


Use, selection, and home range properties: complex patterns of individual habitat utilization

ENDRE GRÜNER OFSTAD ^{1,†}, IVAR HERFINDAL,¹ ERLING J. SOLBERG,² MORTEN HEIM,²
CHRISTER MOE ROLANDSEN,² AND BERNT-ERIK SÆTHER¹

¹Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

²Norwegian Institute for Nature Research (NINA), Trondheim, Norway

Citation: Ofstad, E. G., I. Herfindal, E. J. Solberg, M. Heim, C. M. Rolandsen, and B.-E. Sæther. 2019. Use, selection, and home range properties: complex patterns of individual habitat utilization. *Ecosphere* 10(4):e02695. 10.1002/ecs2.2695

Abstract. Individual patterns of habitat use emerge from behavioral decisions driven by interactions between landscape characteristics and individual traits. Individual traits, such as age and sex, influence the net gain of using habitats and associated resources, and thus the relationship between size and composition of the home range. However, the pathways from individual variation in home range size and composition to habitat selection are rarely fully explored. We investigated how habitat selection in moose (*Alces alces*) was a result of individual traits and home range characteristics, that is, we described the pathway from home range to habitat selection. The study was conducted at two spatial scales during two contrasting seasons. Home range size and composition varied with sex, with season, and to some extent with age. Males had larger home range size, and the composition of their home ranges changed more with home range size than for females. The general trend was that moose used habitats according to availability more in winter than in summer, that is, a weaker habitat selection in winter than in summer. Sex and age explained little of the variation in habitat selection, but sex had a pronounced effect on the relationship between home range size and composition. Because habitat availability (i.e., home range composition) is a component of habitat selection, it suggests that varying habitat use partly compensates for sex-specific differences in home range composition, which in turn results from home range settlement. Hence, although males and females showed similar habitat selection, they differed in the underlying mechanisms generating the pattern of habitat selection. These complex interactions between individual traits and environmental variation have consequences for how we understand the relationships between landscape characteristics, individual behavior, and fitness.

Key words: *Alces alces*; functional response; habitat selection; herbivore; home range composition; home range size; space use; trade-off; ungulate.

Received 24 October 2018; revised 21 February 2019; accepted 25 February 2019. Corresponding Editor: Joseph D. Holbrook.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** endre.ofstad@ntnu.no

INTRODUCTION

Individual variation in resource use reflects the cost-benefit trade-offs in behavioral decisions (Cattarino et al. 2016). In animals, individuals often show large variation in how they trade-off among reproductive effort, predation avoidance, and energetic intake. Because such factors also vary in space and time, we observe spatio-temporal variation in

resource use both within and among individuals (Beyer et al. 2010, Bjørneraas et al. 2011). In turn, such complex relationships among components of resource use affect the demography and dynamics of animal populations by influencing individual vital rates (Losier et al. 2015, Bacon et al. 2017). However, our understanding of the individual variation in the pathways from landscape characteristics to resource use remains limited.

Sex, age, and body size affect resource use through several mechanisms. Body size is expected to be positively related to home range size due to positive relationships with energy requirements (McNab 1963), and better capacity to utilize low-quality forage (Müller et al. 2013). Moreover, since the use of a specific habitat type is assumed to reflect the trade-off between foraging and anti-predation opportunities (Lima and Dill 1990), habitat use is expected to vary with sex and reproductive status (Mysterud et al. 2004, Main 2008). For example, females with offspring tend to maximize offspring survival and exhibit lower use of high-quality resources than males, if such resources are associated with higher mortality risk (White and Berger 2001). As a consequence, males and females often have different habitat use, home range size, and composition (Conner et al. 1999, Main 2008, Ofstad et al. 2016). However, the behavioral mechanisms behind these differences are often unclear.

Habitat selection is defined as the disproportionate use of habitat types relative to their availability (Johnson 1980, Lele et al. 2013), and will therefore vary with changing habitat use and/or availability. In heterogeneous landscapes, individual home ranges will often differ with respect to availability of a given habitat type and its associated resources. Likewise, the availability of different habitat types may vary with the size of the home range at a given location, and consequently, home range size may affect the strength of habitat selection. Availability dependence has been termed a functional response in habitat selection (Mysterud and Ims 1998) and can generate considerable variation in habitat selection among individuals (Beyer et al. 2010). Accordingly, the influence of habitat availability on habitat selection is therefore important to consider (Johnson 1980, Beyer et al. 2010, Lele et al. 2013).

The difference in net gain among habitat types varies with season. In temperate areas, large herbivores often find deciduous leaves and herbaceous plants to be highly digestible and plentiful in summer, but mainly absent in winter, whereas twigs of deciduous trees and conifers are less digestible and often abundant throughout the year (Blair et al. 1977, Rochelle 1980). Accordingly, the cost and benefit of different habitat types may vary among seasons and result in

season-dependent use and selection (Rettie and Messier 2000, Bjørneraas et al. 2011). Moreover, because a high animal density will decrease a habitat's value relative to other habitat types (Fretwell and Lucas 1969), selection for a habitat type may also be affected by the distribution of competitors across the landscape (Fretwell and Lucas 1969, Sutherland 1996, van Beest et al. 2014). This will affect all components of habitat selection described above and may generate complex relationships between individual characteristics and habitat distribution over multiple spatial and temporal scales.

Here, we assessed how habitat selection by moose (*Alces alces*) varies according to sex and age, and across spatial scales and seasons. Moose depend on a variety of resources that vary across the landscape and between seasons (Wam and Hjeljord 2010, Felton et al. 2016), and resource and habitat selection may be influenced by factors occurring at several spatial scales (Herfindal et al. 2009, Van Moorter et al. 2016). This provides an extension of a previous study in the same population (Herfindal et al. 2009) by including GPS locations of moose from both summer and winter, and covering the entire 24-h period. This means that we cover periods of foraging and rumination during both day and night. Like most cervids, the activity level of moose shows circadian variation and is typically highest at dusk, night, and dawn (Godvik et al. 2009, Bjørneraas et al. 2011).

The overall aim of this study was to examine whether individual traits influence the pathway from landscape characteristics to individual habitat selection. To do so, we first assessed the relationship between home range size and composition. Males have larger energetic needs than females (Ofstad et al. 2016), and due to their smaller sizes, females and calves should be less able to utilize lower-quality forage (Müller et al. 2013). Accordingly, with regard to home range properties, we predict females to have smaller home ranges and show a weaker relationship between home range composition and size. Concerning habitat selection, we predict females to be more selective of higher-quality forage than males and show a stronger selection for closed habitats as to reduce predation risk and increase offspring survival (Main 2008). However, since both males and females are likely to benefit from

nutrient-rich forage (Sæther et al. 1996, Markusen et al. 2019), we predict both to show a positive functional response for higher-quality habitat types (Fortin et al. 2008). If the relationship between home range size and composition differs between males and females, it suggests that a similar habitat selection for males and females may occur through differential change in habitat use and/or availability. However, this could result in different functional response in habitat selection.

METHODS

Study area and habitat variables

The study population is located at the island of Vega in northern Norway (65°39'N, 11°54'E), about 30 km from the mainland. The population was founded by three individuals that swam across from the mainland in 1985. In the following years, the population increased, and since 1992, annual harvesting has kept the population size at about 30–50 animals during winter. The population is productive, and 86% of females ≥ 2 yr old are accompanied by offspring with an average of 1.29 calves per cow per year. Natural mortality is very low, and mortality is mainly due to harvesting (Kvalnes et al. 2016).

The climate on the island is oceanic, with mild and wet winters (12 December–26 February, mean temperature is 0.8°C, SD = 4°C; daily precipitation is 4 mm, SD = 6 mm) and short periods with snow cover (mean snow depth of 2.3 cm, SD = 7.4 cm). The mean daily summer (18 May–14 September) temperature and precipitation were 12.7°C (SD = 3°C) and 1.95 mm (SD = 4.4 mm) during the study period.

The landscape of Vega is characterized by forests, open heathland, and farmland (mainly grass production), as well as unproductive and alpine areas above the tree line (8% of total area, based on aerial photograph and ground surveys; Angeloff et al. 2004). The forest consists mainly of deciduous trees (9% of total area), interspersed with Scots pine (*Pinus sylvestris*, 4%) and Sitka spruce (*Picea sitchensis*, 4%; Angeloff et al. 2004). Moose locations were only occasionally found in ocean (0.06%) and in unproductive areas (0.34%), and these areas were excluded from the analyses. We differentiated between open (mainly heathland, farmland, and alpine areas) and forested

habitats, and characterized the habitat types by their understory vegetation. We focused on open areas dominated by grass (>50% grass cover, 36% of the island), short herbs (8%), or heath (*Ericaceae*, 31%), and deciduous forests where the understory was dominated by bilberry bushes (8%) and tall herbs (8%), while the remaining areas consisted of human settlements and unproductive areas such as alpine mountains. These five combinations of cover and understory represent habitat types that are frequently used by moose and expected to influence moose spatial behavior (Bjørneraas et al. 2011, 2012, Van Moorter et al. 2016, Herfindal et al. 2017).

GPS data and ecological seasons

In 1992 and 1993, all moose on Vega were radio-collared, and since 1994, most new recruits and immigrants to the island have been collared (pre-2004, VHF; post-2003, GPS collars). Additionally, moose with malfunctioning collars are routinely recollared (Sæther et al. 2004). In the present study, we used data from 52 adult individuals (1 yr and older) collared with GPS from 2004 to 2015. Relocations were taken at one-hour intervals and were screened for errors following Bjørneraas et al. (2010) before analyses. Individuals were followed for on average 2.8 yr and included relocation data from at least half of their last season (winter, summer). On average, we used 2117 locations per individual during summer and 1252 during winter. Males ($n = 18$) and females ($n = 34$) were on average 5.2 and 6.2 yr old during the study period.

We divided the year into ecological seasons following the clustering method of Basille et al. (2013). We included daily proportional usage of all habitat types and movement parameters, such as turning angle, movement rate, and persistency, as the mean of a 5-d moving window. The method clusters continuous periods of similar behavior, which is assumed to reflect the environmental variables of interest to moose. The season delimitation analysis was done separately for each sex. Onset of autumn was the same for both sexes, but females started summer 14 d earlier than males. Onset of summer for females coincided with calving. Using the summer onset of females, we defined a common summer going from 18 May to 4 September. Females and males showed an onset of early spring at 25 and 27

February, respectively, but no shift in habitat use and movement characteristics marked the onset of winter in females. Using the males' onset of winter, winter started 12 December and lasted to 26 February.

Home range properties

We used Brownian bridge density estimator (BB, Horne et al. 2007) to estimate individual home ranges per season and year. BB estimates the probable location during a given time period and is better for estimating space use in areas with hard boundaries, such as an island (Horne et al. 2007). The Brownian motion drift coefficient, sig1, was estimated with the function `liker` in the package `adehabitatHR` (Calenge 2015) in R version 3.3.2 (R Core Team 2017). GPS accuracy (sig2) was assumed to be 10 m and kept constant for all animals throughout the study period. The Brownian motion parameter (sig1) is a feature of animal movement that reflects among-individual sources of variation such as in behavioral strategies and landscape characteristics (Horne et al. 2007). Using a single Brownian motion parameter for all individuals might introduce a bias or confound among-individual sources of variation in space use. Consequently, we calculated the Brownian motion parameter individually (sig1: median = 1.8, 2.5–97.5% percentile: 0.98–5.34). We could then carry these relationships forward and disentangle them explicitly in habitat selection analyses. We extracted the 90% estimate of the BB home ranges to delineate seasonal home ranges per individual. To avoid that sample size influence of home range size (Börger et al. 2006), we tested at what sample size the estimates of home range size leveled off. We estimated an asymptote after 430 relocations (using the R-package `SiZer`, accounting for moose id, and the three-way interaction between year, season, and sex) and removed all moose-year-seasons with fewer than 430 relocations. As a result, we ended up with 52 individuals and 243 individual moose-year-season home range estimates in the analyses.

Habitat use and selection

Proportional habitat use was calculated as the probability density of the 90% BB that fell inside each habitat type i per moose-year-season. Likewise, we calculated the home range composition as the proportional distribution of different

habitat types within season-year home ranges. At the home range scale, selection ratio was calculated as $\text{proportion use}_i / \text{proportion available}_i$, using habitat availability within each home range (third-order selection). With this approach, the depended variable is similar to the regression coefficients obtained in a resource selection function approach (RSF; Lele et al. 2013). However, by analyzing the selection ratio we get a better understanding of how habitat selection is the outcome of both use and availability. We analyzed these separately to get a better understanding of how individual characteristics influence the individual components of habitat selection.

On the landscape scale, that is, the whole island, we estimated selection ratio as the ratio between home range availability and landscape availability (second-order selection, $\text{Avail}_{i,\text{HR}} / \text{Avail}_{i,\text{LS}}$) to determine whether individual home ranges were a random sample from the landscape. This allowed us to disentangle potential scale-dependent habitat selection. Finally, we estimated spatial variation in population density using the density of locations per season-year-habitat, divided by the total density of locations in the target habitat types, that is, $(n\text{Locs}_i / \text{Area}_i) / \left(\sum_i^{i=5} n\text{Locs}_i / \sum_i^{i=5} \text{Area}_i \right)$. When calculating the mean across years, the estimate of each year was weighted according to the proportion of the population that was marked a given year. The weighting had negligible effect on the results compared to ordinary mean but ensured that the annual sample size was weighed according to parameter certainty. A spatial measure of density allowed us to evaluate habitat use against the level of conspecific competition in the different habitat types.

Statistical analyses of habitat selection against individual traits, landscape, and home range characteristics

Because of large variation in sample size among habitat types, and to simplify the statistical modeling, we analyzed availability and selection ratios separately for each habitat type. Strength of evidence for a given model was assessed using AIC_c (Burnham and Anderson 2002). In models with interaction effects, the presence of higher-order interactions always included their lower-order effects. All analyses

were done in R statistical software version 3.3.2 (R Core Team 2017) using the lme4 package (Bates 2010), with moose identity and year included as random intercepts to account for interdependence in the data (Bolker et al. 2009). Parameter estimates are presented with 95% confidence intervals based on bootstrapping (in square brackets). Home range size was ln-transformed in all analyses where it was the dependent variable, to reduce heteroskedasticity. Age-specific changes in home range characteristics were also evaluated by calculating within-individual changes in home range characteristics and habitat use from year to year (e.g., $\text{HR size}_{\text{Year},t} - \text{HR size}_{\text{Year},t-1}$). The annual changes were then assessed according to two age classes (young = 1–4 yr old and old = 5–14 yr old). This grouping was based on a trade-off between capturing the age-dependent life history characteristics of moose (Sæther et al. 2004, Mysterud et al. 2005, Markussen et al. 2018) and minimizing the sample size differences among age classes (Börger et al. 2006).

Habitat selection was assessed by fitting a linear mixed model with ln-transformed seasonal selection ratios (to restrict predictions to positive values) at both home range and landscape scale, as response variable. The explanatory variables included sex, season, age, and seasonal home range size. If there were sex-specific cost–benefit trade-offs of utilizing a habitat (e.g., dense cover) that differed between seasons, the interaction between sex and season should receive statistical support. Age was included in a three-way interaction with sex and season to account for potential differences between males and females in body mass variation with age, as this may influence the cost–benefit ratios of utilizing a habitat. Finally, we included a three-way interaction between home range size, season, and sex to assess potential differences in the cost–benefit ratios of a habitat type in relation to movement costs associated with the size of the home range.

On home range scale, we assessed functional responses in habitat selection by regressing the individual selection ratios of habitat type i on the individual home range relative availability of habitat type i . We also included the two-way interaction between relative availability and home range size. A significant interaction reflects that moose habitat selection responds to absolute

habitat availability or that there is a trade-off between gains of using a habitat against the costs of acquiring it. Because males and females may differ in behavioral strategies, for example, predation–energy trade-off, we also included the three-way interaction between availability, sex, and season.

To test whether the choice of density estimator affected the results, we also used a fixed kernel density estimator (KDE) to estimate individual home ranges and repeated the above analyses. However, this did not lead to qualitatively different results (see Appendix S2, all other references to supplementary material will refer to Appendix S1).

RESULTS

Home range properties

Home range size.—Males had larger home ranges than females during summer (mean across within-individual means: males = 9.78 km² [SD = 4.71]; females = 3.51 km² [1.49]), but not during winter (males = 3.83 km² [SD = 1.89]; females = 3.66 [1.77], Fig. 1a, Appendix S1: Table S1). Home range size showed a small, but statistically insignificant increase with age (within-individual $\Delta\text{HR} = 0.04$ [−0.94;0.99], Fig. 1b).

Habitat characteristics.—At both the landscape scale and the home range scale, open grassland was the most available habitat type, while the deciduous habitat was the least available, especially among males (Fig. 1c). Open grassland was also used the most and deciduous bilberry forest the least (Fig. 1e). However, when considering the aggregated intensity of use at the population level, that is, density of relocations of all individuals, deciduous forest was most intensively used, and particularly deciduous tall herb forest (Fig. 1e). Among habitat types, only open short herb-land changed in both use and availability with age, and deciduous bilberry forest and tall herb-land changed in use and availability, respectively, with age (Fig. 1d, f; Appendix S1: Tables S2, S3).

Home range composition–size relationship.—As expected, we found that relative habitat availability was related to home range size (Fig. 2, Appendix S1: Table S2). The relationship between the availability of open short herb-lands

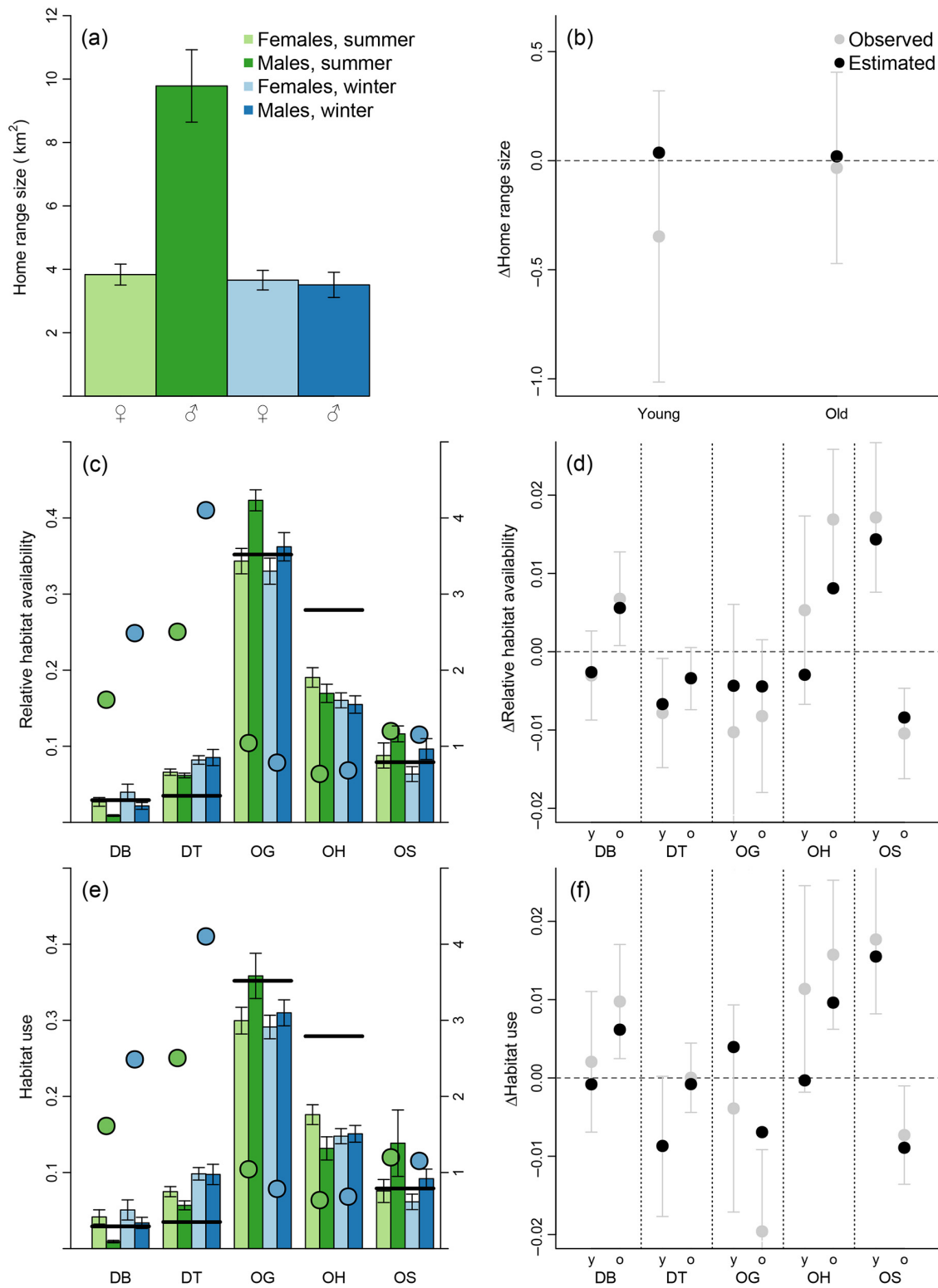


Fig. 1. Variation in home range characteristic according to habitat type (deciduous forests with understorey

(Fig. 1. *Continued*)

consisting primarily of bilberry [DB] or tall herbs [DT], and open landscapes with grass [OG], heath [OH], or short herbs [OS]), sex, season, and age class (young: <5 yr and old: >4 yr) for moose on Vega. Points and bars show the mean and associated standard error, and the mean was first calculated within individual and then across individuals. The influence of age (black dots; panels b, d, f) is estimated using linear mixed models with moose identity and year as random intercepts, and by using only age class as explanatory variable. (a) Home range size (90% Brownian bridge estimate) among females (light) and males (dark) in summer (green), and females and males in winter (blue bars), and (b) change in home range size with age among subsequent years. Habitat composition and use among habitat types (landscape availability in bold line), sex, and season (c, e), and how this change (d, f) between subsequent years for young and old animals. Colored points in panels c and e represent a population density estimate per habitat type compared to overall density per season (relative number of observations per m², right axis).

and home range size changed between seasons, and the availability changed according to both sex and season, that is, two two-way interactions (Fig. 2e; Appendix S1: Table S2). In all other habitat types, the relationship between habitat availability and home range size differed between males and females, and between seasons (three-way interaction between home range size, sex, and season, Appendix S1: Table S2). According to the highest ranked models (Appendix S1: Table S2), composition generally changed more with increasing home range size among males than females (i.e., higher mean effect size, Fig. 2), especially the abundance of poorer habitat types such as open heathland. Moreover, males showed larger seasonal changes in the home range size–composition relationship than females. Finally, there was a general trend that deciduous forest habitats decreased in relative availability with increasing home range size (Fig. 2a, b).

Habitat selection

General patterns of habitat selection.—According to the highest AIC_c-ranked models (Appendix S1: Table S4), we found that home ranges contained more deciduous tall herb forest, and less deciduous bilberry forest and open heathland compared to the overall availability on the island (Appendix S1: Table S6). Within the home ranges, open grassland was available as expected from the landscape composition. At the landscape scale, males selected deciduous bilberry forests and open short herb-land more than females (Appendix S1: Table S4). Within home ranges, males also selected more open short

herb-lands in summer than in winter (Appendix S1: Table S6). Females showed significantly higher landscape selection for deciduous bilberry forests in summer (female–male, across 25–75 percentile of observed home range size and habitat availabilities: deciduous bilberry forests = 0.66 [0.10; 1.24]), but lower landscape selection for short herb-land (open short herb-land = −0.69 [−1.12; −0.16]).

Following the AIC_c ranking (Appendix S1: Table S5), habitat selection on the home range scale was significantly different between males and females for habitat types that showed no sex-specific differences at the landscape scale; that is, sexes differed for all habitat types except for open short herb-land and deciduous bilberry forest. However, only for open grassland in summer did the overall difference significantly deviate from zero (female–male, across 25–75 percentile of observed home range size and habitat availabilities: open grassland = −0.19 [−0.30; −0.07]).

For all habitat types, the selection at the landscape scale differed between seasons (Appendix S1: Table S4) and there was also evidence for seasonal differences at the home range scale for deciduous tall herb forests, open grassland, and open short herb-lands (Appendix S1: Table S5). At the landscape scale, the seasonal differences in habitat selection for open grassland and deciduous bilberry forest differed between males and females (Appendix S1: Table S4). More complex relationships between habitat selection, traits, and home range properties were found at the home range scale. Sex-specific differences were found between habitat selection and age class (deciduous tall herb forests and open heathland), and habitat selection and home range size

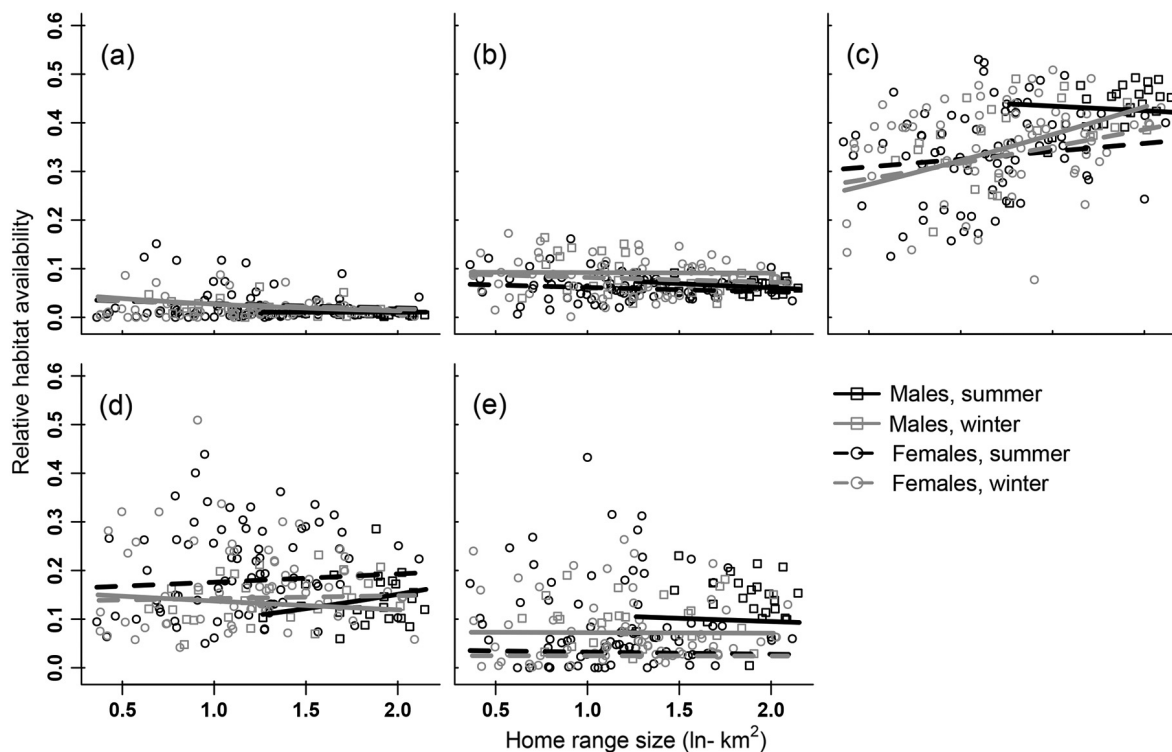


Fig. 2. The relationship between availability of a habitat within the home range and size of the home range in moose on Vega using 90% Brownian bridge home range estimates. Summer and winter are shown with black and gray lines, respectively, and females and males are shown with circles/dashed lines and squares/solid lines, respectively. Plotted lines are the predicted relationships from the highest ranked habitat-specific model in Appendix S1: Table S1 for (a) deciduous bilberry forest, (b) deciduous tall herb forest, (c) open grassland, (d) open heath-land, (e) open short herb-land.

(deciduous tall herb forests, Fig. 3; Appendix S1: Tables S4, S5).

Habitat selection, habitat availability, and home range size.—According to the highest ranked models, there were significant relationships between habitat selection and home range size at both scales for most habitat types (Figure 3; Appendix S1: Tables S4, S5). The landscape selection ratios for open grassland and heathland increased with increasing home range size, whereas selection for deciduous bilberry forest decreased (Appendix S1: Table S4). Seasonal differences in selection ratios were often small and primarily governed by differences in availability and home range size (Fig. 3; Appendix S1: Table S5). At the landscape scale, open habitat types were more selected during summer (summer–winter: open grassland = 0.02 [−0.26; 0.36],

open short herb-land = 0.23 [0.04; 0.42], open heathland = 0.18 [0.10; 0.27]). In contrast, deciduous forest habitat types were more selected during winter, with sex-specific seasonal differences in the selection for deciduous bilberry forest (deciduous bilberry forest_{Female} = −0.17 [−1.25; 0.79], deciduous bilberry forest_{Male} = −0.69 [−1.89; 0.22], deciduous tall herb forest = −0.19 [−0.32; −0.06]). Within home ranges, only open short herb-land was significantly more selected during winter (−0.13 [−0.22; −0.03]).

We found evidence for functional response in habitat selection for all habitat types at the home range scale (Appendix S1: Table S5). Moreover, the relationship between selection ratios and availability was modulated by home range size; that is, animals responded to the absolute amount of available habitat (Appendix S1: Table S5).

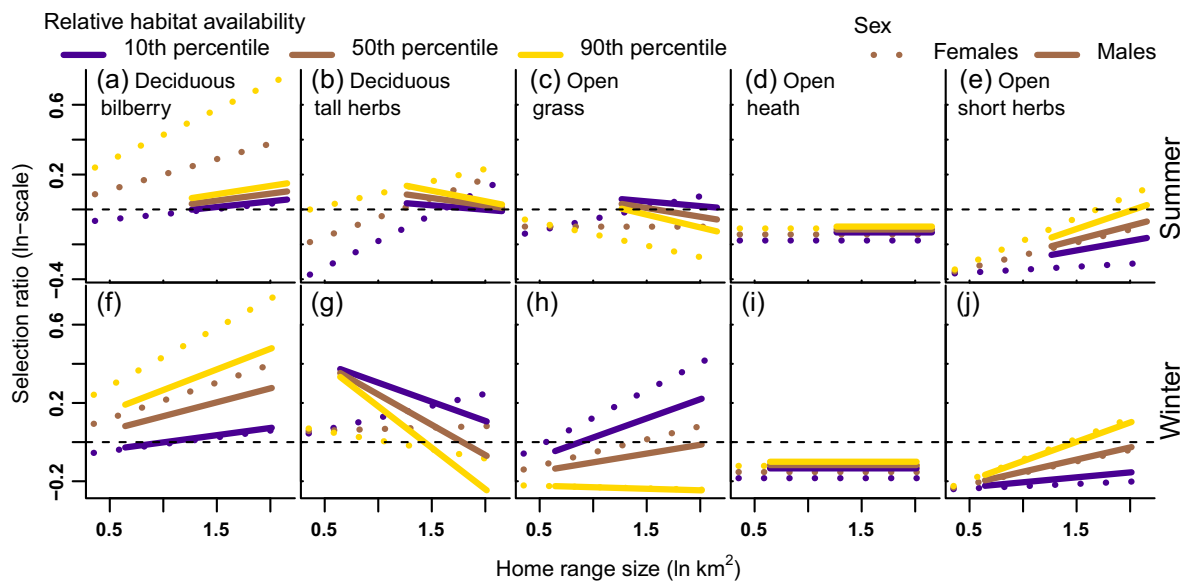


Fig. 3. The relationship between selection ratio of a habitat type within the home range and home range size of males (solid lines) and females (dotted lines) during summer (upper row) and winter (bottom row), at sex-specific 10, 50, and 90 percentile of relative habitat availability (from dark blue to yellow) for moose on Vega. From left, the columns represent (a, f) deciduous bilberry forest, (b, g) deciduous tall herb forest, (c, h) open grassland, (d, i) open heath, (e, j) open short herb-land. The values are predicted for old individuals following the highest ranked habitat-specific models (Appendix S1: Table S6).

Habitat selection ratios tended to increase with increasing home range size (Fig. 3). Only selection for open grassland and deciduous tall herb forest differed between sexes (Appendix S1: Table S5), and female habitat selection increased faster with home range size than male habitat selection (Appendix S1: Table S4). Overall, individuals showed higher selection for habitat types with increasing relative availability, indicating specialization toward that habitat type (Fig. 3).

DISCUSSION

Habitat selection is the outcome of individual characteristics, the landscape animals inhabit, and the relationships among these (Godvik et al. 2009, van Beest et al. 2016, Thurffjell et al. 2017). We found large individual variation in habitat selection ratios in moose, of which only a small proportion was explained by sex, age and season. However, the underlying components, the size and composition of home ranges, as well as their interaction, differed between the sexes as well as between summer and winter. An

understanding of these differences in processes and mechanisms of habitat use and selection would not have been revealed if we focused simply on habitat selection as a function of sex and season. Regardless of how analyses of habitat selection are performed, we need to understand the underlying mechanisms and how they covary due to behavioral strategies and landscape distribution. This understanding enables us to predict how habitat use can be expected to differ between areas according to both individual traits and landscape characteristics.

The amount of resources available to an animal depends on the habitat composition of its home range and the home range size. Several theories such as the metabolic theory (McNab 1963) and marginal value theorem (MVT, Charnov 1976) predict that animals should have larger home ranges in more marginal habitats, a pattern that is confirmed for several taxa (Herfindal et al. 2005, Nilsen et al. 2005, Morellet et al. 2013). Our results provide similar support, even on the high-productive and spatially constrained island of Vega. Regardless of home range size,

females tended to exhibit similar home range composition, whereas males showed large differences in the availability of the different habitat types with increasing home range size (Fig. 2). In general, larger home ranges had lower proportions of habitats that provide cover and higher-quality forage, and females had more than males (Figs. 1, 2). The sex differences in home range composition were most pronounced during summer. Summer is the period when environmental variation has the greatest impact on life history traits in moose (Herfindal et al. 2006). Calves are at their smallest and grow most rapidly during summer, making calves and lactating females highly dependent on nutrient-rich and highly digestible forage (Franzmann and Schwartz 2007). Even small changes in forage quality can therefore have large fitness consequences (the multiplier effect; White 1983).

The sex-specific relationship between home range size and habitat composition did not necessarily translate into sex-specific relationships between home range properties and selection ratios (Fig. 3; Appendix S1: Tables S4, S5). The differences between male and female home range composition (Fig. 1c and e) and home range size–composition relationships (Fig. 2) may explain why the often markedly differences in selection ratios between males and females (Fig. 3) became negligible after accounting for home range properties. Although there was a negative relationship between home range size and availability of deciduous tall herb forests in both males and females (Fig. 2b), only females showed a corresponding increase in the selection of this habitat type with increasing home range size (Fig. 3b). This suggests that females increase their use of higher-quality resources with increasing home range size, but not males. Such sex-specific patterns are expected from sexual segregation theory (Main 2008) because females benefit more from higher-quality forage due to their smaller body mass, and therefore should be less willing than males to trade off forage quality for quantity (Main 2008, Müller et al. 2013). Consequently, females may choose to relocate themselves to areas meeting several requirements, such as forage quality and cover (Main 2008), by landscape scale selection. This will result in more similar habitat compositions across all home range sizes (Fig. 2). Within home range, however, our results

suggest that males and females compensate for variation in habitat quality through different mechanisms: Females adjust their habitat selection, whereas males adjust their home range size.

It is often found that large herbivores at low population densities increase the selection of beneficial habitat types with increasing relative habitat availability, that is, a positive functional response (Losier et al. 2015, van Beest et al. 2016, Mason and Fortin 2017). Fortin et al. (2008) showed how energy maximizing species should specialize their habitat selection with increasing habitat availability when at low density. Our results largely confirm such habitat specialization (Fig. 3), which we also expected given that our study population does not show signs of density dependence in any life history trait (Sæther et al. 2007). However, we did not find support for sex differences in functional responses per se (habitat selection as a function of relative habitat availability, Myrnerud and Ims 1998). This may be because the functional response results from changing use and/or availability. For instance, we found the relative availability of open grasslands to decrease with increasing home range size in summer for males, but the opposite for females (Fig. 2c). Still, there was no sex-dependent functional response in the selection of this habitat type (Appendix S1: Table S5). This suggests that females increase their use of grasslands with increasing home range size, whereas males reduce their use of it. As males and females adjust habitat selection by different mechanisms, the end results may be similar when interpreted as the relationship between habitat selection and relative habitat availability.

We found that the functional response was modified by home range size. This may be because the individual responds to absolute habitat availability, rather than relative habitat availability. Alternatively, it may reflect the effect of changing habitat composition with increasing home range size (Fig. 2) and consequently a change in the cost–benefit ratio in terms of energetic intake of using a specific habitat type (Fig. 3). We generally observe higher selection ratios among animals with larger home range size. The average travel distance between forage patches will in a given landscape increase with home range size, and consequently also increase optimal residence times (Charnov 1976), that is,

stronger habitat selection. The tendency of higher increase in selection among females than males emphasizes the conclusion above about sex-dependent foraging strategy: Females with larger home range also had higher selection ratios, whereas this relationship was weaker for males (Fig. 3).

Negative functional responses in habitat selection is usually attributed to factors resulting in diminishing returns to fitness with increasing relative availability, such as increased predation risk or reduced nutrient uptake (Mysterud and Ims 1998, Godvik et al. 2009). Negative functional responses were observed in open grasslands (Fig. 3c, h) and deciduous tall herb forests during winter (Fig. 3g). Although open grasslands are expected to be favorable for ungulates (Bjørneraas et al. 2012), they provide no cover from predators (Godvik et al. 2009) and may not provide a wide enough diet for browsing ungulates that require a diverse diet (Felton et al. 2016). Moreover, since open grasslands are very common on the island and also within the home ranges (Fig. 1c), individuals may use the habitat type according to availability and therefore not show any selection. Conversely, deciduous tall herb forests provide both higher-quality forage and cover, which could lead to specialization. However, this habitat type has the highest levels of local competition (Fig. 1c, e) and is selected at larger spatial scale. These two factors reduce both fitness benefits of increasing the use of this habitat type (Fretwell and Lucas 1969) and the need for selection at smaller spatial scales (Rettie and Messier 2000, Van Moorter et al. 2016). This illustrates how habitat selection is affected by several mechanisms, not only the habitat type's intrinsic quality.

Performing complex analyses require that we keep in mind the fundamental processes driving the observed patterns (Cagnacci et al. 2010). Our choice of methods is similar to alternative methods of analyzing habitat selection, such as resource selection functions, in terms of questions they address, the importance of defining available habitat, and the influence of habitat availability (Lele et al. 2013, McDonald 2013). However, by analyzing the variation in selection ratio it becomes more transparent that habitat selection is a compound trait consisting of both habitat use and availability, and that both factors vary according to individual and landscape

characteristics. With increasingly detailed sampling of animal movement, future studies can explore how habitat availability and use co-vary over shorter time-frames, and how this varies among species or individuals (Herfindal et al. 2017). In order to make results transferable and capture small-scale patterns, it is also important to account for the local landscape characteristics (Paton and Matthiopoulos 2016). The interaction between home range size and relative habitat availability confirms this conclusion within a selection ratio approach.

Here, we have used a study population with no detectable density dependence (Sæther et al. 2007) combined with extensive information about habitat distribution in a well-defined landscape with known extent. The detailed knowledge about the landscape composition and the population strengthens inferences on the relationships among space use components from the individual level to the population level. Through this approach, we have gained a better understanding of the processes that shape space use and have learned more about individual variation in the mechanisms that shape habitat selection. With this information, we are better equipped to predict habitat selection across study areas and to know where to expect differences to occur.

ACKNOWLEDGMENTS

EGO, B-ES, EJS, and IH developed the concept for the study. EGO with contribution from all co-authors wrote the paper. EGO with input from IH and EJS performed statistical analyses. MH and CMR were in charge of the fieldwork. The authors have no conflict of interests. This work was supported by the Norwegian Research Council (project number: 223257 and 244647) and the Norwegian Environment Agency. We are grateful to Ø. Os, O. A. Davidsen, and B. Aleksandersen for their great effort during fieldwork at Vega.

LITERATURE CITED

- Angeloff, M., P. K. Bjørklund, A. Bryn, and J. Hofsten. 2004. Vegetasjon og skog på Vega. NIJOS Report 21:1–79.
- Bacon, L., Y. Hingrat, F. Jiguet, A. C. Monnet, F. Sarrazin, and A. Robert. 2017. Habitat suitability and demography, a time-dependent relationship. *Ecology and Evolution* 7:2214–2222.

- Basille, M., D. Fortin, C. Dussault, J. P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator-prey interactions. *Ecography* 36:220–229.
- Bates, D. 2010. lme4: mixed-effects modelling with R. <https://cran.r-project.org/web/packages/lme4>
- Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:2245–2254.
- Bjørneraas, K., I. Herfindal, E. J. Solberg, B.-E. Sæther, B. Van Moorter, and C. M. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia* 168:231–243.
- Bjørneraas, K., E. J. Solberg, I. Herfindal, B. Van Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology* 17:44–54.
- Bjørneraas, K., B. Van Moorter, C. M. Rolandsen, and I. Herfindal. 2010. Screening global positioning system location data for errors using animal movement characteristics. *Journal of Wildlife Management* 74:1361–1366.
- Blair, R. M., H. L. Short, and E. Epps Jr. 1977. Seasonal nutrient yield and digestibility of deer forage from a young pine plantation. *Journal of Wildlife Management* 41:667–676.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. Stevens, and J.-S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135.
- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:2157–2162.
- Calenge, C. 2015. Home Range Estimation in R: the adehabitatHR package. <https://cran.r-project.org/web/packages/adehabitatHR>
- Cattarino, L., C. A. McAlpine, and J. R. Rhodes. 2016. Spatial scale and movement behaviour traits control the impacts of habitat fragmentation on individual fitness. *Journal of Animal Ecology* 85:168–177.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- Conner, M., B. Plowman, B. D. Leopold, and C. Lovell. 1999. Influence of time-in-residence on home range and habitat use of bobcats. *Journal of Wildlife Management* 63:261–269.
- Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, S. J. Krizsan, P. O. Hedwall, and C. Stolter. 2016. The nutritional balancing act of a large herbivore: an experiment with captive moose (*Alces alces* L). *PLoS ONE* 11:e0150870.
- Fortin, D., D. W. Morris, and P. D. McLoughlin. 2008. Habitat selection and the evolution of specialists in heterogeneous environments. *Israel Journal of Ecology & Evolution* 54:311–328.
- Franzmann, A. W., and C. C. Schwartz. 2007. Ecology and management of the North American moose. University Press of Colorado, Boulder, Colorado, USA.
- Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710.
- Herfindal, I., U. S. Lande, E. J. Solberg, C. M. Rolandsen, O. Roer, and H. K. Wam. 2017. Weather affects temporal niche partitioning between moose and livestock. *Wildlife Biology* 2017:wlb.00275.
- Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen, and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology* 265:63–71.
- Herfindal, I., E. J. Solberg, B. E. Sæther, K. A. Høgda, and R. Andersen. 2006. Environmental phenology and geographical gradients in moose body mass. *Oecologia* 150:213–224.
- Herfindal, I., J.-P. Tremblay, B. B. Hansen, E. J. Solberg, M. Heim, and B.-E. Sæther. 2009. Scale dependency and functional response in moose habitat selection. *Ecography* 32:849–859.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using brownian bridges. *Ecology* 88:2354–2363.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kvalnes, T., B.-E. Sæther, H. Haanes, K. H. Røed, S. Engen, and E. J. Solberg. 2016. Harvest-induced

- phenotypic selection in an island population of moose, *Alces alces*. *Evolution* 70:1486–1500.
- Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology* 82:1183–1191.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Losier, C. L., S. Couturier, M.-H. St-Laurent, P. Drapeau, C. Dussault, T. Rudolph, V. Brodeur, J. A. Merkle, D. Fortin, and J. Rhodes. 2015. Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *Journal of Applied Ecology* 52:496–504.
- Main, M. B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology* 89:693–704.
- Markussen, S. S., I. Herfindal, A. Loison, E. J. Solberg, H. Haanes, K. H. Røed, M. Heim, and B.-E. Sæther. 2019. Determinants of age at first reproduction and lifetime breeding success revealed by full paternity assignment in a male ungulate. *Oikos* 128:328–337.
- Markussen, S. S., A. Loison, I. Herfindal, E. J. Solberg, H. Haanes, K. H. Røed, M. Heim, and B.-E. Sæther. 2018. Fitness correlates of age at primiparity in a hunted moose population. *Oecologia* 186:447–458.
- Mason, T. H. E., and D. Fortin. 2017. Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. *Journal of Animal Ecology* 86:960–971.
- McDonald, T. L. 2013. The point process use-availability or presence-only likelihood and comments on analysis. *Journal of Animal Ecology* 82:1174–1182.
- McNab, B. K. 1963. Bioenergetics and the determination of home range size. *American Naturalist* 97:133–140.
- Morellet, N., et al. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology* 82:1326–1339.
- Müller, D. W. H., D. Codron, C. Meloro, A. Munn, A. Schwarm, J. Hummel, and M. Clauss. 2013. Assessing the Jarman-Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 164:129–140.
- Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology* 79:1435–1441.
- Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. *Journal of Zoology* 264:209–215.
- Mysterud, A., E. J. Solberg, and N. G. Yoccoz. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *Journal of Animal Ecology* 74:742–754.
- Nilsen, E. B., I. Herfindal, and J. D. C. Linnell. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience* 12:68–75.
- Ofstad, E. G., I. Herfindal, E. J. Solberg, and B.-E. Sæther. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society B* 283:20161234.
- Paton, R. S., and J. Matthiopoulos. 2016. Defining the scale of habitat availability for models of habitat selection. *Ecology* 97:1113–1122.
- R Core Team. 2017. R vers. 3.3.2. R Foundation for Statistical Computing, Vienna, Austria.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- Rochelle, J. A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. University of British Columbia, Vancouver, British Columbia, Canada.
- Sæther, B.-E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology* 77:1493–1500.
- Sæther, B. E., S. Engen, E. J. Solberg, and M. Heim. 2007. Estimating the growth of a newly established moose population using reproductive value. *Ecography* 30:417–421.
- Sæther, B.-E., E. J. Solberg, M. Heim, J. E. Stacy, K. S. Jakobsen, and R. Olstad. 2004. Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment. *Wildlife Biology* 10:51–57.
- Sutherland, W. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2017. Learning from the mistakes of others: how female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PLoS ONE* 12:4.
- van Beest, F. M., P. D. McLoughlin, A. Mysterud, and R. K. Brook. 2016. Functional responses in habitat selection are density dependent in a large herbivore. *Ecography* 39:515–523.
- van Beest, F. M., A. Uzal, E. Vander Wal, M. P. Laforge, A. L. Contasti, D. Colville, and P. D. McLoughlin. 2014. Increasing density leads to generalization in

- both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology* 83:147–156.
- Van Moorter, B., C. M. Rolandsen, M. Basille, and J. M. Gaillard. 2016. Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology* 85:21–31.
- Wam, H. K., and O. Hjeljord. 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. *European Journal of Wildlife Research* 56:745–755.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377–384.
- White, K. S., and J. Berger. 2001. Antipredator strategies of Alaskan moose: Are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* 79:2055–2062.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2695/full>