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Author(s): Ivar Herfindal, Unni Støbet Lande, Erling Johan Solberg, Christer Moe Rolandsen, Ole Roer and Hilde Karine Wam
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I. Herfindal (http://orcid.org/0000-0002-5860-9252) (ivar.herfindal@ntnu.no), Dept of Biology, Centre for Biodiversity Dynamics, Norwegian Univ. of Science and Technology, NO-7491 Trondheim, Norway. – U. S. Lande, Division of Forest and Forest Resources, Norwegian Inst. of Bioeconomy Research, Tingvoll, Norway. – E. J. Solberg and C. M. Rolandsen, Norwegian Inst. for Nature Research (NINA), Trondheim, Norway. – O. Roer, Faun Naturforvaltning AS, Fyresdal, Norway. – H. K. Wam, Div. of Forest and Forest Resources, Norwegian Inst. of Bioeconomy Research, Ås, Norway

Co-existing species at the same trophic level often segregate with respect to diet, habitat use, or spatial distribution, reducing their direct competition for resources. However, temporal patterns in species-specific habitat use, for instance due to climatic variation, may affect the strength of interspecific interactions, and generate temporal variation in niche partitioning. We assessed temporal variation in habitat overlap between a wild ungulate, moose *Alces alces*, and two free-ranging domestic ungulates, sheep *Ovis aries* and cattle *Bos taurus*, on a boreal forest range in southern Norway. We also calculated the distance between species' realised niches, as well as the width of their realised niches to evaluate the extent of temporal niche partitioning under different diurnal weather conditions. Analyses of each habitat variable suggested complex relationships between species-specific habitat use, photoperiod, and weather, related to species-specific behaviour and activity patterns. We found shorter overall niche distance between moose and sheep, compared to moose and cattle, and shorter niche distances during day and night than during the twilight hours. The niche distance between moose and sheep was positively related to temperature during night, but negatively during day. Moreover, niche distance between moose and both sheep and cattle was negatively related to precipitation at daytime. Moose niche width was narrower in periods with short niche distance to sheep, while we did not find such pattern towards cattle. A lack of similar moose response to cattle could be attributed to lower niche overlap between moose and cattle. Our results suggest that temporal niche partitioning between moose and livestock breaks down under the weather conditions that are predicted to become more common as climate change, potentially increasing wildlife-livestock interactions in the future.

Natural or semi-natural habitats used for grazing are a prerequisite for successful pastoralism in many parts of the world (Fratkin 2001, Koocheki and Gliessman 2005), and as such an ecosystem service with potentially high economic value. However, in many such areas livestock are interacting with wild ungulates (Austrheim et al. 2011, Chirichella et al. 2014), which also have a high economic, social and cultural value (Storaas et al. 2001, Austrheim et al. 2011). Following the increasing abundances of wild ungulates in many areas worldwide (Côté et al. 2004, Apollonio et al. 2010, Austrheim et al. 2011), concerns have been raised about the potential negative interactions, such as food competition, spatial displacement, or disease transmission between livestock and wild ungulates (Thomas and Barton 1995).

Studies on co-existing wild and domestic ungulates show contrasting results; from facilitation of food resources for wild ungulates by livestock grazing (Anderson and Scherzinger 1975, Gordon 1988), to range shift by wild ungulates as a response to presence of domestic ungulates (Austin and Urness 1986, DeGabriel et al. 2011, Mason et al. 2014). Other studies report no apparent facilitative or competitive interactions (Dorn 1970, Iranzo et al. 2013). The most common pattern seems to be that low abundance of domestic ungulates improves the foraging conditions for wild ungulates, whereas high abundances of domestic ungulates have a negative effect (Kuiters et al. 2005, Mysterud and Austrheim 2008). However, while negative demographic responses are often reported for wild ungulates (Jenks and Leslie 2003, Madhusudan 2004, Mishra et al. 2004, Marshal et al. 2008), few studies document negative impact on livestock by wild ungulates. Such a directional competition can be due to behavioural modifications caused by domestication, such as the fear response, resulting in a weaker tradeoff between gain and perceived costs (Mysterud et al. 1999). Wild ungulates may also avoid domestic ungulates due to the risk of parasite transmission (Frölich et al. 2002, Fankhauser et al. 2008), and the direction of interaction can be affected by the overlap in species-specific traits, e.g. their location along the grazer-browser continuum (Telfer 1994, Stewart et al. 2003).

A species' habitat association has often been related to the concept of the ecological niche (sensu Hutchinson 1957, Hirzel et al. 2002). The niche concept is useful for assessing habitat utilisation based on observational data (Hirzel et al. 2002, Basille et al. 2008), given that the observations are representative for the species or population in question. Characteristics of the realised niche (e.g. its location in the environmental space) under certain conditions (e.g. for a specific area and time period, and under given levels of predation risk and competition) can be described from sets of environmental variables that may be correlated. Accordingly, for one environmental variable there may be a short distance between two species' utilisation pattern, whereas it may be a long distance for a different environmental variable. In ecological niche modelling (Hirzel et al. 2002, Basille et al. 2008), such environmental variables are decomposed into an environmental space consisting of a set of environmental axes, in line with the conceptual framework of Hutchinson (1957). In a multi-species approach, distances in this environmental niche-space can be used as measures of niche partitioning, given that the environmental axes reflect the environmental variables in the same way for all species in question. Similarly, as the realised niches may vary temporarily according to various factors such as interspecific interactions and environmental variation (Kraan et al. 2013), the location and variation (i.e. niche width) in the niche space will also vary in time (Basille et al. 2013), hence, allowing us to estimate their temporal variation. In similar single-species approaches (Hirzel et al. 2002, Basille et al. 2013), the environmental covariates at used locations are compared to a measure of availability to obtain measures of habitat selection. However, if availability is similar for two species (e.g. sharing a range), and constant over time, any variation in habitat selection, which is the deviation between use and availability (Lele et al. 2013), will be caused by temporal variation in use among species.

Animal habitat use varies over time due to temporal variation in the cost–benefit ratio associated with a specific habitat type (Cornélis et al. 2011, Basille et al. 2013). For instance, the need for hiding cover may be higher during daytime than at night (Mysterud and Østbye 1999, Lykkja et al. 2009), and harsh weather conditions can increase the need for shelter (Dussault et al. 2004, Melin et al. 2014). Likewise, the foraging conditions within a habitat type may vary among seasons, generating and long-term temporal variation in a species' habitat association (Bjørneraas et al. 2011, Melis et al. 2015). The change in habitat association can occur as a shift in habitat used (i.e. a shift in the realised niche), for instance from open areas to forests (Mysterud and Østbye 1999, Lykkja et al. 2009), or as a change in the variation of habitats used (i.e. a change in the width of the realised niche). The latter can for instance involve a change from utilising a mixture of open and closed habitats to only utilising closed habitats on days with high temperatures (Melin et al. 2014), or by clustering around specific resources such as water sources during dry periods (Roever et al. 2012). Because the behavioural response to these factors can vary among species, e.g. due to perceived and actual mortality risk, diet, or tolerance to extreme weather, the level of species interaction will vary accordingly (Fritz et al. 1996). Understanding how niche overlap is related to weather conditions is particularly relevant in view of climate change.

In Norway, the abundance of moose *Alces alces* has increased during the last four decades (Lavsund et al. 2003), and are exceeding the abundance of free ranging livestock in many parts of the country (Austrheim et al. 2011). At the same time, moose hunting and related services have become increasingly more important for the rural economy (Storaas et al. 2001). This creates conflicts among stakeholders, as many are concerned about the potential impact of livestock grazing on moose distribution and demography. To obtain a sustainable management of forest resources for large ungulates, we therefore need more knowledge about the interactions between wild and domestic ungulates utilising the same areas.

To better understand such interactions, we analysed the variation in components of the realised niche of moose and two species of domestic ungulates, sheep *Ovis aries* and cattle *Bos taurus*, on a boreal forest range in southern Norway. Using an extensive set of location data, we 1) estimated the distances between the realised niche of moose, sheep and cattle, and 2) tested whether the realised niche distance co-varied with photoperiod (i.e. diurnally) and weather conditions. In addition, we examined 3) to what extent the width of the realised niche of moose was related to its niche distance to sheep and cattle. The dietary overlap between moose, sheep and cattle is quite low as moose summer diet consists mostly of browse and heather (Mysterud 2000, Wam and Hjeljord 2010a, b) whereas sheep and cattle predominantly eat grass and herbs (Hofmann 1989). Hence, from a diet perspective we expect rather long distances between moose and livestock niches. However, high-quality forage for all species seems to be most abundant in the same habitats, such as clear-cuts and young forest stands (Wam et al. 2010, Bjørneraas et al. 2012), indicating that the niche distances may be smaller than first anticipated. We also predicted niche distances to be shorter during twilight and night, when moose are most active, and to be longer during days of high temperatures. In warm days moose tend to seek shelter in the forest (Dussault et al. 2004, Melin et al. 2014), while livestock tend be resting in open areas (Hjeljord et al. 2014). Moreover, as livestock are tolerant to humans, moose are more likely to avoid areas occupied by livestock than the other way around. Hence, during periods of shorter niche distances, moose may decrease the use of habitats associated with livestock, resulting in a decrease in the niche width of moose. Alternatively, moose may turn to other sub-optimal habitats to compensate for the lower utilisation of preferred habitats, which will result in increased niche width.

Methods

Study area

The study area (approximately 520 km^2) is located in south-eastern Norway (60°16′N, 10°51′E), below the forest line with elevation ranging from 200 to 450 m. asl. and a topography dominated by gentle to moderate slopes (Fig. 1). The forest is dominated by Norway spruce *Picea abies* and Scotch pine *Pinus sylvestris*, mixed with deciduous species such as

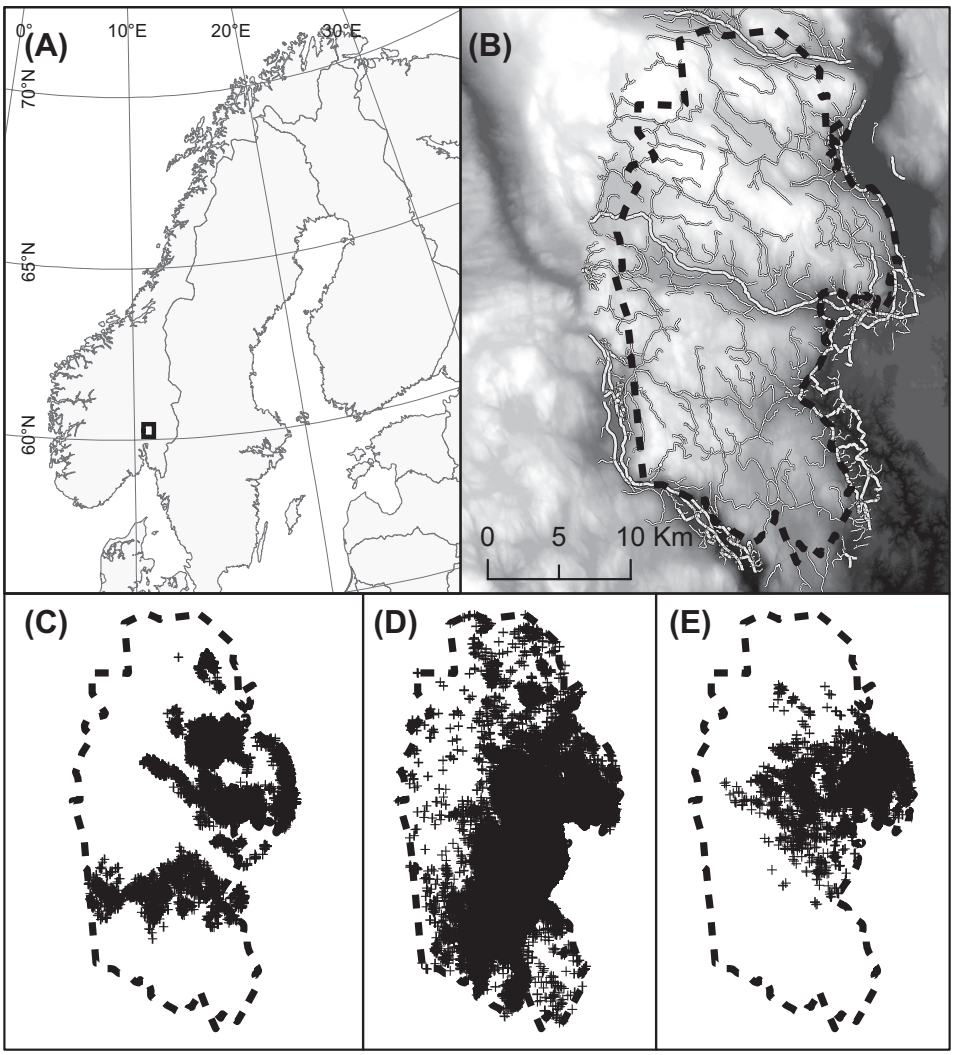

Figure 1. The location of the study area in Norway where we assessed niche partitioning among moose and livestock (A), and elevation and road densities (B, thin lines = private roads, thick lines = public roads, thick black dashed line = boundary of the study area). (C), (D) and (E) show the distribution of GPS-locations from moose, sheep, and cattle, respectively. Only roads closer than 2 km from the boundary of the study area are shown in (B).

birch *Betula pubescens*, rowan *Sorbus aucuparia*, aspen *Populus tremula*, goat willow *Salix caprea* and other salix species (Moen 1999). Open areas are mainly bogs, and meadows at abandoned summer farms, dominated by grasses and herbs. Logging activity creates a diverse age structure of the forest, of which young forest stands in general have particularly high quantity of moose forage (Wam et al. 2010, Bjørneraas et al. 2011). Besides forestry, human infrastructure is rather low in the area. One fenced-off public road crosses the study area (Fig. 1), but has several wildlife crossing corridors. There is also an extensive net of private gravel roads in the area.

The study area is almost entirely fenced in, where sheep and cattle are left free-ranging without any kind of shepherding during summer. Most sheep were transported to the central parts of the area before being released in early June, whereas cattle were released closer to the farms at the periphery of the area. Moose migrate from lower latitudes into the study area during spring (arrival in study area in the end of April or early May, O. Roer unpubl.), and have their summer ranges mainly inside the fenced area. Accordingly, during summer all three species share the same ranges.

Animal, habitat and weather data

Sheep (n = 376) and cattle (n = 15) were fitted with GPS-collars (Telespor; <www.telespor.no>) in the springs of 2010–2012 just before they were released in the grazing area. Moose were captured and fitted with GPS collars from VECTRONIC Aerospace (GPS PLUS/GPS PRO Light collars) during February and March 2009 and 2010, as part of a project to assess moose movement in relation to infrastructure. Capture, handling, and anesthetizing of moose were approved by the Norwegian Directorate for Nature Management and the Research Animal Committee in Norway, and followed the procedure described in Arnemo et al. (2006). Fifteen of the marked moose used the study area as summer range in 2010–2012, for which position data were included in the analyses after being screened for errors following Bjørneraas et al. (2010). Locations where subsampled to a

4-h interval to ensure a standardised sampling interval for all three species. The study period for all species was limited to 6 June–8 September, which corresponds to the period when all three were present within the syudy area. The density of livestock varied only slightly between study years (A. O. Ruud pers. comm.).

To describe the habitat at each animal location, we used elevation (m a.s.l.), slope (degrees), and aspect (radial degrees), obtained from a digital elevation model (DEM) with a spatial resolution of 25×25 m^2 (Norwegian Mapping Authority). Aspect was converted to two continuous variables: cos(aspect) ranging from 1 (north) to –1 (south) and sin(aspect) ranging from 1 (east) to –1 (west). In addition, we used habitat types based on land cover maps that were digitised from aerial photos and field surveys at a spatial scale of 1:5000 (Bjørdal and Bjørkelo 2006), and categorised as follows: High productive coniferous forest, medium productive coniferous forest, low productive coniferous forest, mixed and deciduous forest, grazing land (meadows and abandoned agricultural areas), bogs, and other areas (impediment, other open areas). We also calculated the distance to private roads and public roads. These were combined to one variable ('distance to roads') as they were highly correlated in the ecological niche space, and as the results did not differ qualitatively compared to the results of including private and public roads as two separate variables. To reduce heteroscedasticity in the habitat use regression, and to obtain normal distribution of the continuous variables in the habitat decomposition, slope was ln-transformed and distance to roads was square-root transformed. Elevation and aspect were not transformed.

Weather data (daily mean temperature and daily precipitation) from a nearby weather station located approximately 10 km southwest from the centre of the study area, were obtained from the Norwegian Meteorological Institute. The photoperiod at each animal location was calculated based on the solar elevation at the location at the time of observation, using the function `solarpos` in the package `maptools` (Bivand and Lewin-Koh 2014) in R ver. 3.2.2 for windows (<www.r-project.org>). Daytime was defined as solar elevation $> 0°$ (i.e. sun above the horizon), twilight hours as solar elevation $< 0°$ and $> -6°$, while the night time was defined as solar elevation $< -6°$.

Calculating niche components and distance

We assumed that the observations from marked individuals were random samples of locations from the entire population within the available area at a given time, and that all species had access to the same habitats, i.e. similar habitat availability. All observations from a species at time step t were then pooled to represent the population's habitat utilisation, which we call the realised niche of that species in the given area and time period t.

Following a modified approach of Basille et al. (2008) we first calculated the multivariate environmental space of all observations (all species pooled) described by the matrix $N \times P$ where N is number of observations from a range of time periods and P is the number of variables describing the landscape. Following recommendations in Basille et al. (2008), continuous variables were standardised with mean = 0 and variance = 1. We then used the function `dudi.mix` in the package `adehabitatHS` (Calenge 2006) in R (<www.r-project.org>) to decompose these variables into p environmental axes. This function performs as multivariate analyses where input variables can be a mix of continuous (e.g. elevation, slope) and categorical (habitat types) variables (Calenge 2006). An important output is the eigenvalues, which indicates axes' importance in explaining the variation in habitat characteristics of the observations. Attributes, such as species and time of observations, are distributed along these environmental axes (Fig. 2A). For instance, characteristics of the niche of a species a at time t for environmental axis i can be described by the mean value, $\mu_{a,i,t}$, and the variance $\sigma_{a,i,t}$.

The total niche distance along all p axes between two species, a and b, at time t, can then be calculated as:

$$\delta_{ab,t} = \sqrt{\sum_{i=1}^{p} \left(\mu_{a,i,t} - \mu_{b,i,t}\right)^2} \quad (1)$$

Note that $\delta_{ab,t}$ will always be greater than zero, as the direction of difference (i.e. if $\mu_{a,i,t}$ is greater than or smaller than $\mu_{b,i,t}$) along the environmental axes is discarded. Calculating $\delta_{ab,t}$ for several time steps (e.g. seasons or time of day) makes it possible to assess temporal variation in niche distance. In addition, when including more than two species, differences in niche distance between pairs of species can be directly compared. For instance, if $\delta_{ab,t}$ is higher than $\delta_{bc,t}$, the distance between the realised niche of species a and b is longer than between b and c, measured at the time period t (Fig. 2D).

The niche width for species a at time t in the environmental niche space described by the p axes, can be calculated as the variance of the values along the p axes for the species and time period (Fig. 2C):

$$\sigma^2_{a,t} = Var\left(\sum_{i=1}^{p} x_{a,i,t}\right) = \sum_{i=1}^{p} Var\left(x_{a,i,t}\right) + 2\sum_{i<j} Cov\left(x_{a,i,t}, x_{a,j,t}\right) \quad (2)$$

In further analyses we used the square root of $\sigma^2_{a,t}$ ($\sigma_{a,t}$) as measure of niche width as this gave models with better distribution of residuals (i.e. homoscedasticity). Although axes in the p-dimensional niche space are independent and thus have zero co-variation, there may be co-variation between values along two axes for a subset of the total sample, N, such as for a specific species a at time interval t.

Sample size may differ between species. This can potentially generate bias towards the most data-rich species or time, but can be accounted for by weighting observations according to the sample size of all observations belonging to the species (or time period), e.g. by $1/n$ where n is sample size. However, as the results did not differ qualitatively between analyses based on non-weighted or weighted niche calculations, we only present non-weighted results. The lack of effect of weighting may have occurred because difference in sample size mainly results in a shift of the centre of the environmental space towards the sample-rich species. Consequently, the difference between the species' location in the environmental space (i.e. the niche distances and widths) remains the same because species observations are placed in the same environmental space.

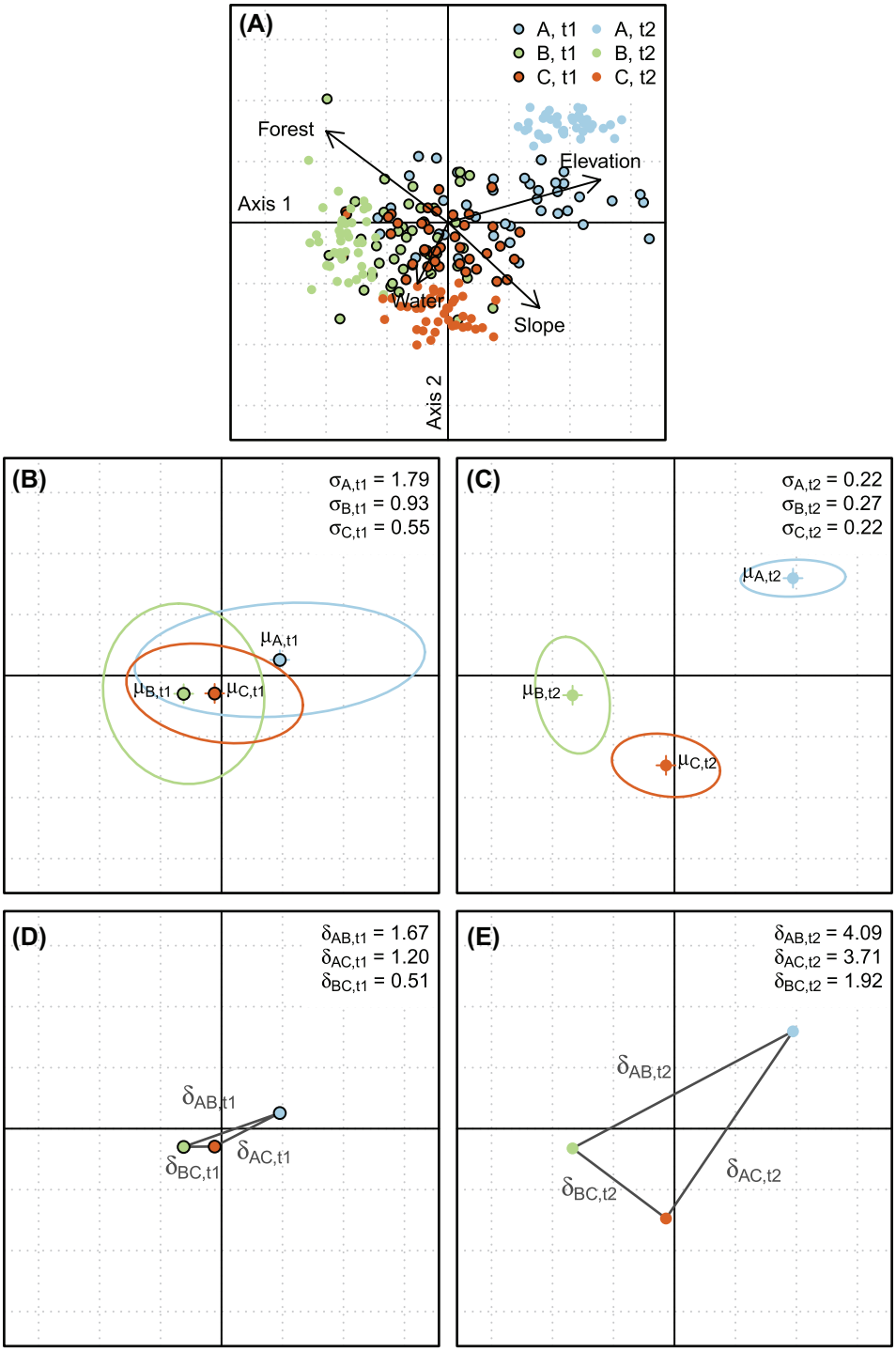

Figure 2. Schematic representation of the procedure to calculate the distance δ between realised niche, and niche width σ for three species and two time steps. (A) Observations from all species at all times are used to decompose the values from habitat characteristics into two environmental axes. (B) and (C) From the species locations in the environmental space, axis-specific means, μ, and total variation, σ (Eq. 2) can be calculated for each species and time step. (D) and (E) The niche distance between two species at a given time step, δ (Eq. 1) is calculated as the total distance in the environmental space described by axis 1 and axis 2. In the example, all species have wider realised niches at time step t1 compared to t2, and species A have the widest realised niche at t1. The distances between species' realised niche are largest during t2. Species A is located further away from B and C in the environmental space (larger δ) whereas species B and C have realised niches that are closer in the environmental space.

We decomposed the variation in habitat characteristics from all animal observations pooled into environmental axes. Based on the eigenvalues of the environmental axes, we chose to retain 5 axes that captured 62.3% of the total variation in landscape characteristics of the observations (Supplementary material Appendix 1 Table A1). From the five environmental axes, we calculated $\mu_{Moose,i,t}$, $\mu_{Sheep,i,t}$ and $\mu_{Cattle,i,t}$ where i is an environmental axis and t is time period defined by the

year, day number, and photoperiod (day, twilight, or night). Accordingly, each $\mu_{s,i,t}$ represents the population mean for a species along an environmental axis at a given day, photoperiod and year. From the sets of $\mu_{s,i,t}$ we calculated the overall environmental niche distance at a given time between moose and sheep, $\delta_{Moose\text{-}Sheep,t}$, and moose and cattle, $\delta_{Moose\text{-}Cattle,t}$ (Eq. 1), as well as the species-specific niche width, $\sigma_{s,t}$ (Eq. 2).

Our approach using ecological niche modelling approaches that takes into account multiple environmental axes differs from previous methods, such as Pianka's statistic (Pianka 1973) by allowing one single model to assess comparable measures of niche distance between several species, groups of individuals, or time periods simultaneously, and that niche locations (and consequently niche distance between species) and niche widths are obtained within the same framework. Note that our approach of examining differences in species habitat utilisation do not depend on the direction of which two species is examined. Measures of niche overlap that compare the overlap between two species niche in the hypervolume (Blonder et al. 2014), will get different answer depending on whether A is compared against B, or vice versa.

Analysing temporal variation in species-specific habitat use and niche components

In all analyses we included year and day number as random factors in (generalised) linear mixed models, (g)lmm, (Bolker et al. 2009) fitted within the lme4-package (Bates et al. 2014) in R (<www.r-project.org>), to account for temporal interdependencies in the observations that was not captured by the explanatory variables. We used AICc (Burnham and Anderson 2002) to rank candidate models. We allowed all variables to be excluded from candidate models, but if an interaction was included its main effects were always retained in the model. Uncertainty of parameter estimates (95% CI) was based on semi-parametric bootstrapping of the models using the function bootMer in package lme4 (Bates et al. 2014).

We first analysed each habitat variable separately to explore differences in habitat use among species and over time. For this, we used habitat variables averaged on species, year, day number, and photoperiod. We used (g)lmm with habitat variable as dependent variable and species, photoperiod, daily mean temperature and daily precipitation as explanatory variables. We also included all two-way interactions and the three-way interactions species × photoperiod × temperature and species × photoperiod × precipitation (see Supplementary material Appendix 2 for model details). Continuous variables (elevation, slope, aspect, distance to roads) were analysed with gaussian error structure. Habitat types were analysed in logistic models (glmm, binomial family and logit link) with the frequency of observations in the focal habitat type in relation to the total number of observation for the species at the time as dependent variables.

The two sets of niche distances ($\delta_{Moose\text{-}Sheep,t}$ and $\delta_{Moose\text{-}Cattle,t}$, see above) were pooled to one dataset where the variable 'livestock species' (LS) indicated whether the measured niche distance was between moose and sheep, or between moose and cattle. Niche distance was then analysed with linear mixed models with temporal covariates and whether niche distance was measured against sheep or cattle (LS) as explanatory variables. A significant effect of LS suggests that the niche distance between moose and cattle was different from the niche distance between moose and sheep. Moreover, we tested if temporal variation in $\delta_{Moose\text{-}Livestock,t}$ (*Livestock* being either sheep or cattle) was related to photoperiod, daily mean temperature, and daily precipitation, where the main effects indicate that niche distance varied between photoperiod or due to weather. The two-way interactions LS × photoperiod, LS × temperature and LS × precipitation were included to assess if temporal patterns in niche distance differed between moose and sheep compared to moose and cattle. Finally, the two-way interactions photoperiod × temperature and photoperiod × precipitation were included to assess if weather effects on niche distance was more pronounced during certain periods of the day. Likewise, the three-way interactions LS × photoperiod × temperature and LS × photoperiod × precipitation were included to see if any diurnal patterns in weather effects on niche distance varied depending on what livestock species moose was compared against. For an overview of the fixed factors and interactions included in the global model (Table 1). $\delta_{Moose\text{-}Livestock,t}$ was ln-transformed to reduce heteroscedasticity.

To assess the temporal variation in the width of the realised niche of moose, we analysed σ_{Moose} in a linear mixed model with respect to photoperiod, temperature, and precipitation. We also included $\delta_{Moose\text{-}Sheep}$ and $\delta_{Moose\text{-}Cattle}$ in order to investigate whether temporal variation in moose niche width was related to the distance in realised niche to livestock niches. A positive relationship between σ_{Moose} and $\delta_{Moose\text{-}Sheep}$ or σ_{Moose} and $\delta_{Moose\text{-}Cattle}$, indicates that moose niche width was narrower when niche distance between moose and livestock was shorter. In the global model, we also included two-way interactions between photoperiod and the other fixed factors.

Table 1. AICc-based ranking of candidate models explaining the variation in niche distance between moose and free-ranging livestock, $\delta_{Moose\text{-}Livestock}$, on a forest range in south-eastern Norway, based on the five axes describing the environmental niche space. Explanatory variables are livestock species (LS = sheep or cattle), photoperiod (PP = day, twilight, night), daily mean temperature (Temp) and total precipitation (Prec). Only the ten highest ranked models are shown.

LS	PP	Temp	Prec	LS× PP	LS× Temp	LS× Prec	PP× Temp	PP× Prec	LS× PP× Temp	LS× PP× Prec	ΔAICc	AICc-w
X	X	X	X	X	X		X	X	X		0.00	0.174
X	X	X	X		X		X	X			0.85	0.114
X	X	X	X	X	X		X		X		1.16	0.098
X	X	X	X		X		X				1.86	0.069
X	X	X	X	X	X	X	X	X	X		1.89	0.067
X	X	X		X	X		X		X		1.92	0.067
X	X	X	X	X	X	X	X	X	X	X	2.53	0.049
X	X	X	X				X	X			2.70	0.045
X	X	X			X		X				2.70	0.045
X	X	X	X		X	X	X	X			2.76	0.044

Results

Temporal variation in species-specific habitat use

For all habitat variables, animal species was included in the highest ranked models, indicating that habitat use varies among species (Supplementary material Appendix 2, Fig. 3). Photoperiod and its interaction with species were included in all of the highest ranked models, except for mixed deciduous forests. Thus, the effect of photoperiod on habitat use seemed to vary between species (Fig. 3). The overall pattern was that moose used areas at higher elevation, further from roads (during day) and at more north-facing slopes than sheep and cattle. In contrast, cattle more often used flatter areas closer to roads, as well as grazing land and bogs. High productive coniferous forest was most used by cattle (during day) and least by sheep (during twilight and night), whereas medium productive coniferous forest was most used by sheep (twilight and night). Low productive coniferous forest was used most by moose (day) and sheep (night), and only to a small extent by cattle. Mixed deciduous forest was mainly used by moose, but overall few observations were found in this habitat type. There were no consistent species-specific patterns between photoperiods for the habitat type "other areas".

The use of habitat types varied with weather conditions (Fig. 3). For all habitat variables except mixed deciduous forests, temperature and/or precipitation were included in the highest ranked model (Supplementary material Appendix 1 Table A1). Moreover, as the two- and three-way interactions between weather variables, species and photoperiod were included in most models, species and photoperiod also seemed important for how weather conditions affected habitat use.

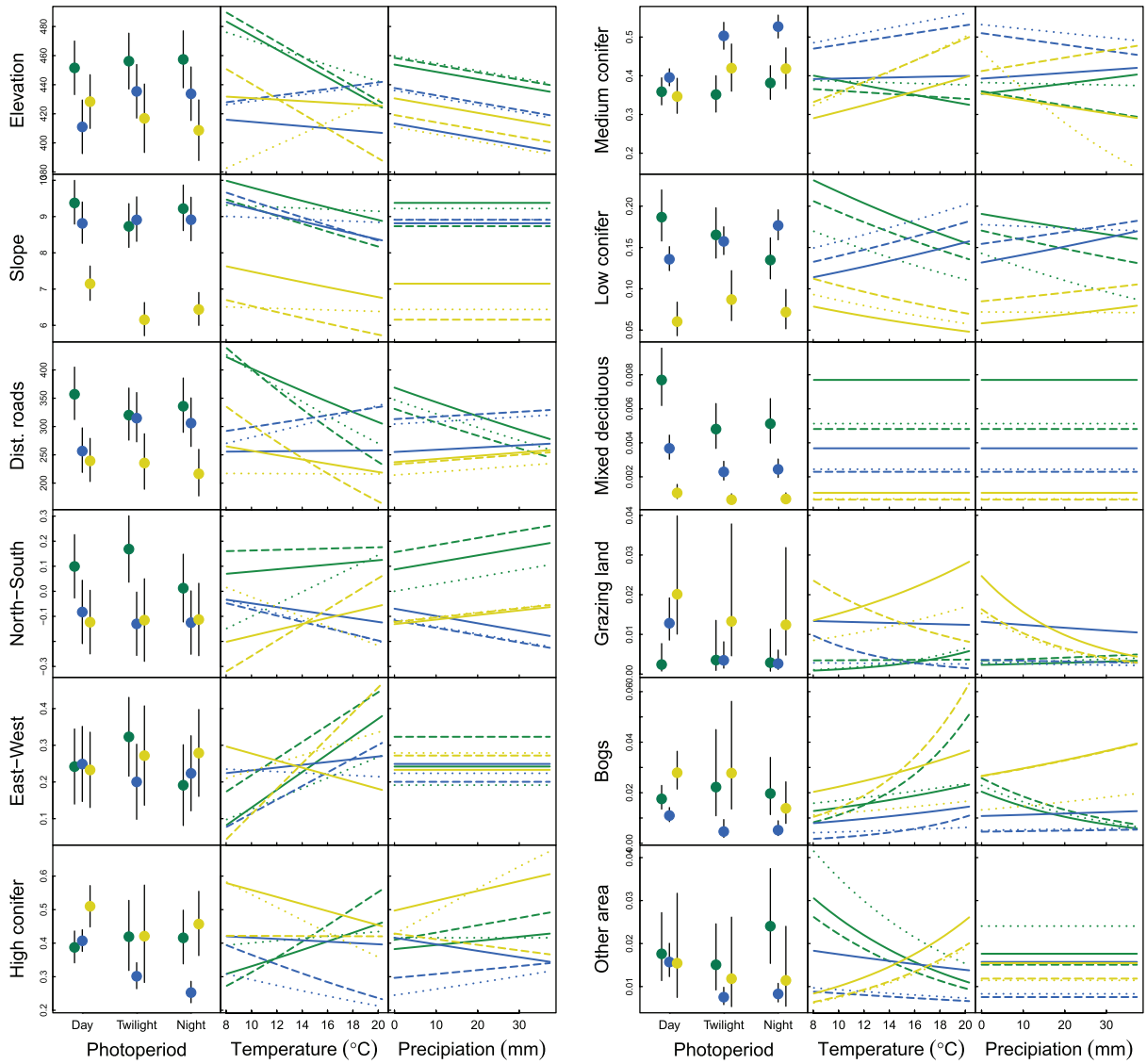

Figure 3. Species-specific temporal variation in habitat use among moose (green lines), sheep (blue lines) and cattle (yellow lines), based on the highest ranked model in the Supplementary material Appendix 1 Table A1. Solid, dashed, and dotted lines represent daytime, twilight, and night, respectively. Temperature is measured as daily mean temperature (°C), and precipitation is total daily precipitation (mm). For panels showing difference in use between photoperiods, mean temperature and precipitation are used to predict values. Bars show standard error of parameter estimates.

The overall pattern was that moose more often used flatter, more east-facing slopes at lower elevations and closer to roads during warm days compared to days with lower temperatures. During warm nights, moose used more north-facing slopes than in cold nights. Moose also increased their use of high productive coniferous forests during day and twilight periods when temperatures were high, and reduced their use of low productive coniferous forests. Finally, moose increased their use of bogs and reduced their use of "other areas" at high temperatures. Temperature-habitat relationships were less clear for sheep and cattle. Most importantly, sheep reduced their use of high productive coniferous forest during night and twilight hours at high temperatures, and increased their use of low productive coniferous forests. Cattle increased their use of medium productive coniferous forests and reduced their use of low productive coniferous forests at high temperatures. Cattle use of grazing land was positively related to temperature in both day and night, but negatively related to temperature in twilight periods. Cattle also used bogs and "other areas" more at high temperatures.

There were fewer and less complex relationships between habitat use and precipitation. All species used areas at lower elevation when precipitation was high. Moose also moved closer to roads and more often used north-facing slopes and high productive coniferous forests when precipitation was high, and spent less time in low productive coniferous forests and bogs. Patterns were weaker for livestock. However, sheep moved to more south-facing slopes at high precipitation, whereas cattle reduced their use of medium productive coniferous forest (during day) and grazing land, and increased the use of high productive coniferous forest (during day and night) when precipitation was high.

Species-specific variation in niche components

Component scores for the five environmental axes explaining the variation in landscape characteristics of the animal locations are found in Supplementary material Appendix 1. The first environmental axis was mainly related to distance to roads, elevation, and habitat types, whereas the second axis was related to slope, north-south aspect, and habitat types. The last three axes were mainly related to habitat types.

The average niche distance between moose and sheep, $\delta_{Moose\text{-}Sheep}$, was 1.17 (95% CI; 0.98; 1.40). The distance between moose and cattle, $\delta_{Moose\text{-}Cattle}$, was 1.59 (95% CI: 1.33; 1.90), which was significantly higher than $\delta_{Moose\text{-}Sheep}$ (95% CI of $\delta_{Moose\text{-}Sheep} - \delta_{Moose\text{-}Cattle}$: –0.53; –0.32). The $\delta_{Sheep\text{-}Cattle}$ was 1.15 (95% CI: 0.87; 1.53).

The mean niche width per time step, σ, was smallest for moose ($\sigma_{Moose} = 1.93$, 95% CI: 1.72; 2.13) and highest for cattle ($\sigma_{Cattle} = 2.23$, 95% CI: 2.03; 2.44), with sheep having intermediate niche width ($\sigma_{Sheep} = 2.09$, 95% CI: 1.89; 2.29). Niche width differed significantly between species (95% CI: $\sigma_{Moose} - \sigma_{Sheep}$: –0.28; –0.04, $\sigma_{Moose} - \sigma_{Cattle}$: –0.44; –0.17, $\sigma_{Sheep} - \sigma_{Cattle}$: –0.27; –0.02).

Temporal variation in niche components

The AICc-based model selection suggested that all temporal variables (photoperiod, temperature and precipitation) were important in explaining the variation in niche distance between moose and livestock (Table 1). The highest ranked model also included the interactions between photoperiod and species, species and temperature, photoperiod and temperature, and photoperiod and precipitation, as well as the three-way interaction between species, photoperiod and temperature. These terms were included in at least four of the six models with $\Delta AICc < 2$ (Table 1, see Supplementary material Appendix 2 Table A3 for parameter estimates for the two highest ranked models). Contrary to our expectations, niche distances, $\delta_{Moose\text{-}Sheep}$ and $\delta_{Moose\text{-}Cattle}$, were longest during twilight and shortest during day (Fig. 4A). The relationship between $\delta_{Moose\text{-}Livestock}$ and temperature differed between the livestock species, and between photoperiods (Fig. 4B). The relationship between temperature and $\delta_{Moose\text{-}Sheep}$ was negative during daytime and positive during night, whereas no clear relationship was found during twilight hours (Fig. 4B). $\delta_{Moose\text{-}Cattle}$ was only weakly related to temperature, with the strongest positive relationship during the twilight hours (Fig. 4B). Precipitation was related to $\delta_{Moose\text{-}Sheep}$ and

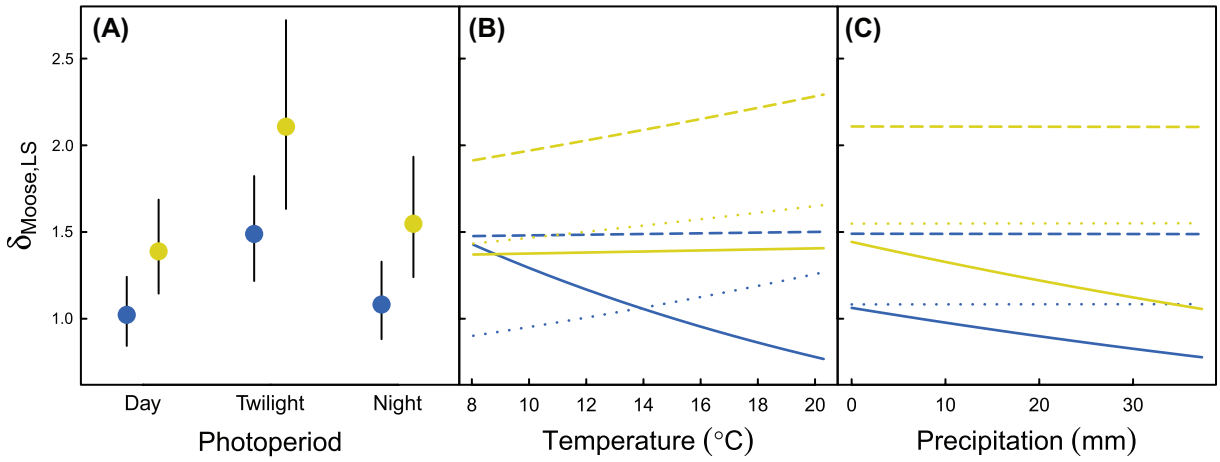

Figure 4. The relationships between realised niche distance between moose and livestock, $\delta_{Moose\text{-}Livestock}$, and daily temperature and precipitation. Blue and yellow lines represent niche distance between moose and sheep, and moose and cattle, respectively. Solid lines show relationships during the day, dashed lines show relationships during the twilight hours, whereas dotted lines show relationships during night. The predicted relationship is from the highest ranked model in Table 2. Bars show standard error of parameter estimates.

Table 2. AICc-based ranking of candidate models explaining the temporal variation in moose niche width, σ_{Moose}, from a forest range in southeastern Norway, in relation to the niche distance to sheep ($\delta_{Moose\text{-}Sheep}$) and cattle ($\delta_{Moose\text{-}Cattle}$), daily mean temperature (Temp), daily precipitation (Prec) and photoperiod (PP = day, twilight, night). Only the ten highest ranked models are shown.

PP	$\delta_{Moose\text{-}Sheep}$	$\delta_{Moose\text{-}Cattle}$	Temp	Prec	PP×$\delta_{Moose\text{-}Sheep}$	PP×$\delta_{Moose\text{-}Cattle}$	PP× Temp	PP× Prec	ΔAICc	AICc-w
X	X		X		X		X		0.00	0.303
X	X	X	X		X		X		1.24	0.163
X	X		X	X	X		X		1.98	0.113
X	X	X	X		X	X	X		3.15	0.063
X	X	X		X	X		X		3.20	0.061
X	X		X		X				3.23	0.060
X	X				X				4.24	0.036
X	X	X	X		X				4.28	0.036
X	X	X	X	X	X	X	X		5.03	0.024
X	X	X	X		X				5.17	0.023

$\delta_{Moose\text{-}Cattle}$ in a similar manner, with a negative relationship during daytime and no clear relationship during twilight or dark hours (Fig. 4C).

According to the AICc-based model selection, the temporal variation in moose niche width, σ_{Moose}, was best explained by photoperiod, temperature, and $\delta_{Moose\text{-}Sheep}$ (Table 2). The highest ranked model also included the interactions between photoperiod and $\delta_{Moose\text{-}Sheep}$, and photoperiod and temperature. These terms were included all candidate models with ΔAICc < 2 (see Supplementary material Appendix 2 Table A4 for parameter estimates for the two highest ranked models). σ_{Moose} was lowest during twilight and highest during night, but their associated 95% confidence intervals were quite high (Fig. 5A). Thus, there was only weak evidence for diurnal variation in σ_{Moose}. However, σ_{Moose} was positively related to $\delta_{Moose\text{-}Sheep}$, and more so during night, indicating that the realised niche of moose was wider when the niche distance to sheep was long (Fig. 5B). This is in accordance with the prediction that livestock presence may restrict habitat use by moose. During twilight hours the relationship between σ_{Moose} and temperature was negative while the relationship was weakly positive during night and day (Fig. 5C).

Discussion

Using location data from wild (moose) and domestic (sheep and cattle) ungulates that use the same forest range during summer, we show how niche partitioning between species varied with photoperiod and weather (Fig. 3, 4). The width of the moose niche also showed temporal variation related to photoperiod, temperature, and to the realised niche distance between moose and sheep (Fig. 5). Combined, these results suggest that the temporal variation in realised niche of wild and domestic ungulates is related to species-specific patterns of habitat utilisation varying over time.

Co-existing species with overlapping dietary or habitat requirements often show segregation in the form of dietary shifts or spatial displacement (Anderwald et al. 2015, Witczuk et al. 2015). In many cases, such segregation is the result of co-evolution towards less interspecific competition (Schlaepfer et al. 2005), facilitating the co-existence of species. However, in most cases domestic and wild ungulates have only a short history of co-existence, and they often interact during part of the year only (Chirichella et al. 2014). Accordingly, any behavioural response in the wild ungulate, such as spatial or niche segregation (Austin and Urness 1986, Fritz et al. 1996, La Morgia and Bassano 2009, Brown et al. 2010) is more likely to be a response to environmental perturbations, i.e. the presence of livestock, than to evolution.

In our study system, the distance between niches as described by habitat characteristics was shorter between moose and sheep compared to moose and cattle. Specifically, cattle used areas with less slope, closer to roads, and more dominated by high coniferous forest (day-time only) and grazing land, compared to moose and sheep. Both sheep and cattle are categorized as grazers (Van Soest 1994), and would

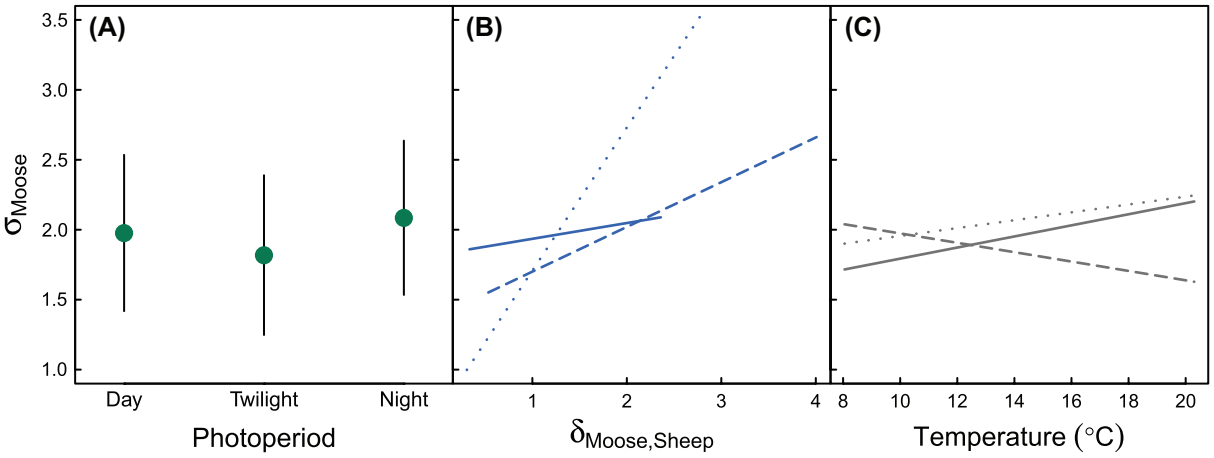

Figure 5. The relationships between moose realised niche width, and (A) photoperiod, (B) niche distance between moose and sheep, $\delta_{Moose\text{-}Sheep}$, and (C) daily temperature. Solid lines show relationships during the day, dashed lines show relationships during the twilight hours, whereas dotted lines show relationships during night. The predicted relationship is from the highest ranked model in Table 2. Bars in (A) show standard error of the parameter estimates.

therefore be expected to have similar habitat requirements with regard to foraging. However, as cattle are considerably larger than sheep, they may also be better in trading off forage quality for quantity (Demment and Van Soest 1985, but see Clauss and Hummel 2005), which can explain why they spend more time in open grazing land and bogs with higher abundance of grass. Conversely, sheep are smaller and less able to digest low-quality forage, and hence are forced to be more selective when foraging (Hofmann 1989). Forests, with their fine-scaled mixture of open and closed patches could therefore better accommodate the needs of sheep. Indeed, because such habitats also provide the most suitable foraging landscape for moose (Wam and Hjeljord 2010a, Bjørneraas et al. 2011), this can explain the shorter niche distance between sheep and moose than cattle and moose. It is worth noting that observations of sheep and moose were distributed over larger parts of the study area compared to cattle (Fig. 1), which could have created a similar pattern in case of considerable habitat differences e.g. between the southern and eastern part of the study area. However, the niche width was highest for cattle, which suggests that this species utilised the broadest range of habitats. Accordingly, there is no indication that cattle were particularly restricted by the habitat types available.

Habitat use differed between photoperiods, seemingly in accordance to species-specific diurnal activity patterns. For instance, moose are found to be least active during the day (Cederlund 1989, Lykkja et al. 2009), and in our study spent this time period mainly in the cover of low productive coniferous forest. In contrast, sheep and cattle seemed to spend most of the day in typical feeding habitats, but did otherwise show several contrasting diurnal patterns. While sheep was at lower elevations during day and moved to higher elevations in the twilight and night-time, cattle moved from higher to lower elevations. Similarly, sheep spent more time closer to roads in high productive coniferous forest during daytime; a pattern that was not found for cattle (Fig. 3). Hence, sheep and cattle utilise different parts of the landscape at different times (i.e. temporal habitat partitioning), leaving fewer habitats exclusively available for moose.

Through species-specific habitat-responses, weather can also affect the distance between species niches (Fritz et al. 1996). For instance, moose are not tolerant to heat during summer (Franzmann and Schwartz 1997), but can adjust by using habitats with denser canopy cover (Melin et al. 2014). This may explain why moose were more often using north-facing slopes at lower elevation and closer to roads during daytime when temperatures were high, and spent less time in low productive coniferous forest (Fig. 3). We found no such pattern in sheep and cattle, with the consequence that particularly the niche distance between sheep and moose decreased during periods with high temperature.

The complex patterns of habitat use in relation to photoperiod and weather suggest that animals make decisions based on tradeoffs between foraging, risk avoidance, and protection from stressful environmental conditions. In traditional habitat utilisation analyses, such results may be confounded by correlated habitat characteristics (Engen et al. 2008). By decomposing all habitat characteristics into one measure of niche distance, we could measure the temporal variation in overlap for all habitat variables combined. This analysis confirmed the results of the univariate analyses; i.e. that moose niche distance to sheep was shorter than to cattle, and shorter during the day and night than in the twilight hours (Fig. 4A). This emphasizes the importance of addressing temporal variation in niche overlap (Basille et al. 2013). In addition, the niche distance to livestock depended on weather conditions (Fig. 4B–C). The positive relationship between moose niche width and niche distance to sheep (Fig. 5B), also suggests a behavioural response by moose to sheep presence. Possibly, this is because moose avoid habitat types used by sheep, which has been reported for wild ungulates facing intrusion of livestock on their ranges (Cooper et al. 2008, Fritz et al. 1996, Chirichella et al. 2014, Traba et al. 2017), or it may be related to temporal correlation in the responses of niche width and niche distance to varying weather conditions. The niche distance between moose and sheep was related to temperature, and as niche distance was included in the model explaining the variation in moose niche width it may have captured some of the variation attributed to temperature.

In most areas where wild and domestic ungulates co-exist, the abundance of livestock is considerably higher than the abundance of wild ungulates (Austrheim et al. 2011, Chirichella et al. 2014). Accordingly, even small changes in their niche overlap can have high impact on the less abundant species, irrespective of its competitive abilities (Abrams 1980). The shorter niche distance between sheep and moose at high temperatures suggests that interactions between these species will increase following the predicted warmer and wetter weather in boreal forests (Benestad 2011). For moose, where summer is the main season for body growth and development (Herfindal et al. 2006), the combination of increased environmental stress from high temperatures (Melin et al. 2014) and higher level of interspecific interactions with livestock, can affect fitness through reduced foraging opportunities. Other mechanisms such as increased risk of disease transmission (Frölich et al. 2002, Stuen et al. 2013) may affect both livestock and wildlife. However, we need more knowledge about the fine-scale spatial interactions as well as dietary consequences of co-existence in order to predict any demographic consequences.

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Supplementary material (available online as Appendix wlb-00275 at <www.wildlifebiology.org/appendix/wlb-00275>). Appendix 1–2.