

Ecological dynamics in habitat selection of reindeer: an interplay of spatial scale, time, and individual animal's choice

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Abstract While striving for “global” species models of habitat selection, spatiotemporal variation in utilization patterns within a particular habitat and intraspecies variation in space use are still poorly understood. We addressed these challenges by exploring habitat use of domesticated reindeer (*Rangifer tarandus tarandus*), focusing on factors that underlie ecological dynamics in habitat selection. We analyzed habitat selection of 15 (± 2) female reindeer in southern Norway separately for (a) region and home range, (b) seasonality, and (c) each Global Positioning System (GPS)-collared reindeer. We explicitly evaluated spatiotemporal and intraspecies variability in habitat selection by applying multivariate ordination techniques based on the niche concept. In contrast to global assumptions, our results reveal a considerable and partly unpredictable amount of variation in habitat selection resulting from the interplay of spatial scale, time, and individual animal choice. Thus, we conclude that across-scale approaches describing animal space use facilitate better understanding of habitat selection instead of finding a single “best” model that indicates the strongest species–habitat relationships.

Keywords GPS telemetry · Habitat preferences · Home range · Niche concept · Arctic–alpine ecosystems

Introduction

In Fennoscandia, reindeer (*Rangifer tarandus tarandus*) play an important ecological and cultural role: as a natural component of arctic–alpine ecosystems (Oksanen et al. 1995), reindeer act as ecosystem engineers, affecting ecosystem structure and processes such as phytodiversity, nutrient cycling, and primary productivity, at broad spatial scales (see Suominen and Olofsson 2000 for a review; Löffler 2000; Löffler and Pape 2008; Pajunen et al. 2008). Though the last remnants of the original wild reindeer population are still found in Norway, due to extensive conservation efforts (Panzacchi et al. 2013), currently 40 % of the land area is used as pasture for herded [or, following the nomenclature of Skarin and Åhman (2014), “domesticated”] reindeer (Tyler et al. 2007; Moen 2008). This traditional pastoral system of reindeer husbandry represents a model of sustainable exploitation and management of northern terrestrial ecosystems (Magga et al. 2009), forming an essential part of the livelihood of the indigenous Sámi people that is tightly connected to their sociocultural identity (Jernsletten and Klokov 2002; Skarin and Åhman 2014).

Both wild and domesticated reindeer depend on the diversity of accessible natural pastures to cover their seasonally different needs (Pape and Löffler 2012). However, nearly one-third of traditional reindeer husbandry ranges have been physically or functionally lost due to human impact (UNEP 2001; Jernsletten and Klokov 2002), threatening contemporary reindeer husbandry (Pape and Löffler 2012).

Due to the ever-increasing human impact on natural systems, the quest to understand key concepts in animal ecology, such as resource use, home range, and dispersal, becomes more crucial than ever (Salinas-Melgoza et al. 2013; Campos et al. 2014). Hence, ecologists devote more

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attention to habitat selection than to any other branch in this discipline (Mayor et al. 2009).

The questions of where, when, and why animals move, and the associated mechanistic forces, are obviously scale dependent and hierarchically structured (Johnson 1980). Though the matter of scale has long been identified as a critical topic in habitat selection studies (see Mayor et al. 2009 for a review), efforts to analyze the relative effects of resources and disturbances on habitat selection remain hindered by the difficulty in accounting for the multiple scales on which this selection occurs (Leblond et al. 2011). In addition to a spatial component, animal behavior is affected by a temporal component, for example, due to biological (e.g., calving, rutting) or seasonal (e.g., phenology, snow cover) constraints. A common approach has been to analyze space use by animals separately for different times of the year (McLoughlin et al. 2010). Despite an increasing number of publications dealing with spatiotemporal perspectives (Benhamou and Riotte-Lambert 2012; Wilson et al. 2012), the results of habitat selection studies are often still simplified to “global” models of “the species as a rule does this.” This leads to loss of important information regarding the spatiotemporal factors of animal habitat use and the variability among individual animals. Intraspecific variation in habitat selection, not only between different populations in different ranges (Putman and Flueck 2011) but also among individuals in the same population, was recently proven to be extremely significant and of great importance (Gillingham and Parker 2008; Anderson and Johnson 2014; Campos et al. 2014).

Many habitat selection studies have focused on reindeer (Nellemann et al. 2001; Mårell and Edenius 2006; Skarin et al. 2008; Anttonen et al. 2011), contributing—together with earlier reports (Kelsall 1968; Skjenneberg and Slagsvold 1968)—much to our knowledge about the general habitat preferences of this species. However, multiple issues remain unclear, including (1) the temporal variations in space use within a particular habitat, (2) its driving forces (Blix et al. 2014), and (3) the intraspecific variations in space use patterns (Anderson and Johnson 2014). In this study, we aim to explicitly address both the spatiotemporal and individual variations in habitat selection by domesticated reindeer in the southern fringe of their range in Norway.

We expected:

1. Habitat selection [expressed as marginality, i.e., the difference between the average habitat conditions used by an organism and the average habitat conditions available to it (Calenge et al. 2005)] to be more pronounced within the regional context rather than the home range context, due to the proposed hierarchical

nature of habitat selection (Johnson 1980; Senft et al. 1987).

2. Explanatory variables of habitat selection to be scale specific, as Johnson’s designation of selection levels implies that habitat selection is likely to differ among spatial scales (Gaillard et al. 2010).
3. Temporal variability in habitat selection and its mechanistic forces to be pronounced due to the proven importance of plant phenology for reindeer (Albon and Langvatn 1992; Myrsetrud et al. 2001; Iversen et al. 2014) in these extremely seasonal environments.
4. Intraspecific variability in habitat selection to be low due to the general view of reindeer as a highly gregarious species, further promoted by domestication (Hemmer 1990) with proven in-group synchronicity between individuals (Colman et al. 2004).

Materials and methods

Study area

The habitat use of domesticated, but mostly free-ranging reindeer was studied in the southern part of central Norway in cooperation with the reindeer herders of Filefjell Reindrift, the southernmost reindeer husbandry unit in Norway. Their ranges cover an area of approximately 2000 km² (Reindrifftsforvaltningen 2014), spatially separated into winter pastures in the southeastern part of the study area and summer pastures in the northwestern part (Fig. 1). The winter pastures are situated between 140 and 1290 m above sea level in a gently rolling topography dominated by forests and alpine heaths, whereas the summer pastures lie between 740 and 1918 m above sea level in a more rugged topography dominated by alpine vegetation. The size of the winter herd has been stable at about 3000 (± 150) animals for more than a decade, with the majority of animals being females (77 % in 2013), followed by calves (22 %) and just 1 % males (Reindrifftsforvaltningen 2012, 2014). Except during seasonal migrations between the summer and winter pastures, the reindeer are allowed to roam freely under daily surveillance of the borders of their ranges. Reindeer gathering for calf-marking and slaughter is restricted to the migration towards the winter pastures in December.

Telemetry data

In December 2007, during the annual roundups for calf-marking and slaughter, 20 female reindeer were equipped with GPS/Global System for Mobile Communications

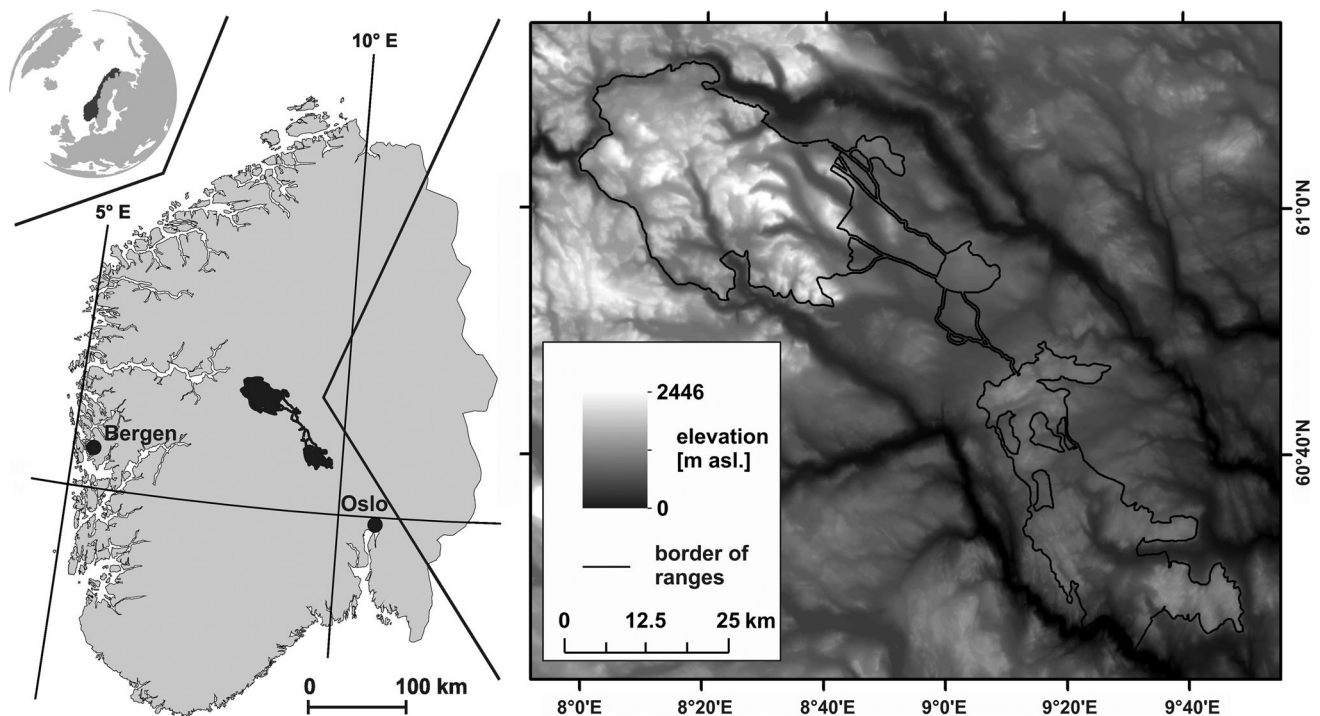


Fig. 1 Location of the study area, the ranges of Filefjell Reinlag, southern Norway

(GSM) collars (Vectronic Aerospace GmbH, Berlin, Germany). As a highly gregarious species, reindeer are known to synchronize their behavior among group or herd members (Maier and White 1998; Colman et al. 2004), such that each collared individual was expected to represent a larger number of animals. However, to ensure a certain degree of independence between the collared animals, and to ease herd management, the herders tried to select the animals to be collared from different subherds or groups.

The collars weighed approximately 900 g and had an average battery life of 1 year. The monitoring equipment acquired one position per hour and stored the data locally until transmission to the GSM ground station at the Norwegian Institute for Nature Research (NINA). Data access was provided by NINA's web-based map service at <http://www.animalpositions.com>. We based our analyses on the GPS fixes of $n = 15 (\pm 2)$ animals (since not all of the 20 GPS units were operational at any given time) between December 2008 and November 2009.

Environmental data

For environmental characterization of the ranges and the subsequent analyses of habitat selection, we derived a set of 14 variables (see Table 1 for further details). These variables reflect factors commonly considered to be important for habitat selection by reindeer (Skarin et al. 2008), such as topographic conditions, human

infrastructure (as a potential measure of disturbance; Vistnes and Nellemann 2008), vegetation properties, and snow cover. Apart from accounting for wind exposure and delimiting the seasons (see below), we did not explicitly account for harassment of the animals by biting insects, e.g., oestrid flies. This is due to the obvious mismatch in temporal scale between high insect activity (restricted mostly to warm and windless periods; Hagemoen and Reimers 2002; Skarin et al. 2010) and animal positions aggregated over a period of several days or weeks.

All spatial data were provided at 30 m resolution, except for the MODIS-derived normalized difference vegetation index (NDVI) at 250 m resolution (Carroll et al. 2010) and the snow cover fraction at 500 m resolution (Hall et al. 2006), which were both resampled to 30 m resolution. Data were processed using ArcGIS 10 (ESRI 2010) and R 3.1.0 (R Core Team 2014) with the raster package (Hijmans 2014).

Analyses: general approach

We based our analyses of habitat selection on the ecological niche concept (Hutchinson 1957), as it provides a sufficient framework to analyze presence-only data such as GPS fixes of animals. Here, the niche is defined as the subspace of sites used (i.e., GPS locations) within the hyperspace spanned by the environmental conditions of the sites considered to be available to the species (Hirzel et al. 2002).

Table 1 Environmental variables used in this study

Variable	Description	Source
Topography		
Elev	Elevation above sea level	Digital elevation model (DEM) based on 1:50,000 topographical maps from the Norwegian Mapping Authority
Slope	Slope gradient	Derived from DEM following Horn (1981)
Aspect	Cosine-transformed aspect	Derived from DEM following Horn (1981)
TRI	Terrain ruggedness index	Derived from DEM within a 5 × 5 moving window following Wilson et al. (2007)
TPI	Topographic position index	Derived from DEM within a 5 × 5 moving window following Wilson et al. (2007)
Wind	Windward exposure	Derived from DEM and mean wind direction for the time period considered (stations #23410 Fagernes Airport for summer pasture and #24890 Nesbyen–Todokk for winter pasture)
Infrastructure		
DMjR	Distance to major (asphalted two-lane) roads	1:50,000 topographical maps from Norwegian Mapping Authority
DMnR	Distance to minor (gravel) roads	1:50,000 topographical maps from Norwegian Mapping Authority
DCab	Distance to cabins	1:50,000 topographical maps from Norwegian Mapping Authority
DTrail	Distance to hiking trails	1:50,000 topographical maps from Norwegian Mapping Authority
Vegetation		
Value	Reindeer-specific grazing value [low, medium, good] of vegetation, differentiated for summer and winter pastures	Reclassification of the SatVeg vegetation map with 25 vegetation types (Johansen 2009) based on Skogsstyrelsen (n.d.) and Tømmervik (2007)
NDVI	Maximum value of the normalized difference vegetation index (NDVI) for the time period considered, based on 16-day composites	MODIS product MOD13Q1 (Carroll et al. 2010)
Snowcover		
Snow	Median of snow cover fraction (SCF) for the time period considered, based on daily data	MODIS product MOD10A1 (Hall et al. 2006)
Δ-Snow	Change in SCF compared with the previous time period	MODIS product MOD10A1 (Hall et al. 2006)

All of our analyses were based on explorative multivariate techniques (more specifically, direct gradient ordination), as these techniques are well suited to analyze habitat selection (Hirzel et al. 2002; Calenge et al. 2005; Calenge and Basille 2008) for three reasons: (1) Robust against autocorrelation of location data (Calenge et al. 2005), the techniques make use of a dense network of observations instead of requiring spatially and temporally independent observations (Boyce and McDonald 1999; Fieberg 2007); (2) Contrary to the often-used resource selection functions (Manly et al. 2002), the techniques do not require a priori knowledge of the factors affecting the probability of selection (Guisan and Zimmermann 2000); (3) The techniques facilitate the exploration of the used ecological space (the niche) relative to the available space, enabling assessment of both the amount and direction of niche specialization (Dolédec et al. 2000; Calenge et al. 2005).

Prior to the actual analyses of habitat selection, less than 0.1 % of the location data were labeled as erroneous and removed based on the movement characteristics, following the approach of Bjørneraas et al. (2010). Fixes were

considered to be erroneous if they exceeded distances of 100 km from the median and 20 km from the mean of the locations within a moving window of six fixes (i.e., an outlier), or if the movement rate and turning angle between three consecutive fixes exceeded thresholds of 6.0 km h⁻¹ and 165°, respectively (i.e., a spike).

All analyses of habitat selection were performed in R 3.1.0 (R Core Team 2014) using the “adehabitat” family of packages (Calenge 2006). Statistical significance of habitat selection at each scale considered was assessed using randomization tests with $n = 999$ repetitions.

Analyses: effect of spatial scale

To address our first two expectations, i.e., that habitat selection and its mechanistic forces are scale dependent and more pronounced within the region than within the home range, we analyzed habitat selection at both regional and home-range scales.

At regional scale, corresponding to the “second-order” habitat selection of Johnson (1980), which characterizes the placement of the home range within the available

region, we explored the utilization of the area individually for each collared reindeer but assumed that the region was commonly available (“design II” study of Thomas and Taylor 1990). In this context, the region consisted of either the entire summer pasture or winter pasture (as shown in Fig. 1), depending on the season considered. This definition of region reflects the herding praxis of free-roaming animals under surveillance of the borders of the pastures. To analyze habitat selection within the region, i.e., to distinguish between utilized and nonutilized habitat conditions, we applied direct gradient ordination in the form of outlying mean index (OMI) analysis, which provides an integrated description of species–environment relationships (Dolédec et al. 2000). Briefly, the OMI approach yields a two-dimensional coordinate system with axes corresponding to the combination of environmental variables that are most relevant for the species under study. While the origin of this coordinate system represents the mean habitat condition of the available area (the region), individual animals are located in this coordinate system according to their mean utilized habitat conditions. The OMI is simply the distance between the origin and the individual animal’s centroid (marginality), i.e., a measure that integrates the niche specialization of an individual according to the selected habitat.

Focusing further on differences in utilization patterns within the area generally used by an individual reindeer (its home range) led us to the analysis of “third-order” habitat selection (Johnson 1980) at the home-range scale. Here, both utilization and availability were assessed individually for each collared reindeer, corresponding to “design III” studies of Thomas and Taylor (1990). To determine the individual home ranges, we used a Brownian bridge approach that estimated the utilization distribution of each animal based on serially autocorrelated relocations (Horne et al. 2007). The home range was then defined as the 95 % contour of the utilization distribution. Within each individual’s home range (the available area), habitat selection (expressed as differences in utilization density) was then explored using K-select analysis (Calenge et al. 2005). This analysis consists of noncentered principal component analysis performed on the table containing the marginality vector coordinates of each animal for the habitat variables. This method provides a linear combination of habitat variables for which the average marginality is greatest and is a synthesis of the variables that contribute the most to habitat selection. Due to this approach, the method nicely handles multicollinearity between explanatory variables (Calenge et al. 2005). The outcome of the analysis is a coordinate system based on the environmental variables important for the species, in which both the mean of the habitat conditions within the home range and the mean of the habitat conditions of the space utilized within the home

range are placed for each individual animal. The difference between both means defines the marginality vector, with its length being proportional to the importance of habitat selection and its direction indicating which variables are selected (Calenge et al. 2005).

Analyses: temporal variability

Multiple spatiotemporal scales are involved in the process of habitat selection due to variations in the animal’s perception of the environment over time and space (Leblond et al. 2011). This issue is likely to be of particular importance for animals living in environments with high spatial and temporal variability (Campos et al. 2014) such as reindeer. Because of this variability, the reindeer herding year is traditionally divided into different seasons (Sandström et al. 2003) based on climatic conditions, animal behavior, and herding logistics.

To derive seasons, we primarily used climate data, especially air temperature and snow condition, from the Norwegian Meteorological Service (DNMI) and the Norwegian Water Resources and Energy Directorate (NVE). For the summer pasture, we acquired snow data from meteorological station #54600 Maristova at 806 m above sea level and air temperature data from station #54710 Filefjell at 956 m above sea level (with missing data filled in by the NVE-station Sula, <1 km away from the Filefjell station). For the winter pasture, we used snow data from station #22840 Reinli at 628 m above sea level and air temperature data from station #23160 Åbjørsbråten at 639 m above sea level. In addition, data on spatial snow cover and thickness were derived from MODIS data (Hall et al. 2006) and NVE data. Different phases of herd management (animal gathering prior to migration and the migration itself) were derived from the telemetry data and information provided by the herders. Due to the predominating human impact on animal behavior caused by seasonal migrations, we excluded the migration periods during December and April, each period lasting approximately 3 weeks. The calving period as a biological constraint was derived from the GPS fixes of the reindeer, following the time-series analysis approach of Strand et al. (2011); individual calving dates were indicated by a sharp decline in movement rates. To handle slight deviations from the observed general synchronicity in calving, we set the duration of the calving season to 2 weeks. Based on the final hierarchical overlay of herd management (animals staying on either winter or summer pastures, migration to be excluded), climatic conditions (temperature thresholds and snow cover), and biological constraints (calving), we inductively delineated nine seasons to be analyzed further. The detailed criteria that led to the delineation of these seasons, their characteristics, and time spans are outlined in Table 2.

Table 2 Inductive delineation of annual seasons to acknowledge the temporal variability of both environment and animal behavior, based on a hierarchical overlay of constraints related to management, climatic conditions, and reindeer biology

Management: pasture used	Criteria for delineation of seasons, and seasons' characteristics	Resulting time span	Season name
<i>Spring migration</i>			
Winter	Starts 1 week after the animals' release to their winter pasture and covers the first half of their stay there: permanent snow cover with increasing depth, period of lowest temperatures	22/12/2008 13/02/2009	Winter
	Second half of the animal's stay at their winter pasture, ends 1 week before gathering for the spring migration starts: time of maximum snow cover and depth until beginning of snow melt	14/02/2009 06/04/2009	Late winter
<i>Winter migration</i>			
Summer	Starts 1 week after the animals' release to their summer pasture, ends with the onset of the calving period: snow melt continues, daily mean temperatures >0 °C	23/04/2009 06/05/2009	Spring
	Pronounced immobility of the animals: snow restricted to elevations >1000 m, increasingly patchy	07/05/2009 21/05/2009	Calving
	Period between calving and daily mean temperatures exceeding 6 °C: increased mobility of the animals after calving, snow melting continues	22/05/2009 12/06/2009	Early summer
	First half of the time period with daily mean temperatures ≥6 °C, indicative of high insect activity and harassment (Mörschel 1999): total melt-out of snow due to high temperatures	13/06/2009 31/07/2009	Summer
	Second half of the time period with daily mean temperatures ≥6 °C, with decreasing insect activity: gradual temperature decrease	01/08/2009 14/09/2009	Late summer
	Period of daily mean temperatures between 0 and 6 °C: first snow, rutting	15/09/2009 30/09/2009	Autumn
	Daily mean temperatures <0 °C: snow cover remains thin but ultimately does not melt	01/10/2009 15/11/2009	Early winter

To test our third expectation, i.e., that temporal variability is pronounced in both habitat selection and its mechanistic forces, we analyzed habitat selection in the regional and home range context separately for each delineated season by applying the OMI and K-select analysis as outlined above.

Analyses: intraspecies variability

The analysis approaches allowed us to easily test our fourth expectation, i.e., that intraspecies variability in habitat selection is low. Restricting the OMI and K-select analysis to a factorial plane of two principal components containing most of the observed variance allowed for a visual investigation of each individual's selection. Apart from the direction of habitat selection within the ecological space for each animal, the similarity of habitat selection between multiple animals can be determined visually from the resulting diagrams.

Results

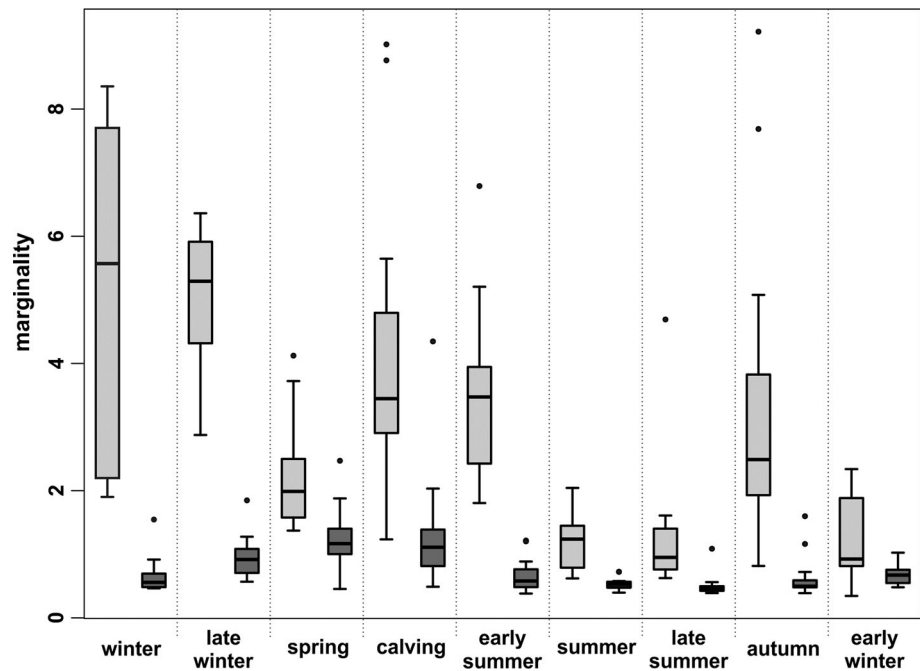
Effect of spatial scale

Regarding the amount of habitat selection (the marginality), our analysis revealed pronounced differences between

the region and home range, with significantly ($p < 0.001$) lower marginality within the home range throughout the year (Fig. 2). Furthermore, we found that habitat selection within the region was usually statistically significant (Fig. 3), whereas the significance of habitat selection within the home range varied with the time of year, being less significant during autumn and early winter (Fig. 4).

With regard to explanatory variables, we found habitat selection at both spatial scales (region and home range) to be related to a similar set of environmental variables: elevation, snow, productivity, and human infrastructure (the vectors in Figs. 3, 4). The effect of infrastructure, however, was more pronounced within the region than within the home range: As evident from a disproportionately low utilization, the reindeer avoided areas closer than 3000 m (on average) to infrastructure. Similarities and differences in habitat selection between the spatial scales also revealed a clear seasonal dependence. During the winter and late winter, elevation, snow conditions, and NDVI affected habitat selection within the region and home range in the same way, whereas scale-dependent contrasting effects of elevation and NDVI occurred during the summer: The preference for higher elevations at the expense of NDVI within the region turned into habitat selection irrespective of elevation but with a slight preference for more highly productive sites (higher NDVI)

Fig. 2 Marginality as the amount of habitat selection per season within the region (*light grey*) and home range (*dark grey*). *Boxplots* were based on the marginality of each collared reindeer, i.e., the difference between the average habitat conditions used by the animal and the average habitat conditions available to the animal. The median (*thick line*), interquartile range (*boxes*), min/max (*whiskers*), and outliers (more/less than 1.5 times the upper/lower quartile, shown as *black dots*) of the marginalities are shown



within the home range. During autumn and early winter, elevation was found to be important within the home range but less so within the region.

Effect of season

Apart from scale-dependent differences in marginality, our analysis also revealed a pronounced temporal variability in marginality (Fig. 2): in the region, marginality was most pronounced during winter and late winter, followed by calving, early summer, and autumn. The lowest marginality occurred during late summer, early winter, and to a lesser extent, spring. The comparatively low marginality within the region during spring, however, was found to be contrasted by a high marginality within the home range. The highest marginality within the home range occurred during calving.

With regard to the explanatory variables, we detected a pronounced effect of snow or snow-cover change on habitat selection; For example, during spring, the animals showed a preference for higher elevations within the region, still covered with snow but also wind exposed, and a strong preference for ridge positions (higher TPI value) within the home range. During early summer, the animals moved to productive sites at low elevations, in contrast to their preference for higher elevations during the rest of the year.

Intraspecies variability

The variability in habitat selection among the collared animals within the region and within the home range is

shown in Figs. 3 and 4 by the scatter among the points representing the individual animals. The change from winter to spring reveals two contrasting strategies among the animals: though both groups were rearing calves, one group preferred wind-exposed higher elevations whereas the other group preferred more highly productive sites with low snow cover at lower elevations. Within each of these two groups, variance was minor. The situation was completely different during calving, with enormous variance in habitat preferences among individuals, within both the region and the home range. During the rest of the year, the scatter among individuals along the X-axis of both analyses (the axis that explains most of the variance) was minor, indicating predominantly similar preferences among the animals. The scatter along the Y-axis also revealed some intraspecies variability; for example, during early summer, most (64 %) of the variance in habitat selection within the region was related to NDVI, but the large scatter along the Y-axis (related to distance from major roads) indicated a fair amount (15 %) of variance in habitat selection related to human infrastructure.

Discussion

Not surprisingly, our findings corroborate research on the general habitat preferences of reindeer, but also reveal important spatiotemporal and individual effects on the general model of habitat selection. We found marginality to be generally more pronounced within the region than within the home range, as expected from the hierarchical

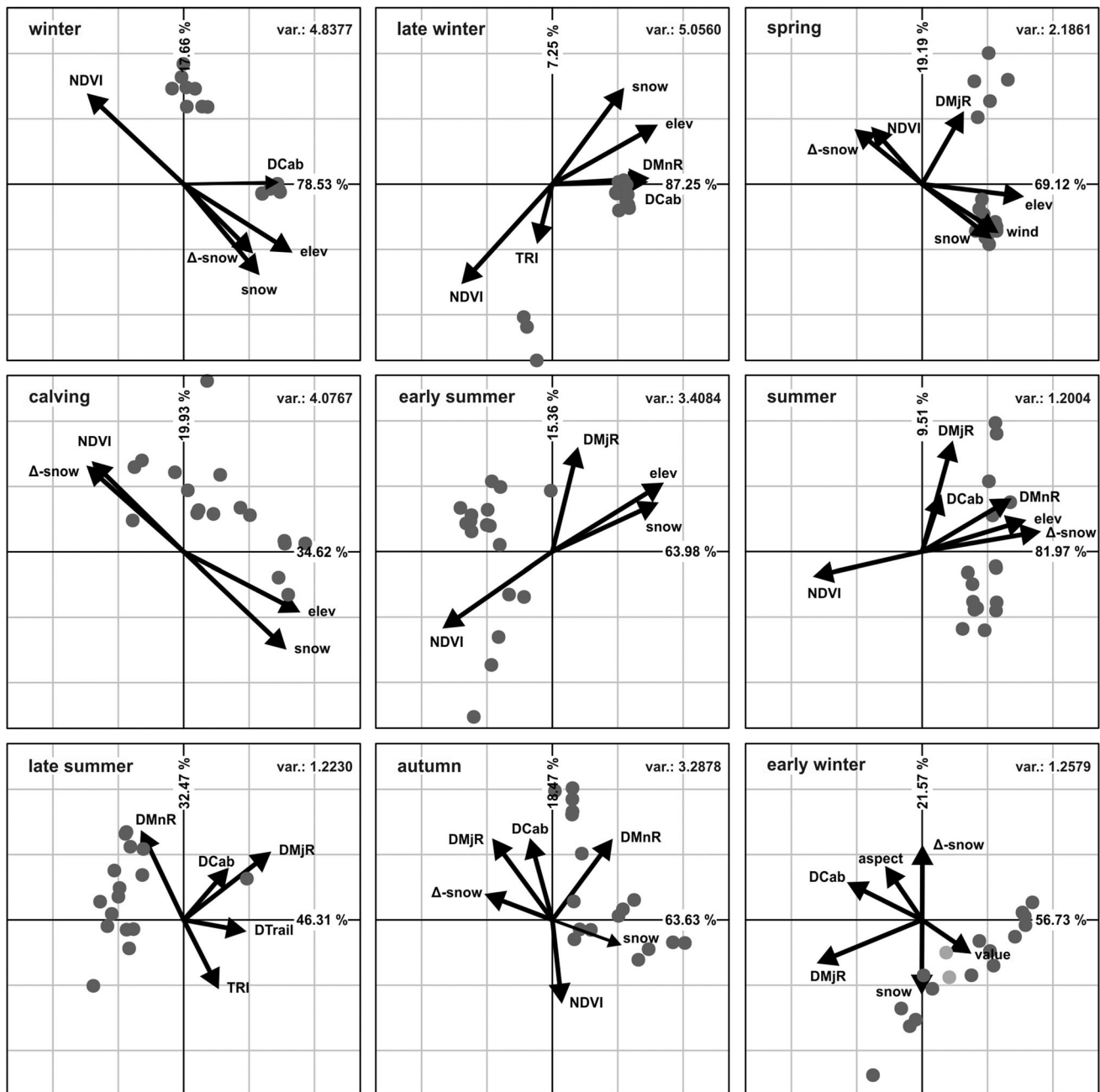


Fig. 3 Seasonal habitat selection of each collared reindeer within the region. For each of the nine seasons, *filled circles*, plotted onto the first factorial plane of the OMI analysis, represent the mean of the utilized habitat conditions for each animal. The origin of the coordinate system represents the mean over the habitat conditions available to all individuals. The location of *each circle* represents its deviation in habitat use from the mean habitat availability and can be interpreted using the *arrows* of the significant environmental variables which indicate the correlation of those variables with the first two OMI axes (Pearson's r ; the raster in the background corresponds to 0.5). Thus, a *circle* further from the origin represents an individual with more specialized habitat use than an individual represented by a

circle close to the origin. *Circles* are shown in *dark grey* if habitat selection is significant at the $p < 0.05$ level. As an example, during winter, the habitat use of all of the animals differed significantly from the mean habitat availability (large distance from the origin, all *circles* shown in *dark grey*), with one group of animals preferring areas with high NDVI values at lower elevations with less snow (cluster of *circles* at the *top* of the diagram), and a second group preferring higher elevations, more snow, and a larger distance from cabins (cluster of *circles* to the *right*). The amount of variance explained by each axis is given in percent, whereas the amount of total variance is shown in the *upper-right corner* of each diagram

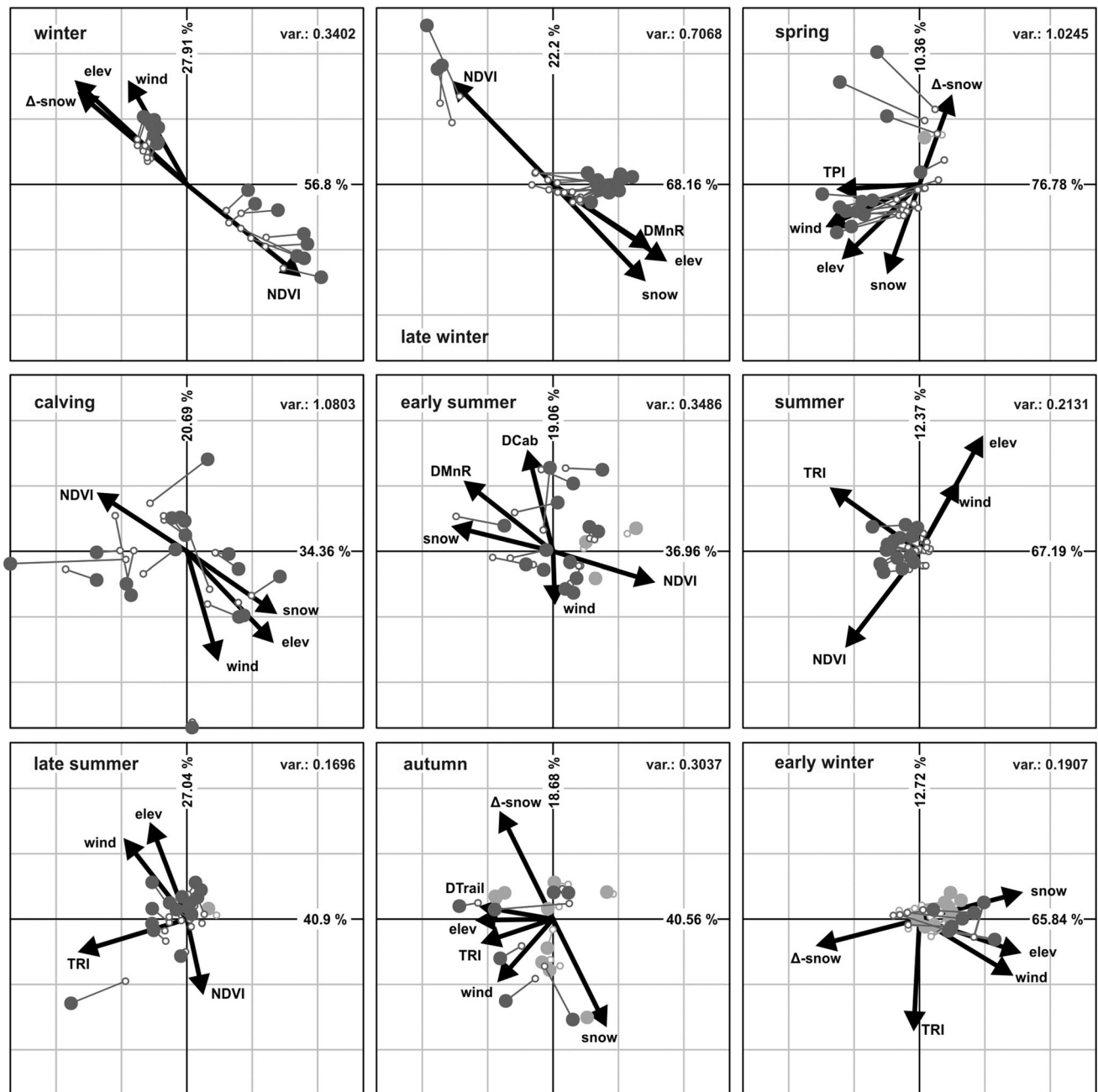


Fig. 4 Seasonal habitat selection of each collared reindeer within its respective home range. For each of the nine seasons, circles, plotted onto the first factorial plane of the K-select analysis, represent the mean availability of habitat conditions within each animal's home range (small open circles) and the mean of the utilized habitat conditions within this home range (filled circles). The connecting vector between each pair of open and filled circles represents the amount (marginality) and direction of habitat selection. These can be

interpreted using the arrows of the significant environmental variables which indicate the correlation of those variables with the first two K-select axes (Pearson's r ; the raster in the background corresponds to 0.5). Significant selections ($p < 0.05$) are shown in darker grey. The amount of variance explained by each axis is given in percent, whereas the amount of total variance is shown in the upper-right corner of each diagram

nature of habitat selection (Johnson 1980; Senft et al. 1987): selecting a home range within a region results in less selectivity within that home range.

Our findings failed to fully support our second expectation, i.e., that explanatory variables of habitat selection

are scale dependent (Gaillard et al. 2010). Consistent with Vistnes and Nellemann (2008) and Skarin and Åhman (2014), who reviewed the effects of human infrastructure on reindeer habitat selection, we found infrastructure to be more important within the region than within the home

range. Avoiding infrastructure while selecting a home range within a region suggests that habitat use within the home range is less affected by infrastructure, reflecting again the hierarchical nature of habitat selection. However, since infrastructure is not placed randomly in the landscape, it is likely that related factors (e.g., elevation) confound the assessment of the effect of infrastructure. Apart from infrastructure, however, none of the other explanatory variables were more important for one scale than the other. Instead, our analyses revealed that the effects of explanatory variables are dependent on the interaction between spatial scale and time. This result verifies the assumption of Leblond et al. (2011) and Thornton et al. (2011) that habitat selection is controlled across multiple interacting spatiotemporal scales.

We found pronounced differences between the seasons with regard to the amount and direction of habitat selection. During spring and calving, marginality (and thus selectivity) was high due to the search for high-quality food after the winter and secure calving sites. In contrast, habitat selectivity was low during summer and late summer, presumably due to homogenized forage availability (Iversen et al. 2014). The highest selectivity occurred during winter and late winter, when snow cover and wind exposure are important parameters (Skjenneberg and Slagsvold 1968). The availability of lichens as major winter fodder for reindeer depends on the ecological causal chain initialized by the “conservative nature of snow” (Gjærevoll 1956), i.e., annually recurrent patterns of snow distribution that result from the interplay of topography and wind. Spatial variations in microclimatic conditions due to snow cover and topography (Pape and Löffler 2004; Löffler et al. 2006) result in distinct spatial patterns of biocoenoses in general (Löffler and Finch 2005), vegetation types, plant growth (Bär et al. 2008), and ultimately utilization by herbivores. The reindeer also preferred higher, snow-covered elevations during calving in May; however, this preference was likely due to the reduced risk of predation, since reindeer predators and their alternative prey are less suited to live at high elevations (Skjenneberg and Slagsvold 1968; Gustine et al. 2006; Pinard et al. 2012). The subsequent move to lower elevations in early summer could be attributed to the surge for the onset of the vegetation green-up at lower elevations. Consequently, during the snow-free seasons, the NDVI (as a proxy for the state of vegetation and its productivity; Pettorelli et al. 2006) gained importance. Hence, and in accordance with our third expectation, fodder availability and plant phenology in this extremely seasonal environment led to pronounced temporal differences in habitat selection and its mechanistic forces.

Regarding intraspecies variability in habitat selection within the studied population, we found no general support for our fourth expectation that low variability occurred among

individuals. This expectation arose from the global model of domesticated reindeer as highly gregarious animals. However, the highest variability in habitat selection occurred during calving, as female reindeer exhibited obvious spatial segregation to reduce detection by predators (Pinard et al. 2012). This segregation is likely to result in a “functional response in habitat selection” (Mysterud and Ims 1998), reflecting a change in habitat preference with an altered habitat availability. The same functional response became obvious in winter and late winter, when two clusters of animals with different habitat preferences were discovered. One group sought fodder in wind-blown ridges above the tree line, whereas the other group preferred to eat in the forests with more evenly distributed snow and a lesser tendency to form crusts (Skjenneberg and Slagsvold 1968). During the rest of the year, the individual animals often showed similar selection along the *X*-axis of the analyses, but with a fair amount of variability along the less important *Y*-axis.

Framing our specific findings in the larger context of reindeer as a species, it is important to distinguish between the fundamental niche and the realized niche, as recently shown by Panzacchi et al. (2015). While the fundamental niche represents a kind of “global” species model, the realized niche, as analyzed in habitat selection studies, is necessarily restricted to a subset of resources available to a specific population, constrained by physical, biotic, historical, and—in the case of domesticated reindeer—management boundaries. Two implications arise from this setting. Firstly, given that the availability of resources is constrained by management, it is challenging to disentangle the key role that the herdsmen might play in the spatial and temporal range use of the majority of reindeer in Scandinavia. Though the reindeer under study were allowed to range freely under the surveillance of the borders, some of our findings (e.g., different strategies during winter; the larger the scale, the greater the selectivity) would fit well with the herdsmen’s choices. Secondly, even though our findings on the habitat selection of reindeer in the Filefjell area are consistent with what is generally known about reindeer as a species, population-based studies of habitat selection are valid only for the specific population studied, with upscaling to species level remaining difficult (Panzacchi et al. 2015). Apart from the strive for “global” species models that are often a practical approach for the study and ultimately the management of wildlife populations (Saher and Schmiegelow 2005; Anderson and Johnson 2014), our findings also imply the need to account for disparate habitat selection strategies depending on the interplay of spatial scale, time, and individual animal choice. This interplay would have been masked by pooling the data, which is undesirable since such behavioral plasticity is important for evaluating the potential effects of habitat change (Anderson and Johnson 2014).

Conclusions

Exploring the ecological dynamics inherent in the habitat selection of domesticated reindeer, we explicitly focused on variations related to spatial scale, time, and individual animal behavior. We found specific spatial, temporal, and spatiotemporal patterns of habitat selection, and these patterns were interlaced with a pronounced variability among conspecifics. To explain animal space use with the common simplification “the species as a rule does this,” and to attempt to find the single “best” model for which species–habitat relationships are strongest, proved to be unsatisfactory. Thus, we strongly advocate using additional across-scale approaches when considering ecological dynamics in habitat selection, as revealed by the interplay of spatial scale, time, and individual animal choice.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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