What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?

Floris M. van Beest[1,2]*, Inger M. Rivrud[2], Leif E. Loe[2,3], Jos M. Milner[1] and Atle Mysterud[2]

[1]*Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, Evenstad, NO-2480 Koppang, Norway;* [2]*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, NO-0316 Oslo, Norway; and* [3]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Aas, Norway*

Summary

1. Most studies of intraspecific variation in home range size have investigated only a single or a few factors and often at one specific scale. However, considering multiple spatial and temporal scales when defining a home range is important as mechanisms that affect variation in home range size may differ depending on the scale under investigation.

2. We aim to quantify the relative effect of various individual, forage and climatic determinants of variation in home range size across multiple spatiotemporal scales in a large browsing herbivore, the moose (*Alces alces*), living at the southern limit of its distribution in Norway.

3. Total home range size and core home range areas were estimated for daily to monthly scales in summer and winter using both local convex hull (LoCoH) and fixed kernel home range methods. Variance in home range size was analysed using linear mixed-effects models for repeated measurements.

4. Reproductive status was the most influential individual-level factor explaining variance in moose home range size, with females accompanied by a calf having smaller summer ranges across all scales. Variation in home range size was strongly correlated with spatiotemporal changes in quantity and quality of natural food resources. Home range size decreased with increasing browse density at daily scales, but the relationship changed to positive at longer temporal scales. In contrast, browse quality was consistently negatively correlated with home range size except at the monthly scale during winter when depletion of high-quality forage occurs. Local climate affected total home range size more than core areas. Temperature, precipitation and snow depth influenced home range size directly at short temporal scales.

5. The relative effects of intrinsic and extrinsic determinants of variation in home range size differed with spatiotemporal scale, providing clear evidence that home range size is scale dependent in this large browser. Insight into the behavioural responses of populations to climatic stochasticity and forage variability is essential in view of current and future climate change, especially for populations with thermoregulatory restrictions living at the southern limit of their distribution.

Key-words: climate, forage availability, movement, reproduction, scale dependence, supplementary feeding

Introduction

Movements of individual animals are often restricted to a specific area, defined as a home range, likely due to increased benefits of familiarity with that area (Stamps 1995; van Moorter *et al.* 2009). Understanding why home range size varies between and within species remains a fundamental issue in ecological research (McLoughlin & Ferguson 2000; Börger, Dalziel & Fryxell 2008). While interspecific variation

in home range size is largely driven by body-size-dependent metabolic requirements (Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Carbone *et al.* 2005), intraspecific variation in home range size may be caused by a range of intrinsic and extrinsic factors (Table 1). In most studies, only a single or a few factors have been used to describe intraspecific variation in home range size and often at one specific spatial or temporal scale (e.g. Table 1).

Clearly, the mechanisms underlying intraspecific variation in home range size involve scale dependence (Kie *et al.* 2002; Rivrud, Loe & Mysterud 2010), an important component of

Table 1. Summary of a literature review on the effect of various individual, forage and climatic determinants of home range size in cervids. For more details on the predictions see Introduction. For each study reviewed, we state the spatial and temporal scales under investigation, home range size (HR) estimator used (minimum convex polygon is abbreviated as MCP), the direction of the relationship (+ for positive relationships, − for negative relationships and 0 for no relationships) and the cervid species under investigation. The review was restricted to variables available in this study

Factor & predictions	Temporal scale	Spatial scale and HR estimator	Effect on home range size	Species	Reference
Intrinsic					
Individual variation (P. 1·1)	Seasonal	100% MCP	Large	Moose	Stenhouse et al. (1995)
	Seasonal	60 & 95% MCP	Large	Moose	Dussault et al. (2005a)
	Seasonal	95% MCP & fixed kernel	Large	Mule deer	Nicholson, Bowyer & Kie (1997)
	Multiple	50–90% fixed kernel	Large	Roe deer	Börger et al. (2006)
Body mass (P. 1·2)	Annual	95% harmonic mean	+ (males only)	Mule deer	Relyea et al. (2000)
	Summer	50 & 95% fixed kernel	0	Roe deer	Saïd et al. (2005)
	Seasonal	95% fixed kernel	0	Roe deer	Saïd et al. (2009)
Age (P. 1·3)	Annual	90% MCP	0 (females), + (males)	Moose	Cederlund & Sand (1994)
	Seasonal	95% fixed kernel	−	Roe deer	Saïd et al. (2009)
	Seasonal	50 & 95% fixed kernel	0	Roe deer	Saïd et al. (2005)
	Multiple	50–90% fixed kernel	− (yearly scale only)	Roe deer	Börger et al. (2006)
Reproductive status (P. 1·4)	Annual	90% MCP	Calf > no calf (autumn only)	Moose	Cederlund & Sand (1994)
	Summer	90% adaptive kernel	Calf > no calf	Roe deer	Tufto, Andersen & Linnell (1996)
	Summer	50 & 95% fixed kernel	2 calves > no calf	Roe deer	Saïd et al. (2005)
Extrinsic (Forage related)					
Browse density (P. 2·1)	Seasonal	60 & 95% MCP	− (winter) + (summer)	Moose	Dussault et al. (2005a)
	Seasonal	95% fixed kernel	−	Red deer	Anderson et al. (2005)
	Seasonal	95% fixed kernel	−	Roe deer	Saïd et al. (2009)
Browse quality (P. 2·2)	Summer	50 & 95% fixed kernel	−	Roe deer	Saïd et al. (2005)
	Seasonal	95% fixed kernel	−	Roe deer	Saïd et al. (2009)
Use of feeding stations (P. 2·3)	Winter	95 & 50% MCP & harmonic	−	Roe deer	Guillet, Bergstrom & Cederlund (1996)
	Winter	Mean 95% adaptive kernel	−	White-tailed deer	Kilpatrick & Stober (2002)
Extrinsic (climate related)					
Temperature (P. 3·1)	Multiple	50–90% fixed kernel	−	Roe deer	Börger et al. (2006)
	Daily	100% MCP	−	Red deer	Kamler, Jedrzejewska & Jedrzejewski (2007)
	Multiple	50–90% MCP & fixed kernel	− (summer), + (winter)	Red deer	Rivrud, Loe & Mysterud (2010)
Snow depth (P. 3·2)	Winter	60 & 95% MCP	−	Moose	Dussault et al. (2005a)
	Winter	95% MCP & fixed kernel	−	Red deer	Luccarini et al. (2006)
	Winter	50–90% MCP & fixed kernel	−	Red deer	Rivrud, Loe & Mysterud (2010)
Rainfall (P. 3·3)	Multiple	50–90% fixed kernel	−	Roe deer	Börger et al. (2006)
	Daily	100% MCP	0	Red deer	Kamler, Jedrzejewska & Jedrzejewski (2007)
	Multiple	50–90% MCP & fixed kernel	+	Red deer	Rivrud, Loe & Mysterud (2010)
Daylight (P. 3·4)	Multiple	50–90% fixed kernel	− (summer), + (winter)[a]	Roe deer	Börger et al. (2006)
	Multiple	50–90% MCP & fixed kernel	− (daily scale)	Red deer	Rivrud, Loe & Mysterud (2010)

[a]Börger et al. (2006) analysed the effect of daylight on home range size of roe deer over a full year. The effect cycled over time and as such was negatively related during the period corresponding to summer and positively related during the period corresponding to winter.

ecological theory (Wiens 1989). For example, Börger et al. (2006) showed how the effects of local climate on home range size of roe deer (*Capreolus capreolus* L.) differed between total home range area and the core home range area. Similarly, the effect of home range determinants can change across temporal scales. Spencer, Cameron & Swihart (1990) found a significant relationship between weekly home range

size and body mass of cotton rats (*Sigmodon hispidus* Say and Ord), but the effect was absent at shorter (daily) time-scales.

The overall objective of this study is to examine how individual, forage and climatic factors influence variation in home range size of a large browser, the moose (*Alces alces* L.) in southern Norway, across multiple spatial (core area to total home range area) and temporal (daily to monthly)

scales. Based on previous findings of cervid home range size (Table 1), we test the following predictions:

Individual-level determinants: We expect large individual variation in home range size across all scales (P. 1·1). Variation in body mass and age is typically poor predictors of within-species home range size (Table 1), and we therefore expect to find no effects of body weight or age on home range size over space or time (P. 1·2 and P. 1·3, respectively). In contrast, the effects of reproductive status on ungulate space use are typically greater as females change their behaviour in response to changes in energetic requirements, mobility and vulnerability to predation (Tufto, Andersen & Linnell 1996; Grignolio *et al.* 2007; Long *et al.* 2009). Contrasting empirical evidence has been found, whereby females accompanied by offspring either enlarged their summer home range during lactation (e.g. roe deer: Tufto, Andersen & Linnell 1996; Saïd *et al.* 2005), reduced it (e.g. white-tailed deer (*Odocoileus virginianus* Zimmermann): Schwede, Hendrichs & McShea 1993; Alpine ibex (*Capra ibex ibex* L.); Grignolio *et al.* 2007) or showed no change (e.g. moose; Cederlund & Sand 1994). Based on energetic requirements, we would expect females with a calf at heel to have larger home ranges than barren females (P. 1·4$_a$), while based on mobility arguments, we would expect smaller ranges because of the restricted mobility of the offspring (P. 1·4$_b$).

Forage characteristics: Forage variability is considered a primary factor in herbivore space use (Tufto, Andersen & Linnell 1996; McLoughlin & Ferguson 2000). We therefore expect overall density of browse and the proportion of high-quality browse to have a marked negative effect on moose home range size across all temporal scales (P. 2·1 and P. 2·2, respectively). The presence of winter supplementary feeding stations may also affect animal movement and habitat selection patterns within seasonal home ranges (Guillet, Bergstrom & Cederlund 1996; van Beest *et al.* 2010a). We expect winter home range size to decrease as the time spent at supplementary feeding stations increases (P. 2·3).

Climatic determinants: Recently, the effect of climatic determinants on home range size has received increased attention because of climate change issues. Mechanisms might include both direct effects associated with thermoregulation or increased costs of moving in deep snow at short temporal scales, as well as indirect effects operating through plant growth, typically at longer temporal scales (Rivrud, Loe & Mysterud 2010). Moose are adapted to cold environments but may suffer from heat stress at warm ambient temperatures in all seasons (Dussault *et al.* 2004). We therefore expect moose home range size to be negatively correlated with temperature across all spatiotemporal scales, but most clearly at short temporal scales (P. 3·1). Similarly, we expect winter home range size to decrease with increasing snow depth across all scales (P. 3·2). Although contrasting results have been found for the effect of precipitation on home range size (Table 1), precipitation is known to increase heat loss in ungulates (Parker 1988). We therefore expect precipitation to negatively affect moose home range size with the effect being most pronounced at short temporal scales (P. 3·3). Finally,

the effect of day length is known to be a key determinant of activity and home range size (Börger *et al.* 2006). We expect hours of daylight to be consistently important on moose home range size across all scales with a positive relationship during winter and a negative relationship during summer (P. 3·4).

Materials and methods

STUDY AREA

The study area (1733 km^2) is located in southern Norway within parts of Telemark, Buskerud and Vestfold counties (59°21′N, 9°38′E) and ranges in altitude from 20 to 800 m with the forest line at approximately 750 m. The area is in the boreonemoral zone and is mostly covered by commercially managed coniferous forest (82%). Stands are dominated by Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.), but some mixed deciduous stands also occur. Average ± SE temperatures in the area over the last 30 years were 15·5 ± 0·9 °C in summer (June–September) and −2·1 ± 1·4 °C in winter (January–April). Average ± SE snow depth in the area over the last 30 years was 35 ± 14·4 cm (The Norwegian Meteorological Institute; http://eklima.met.no). Moose winter densities in the area are approximately 1·5 individuals per km^2 (Norwegian Institute for Nature Management). Red deer (*Cervus elaphus* L.) and roe deer densities are 0·5 and 0·2 individuals per km^2, respectively. Large predator species are scarce, and hunting is the single most important cause of moose mortality in this area.

MOOSE AND GLOBAL POSITIONING SYSTEM (GPS) DATA

A total of 34 adult female moose accompanied by a calf were tranquilized by dart gun from a helicopter, using established techniques (Arnemo, Kreeger & Soveri 2003), during January 2007 and January 2008 (van Beest *et al.* 2010b). Body mass (range: 235–430 kg) was recorded by weighing the restrained moose from the helicopter. Moose were fitted with GPS collars with a VHF radiotransmitter (Tellus Remote GSM, Followit AB, Lindesberg, Sweden), programmed with a 1-h relocation schedule. GPS locations were collected from January to November ($N = 16$ in 2007 and $N = 18$ in 2008). Marked individuals were, where possible (25/34 individuals), harvested during the hunting season (10th of October to 30th of November) as part of the annual quota set by the local wildlife board. Age of the marked individuals (range: 2–14 years) was determined by counting tooth annuli (Rolandsen *et al.* 2008). Missing data on age estimation reduced the total sample size to 24 individuals ($N = 10$ in 2007 and $N = 14$ in 2008). All marked adult females were located and approached carefully on foot in early June to determine the presence of a newborn calf. If no calf was observed, we located the female again at intervals of several days until we were confident of calving status. Fourteen adult females were observed with a calf during summer (58%), and none of the females were accompanied by twins. These values are representative for this part of Norway (Lavsund, Nygren & Solberg 2003).

All GPS locations collected within 24 h of marking were excluded. The GPS data were screened for positional outliers using an established technique based on moose movement characteristics (Bjørneraas *et al.* 2010). With this approach, we removed 498 erroneous locations (< 0·5% of the full GPS data set).The average GPS-collar fix rate was 93% (range: 83–99%), and the mean location error was 29·9 m (range: 8–49 m) which was less than the resolution of our

forage availability maps (see below). We therefore judged the potential bias of these factors on home range size to be low. Long directional movements, such as during migration, can seriously affect home range size (Luccarini *et al.* 2006) so we excluded GPS locations from each individual's migration period (Ramanzin, Sturaro & Zanon 2007; Rivrud, Loe & Mysterud 2010). To do so, we classified individuals as migratory or resident, we used the first GPS location of each individual (i.e. reference point) and calculated the net displacement distance (using Euclidean distances in metres) between each subsequent location and the reference point. For individuals displaying a distinct migratory pattern ($N = 22$ of 24), we identified the start and end dates of migration using piecewise regression in the library 'segmented' (Muggeo 2008) implemented in the statistical software R (R Development Core Team 2009). With this approach, we removed 10 029 locations (5·9% of the full GPS data set).

FORAGE VARIABILITY AND LOCAL WEATHER DATA

Large herbivores are often confronted with spatial and temporal variation in the quality and quantity of their food resources. We used forage availability maps (50 m^2 pixel resolution), for both summer and winter seasons, based on field estimates of available biomass of the six most common browse species eaten by moose in southern Norway; full details are given in van Beest *et al.* (2010b). We considered silver birch (*Betula pendula* Roth.), downy birch (*Betula pubescens* Ehrh.) and Scots pine as low-quality browse species and rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.) and willow (*Salix* spp.) as high-quality species (van Beest *et al.* 2010b). We extracted the total amount of summer and winter forage biomass within each moose home range from the forage availability maps using Spatial Analyst in ArcGIS (2006 ESRI, Redlands, CA, USA). We divided the total amount of forage biomass by home range size (ha) to obtain a measure of forage density (dry mass g ha^{-1}). The proportion of high-quality browse within each home range was calculated by dividing the amount of quality browse biomass by the total amount of forage biomass. On some occasions, the marked individuals ventured completely or partly outside the area for which we had forage availability data. We therefore excluded individuals with <95% home range overlap with the forage availability maps at each spatiotemporal scale. To quantify use of supplementary feeding sites in winter by each individual at each spatiotemporal scale, we determined the proportion of time spent within 100 m of feeding stations (sensu van Beest *et al.* 2010a). We did so by calculating the number of GPS locations within a 100 m buffer around feeding stations and dividing this by the total number of GPS locations obtained for that individual at a specific spatiotemporal scale. Because feeding stations were small (<20 m^2) and because the location in between the hourly fixes is not known, we assumed that moose located within a 100 m buffer from feeding sites had indeed visited the station.

To assess the effect of climate on home range size, we obtained data on daily temperature, rainfall and snow depth from the nearest available meteorological station. Mean daily temperature data (°C) during 2007 and 2008 were taken from a weather station located 18 km east of the centre of our study area (100 m above sea level). Data on daily rainfall (mm) and snow depth (cm) were obtained from a different weather station located 15 km south of the centre of our study area (450 m above sea level; The Norwegian Meteorological Institute; http://eklima.met.no). To evaluate whether the climatic conditions observed during the study period were typical of the long-term pattern in local climate, we used monthly temperature, snow depth and precipitation averages for both summer and winter over the last 30 years (Fig. S1, Supporting Information). We regressed daily temperature, rainfall and snow depth against Julian day using generalized additive models (GAM) in the R library 'mgcv' (Wood 2006) and used the residuals of each covariate as fixed effects to analyse variation in home range size. This approach removes the seasonal pattern from the weather data but retains the unpredictable climatic variability over time. Day length (hours of daylight) in the southern part of Norway during our study period was obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil).

SPATIOTEMPORAL SCALES AND HOME RANGE SIZE ESTIMATION

We considered four temporal (daily, weekly, biweekly (two weeks) and monthly) and two spatial scales, delimited by the core area (50% isopleths) and total home range area (90% isopleths). All scales were analysed separately for both summer and winter. Annual snow conditions were used to define winter length (period with ≥30 cm snow depth). As such, winter in 2007 stretched from 21st January until 8th April and in 2008 from 4th January until 30th April. Summer was defined as the period 1st of June till 15th of September for both years. Spring and autumn were excluded to avoid the inclusion of long distance movements during migration and the autumn breeding season and because we lacked forage availability maps for these periods.

Home range sizes (ha) were estimated with the nonparametric local convex hull (LoCoH) method (Getz *et al.* 2007) and the fixed kernel method (Worton 1987), using the R library 'adehabitat' (Calenge 2006). We employed the k-LoCoH method, where k is the number of nearest neighbour points from which local hulls were constructed to obtain a utilization distribution. Following Getz *et al.* (2007), k was calculated by $k = \sqrt{n}$, where n is the mean number of locations per marked individual at a specific temporal scale. For the fixed kernels, we employed the reference technique for the calculation of the smoothing factor h (Kernohan, Gitzen & Millspaugh 2001). We only estimated home ranges for individuals with at least 95% coverage in a given temporal scale.

MODEL DEVELOPMENT AND STATISTICAL ANALYSES

To examine variation in moose home range size across spatiotemporal scales, we used linear mixed models in the R library 'nlme' (Pinheiro *et al.* 2009). Log-transformed home range size (ha) was fitted as the response variable in all models. Depending on the season, we included the following fixed effects (defined in Table 2) in the models: age, body mass, calf at heel (yes or no; summer models only), proportion of time spent at feeding stations (winter models only), browse density, proportion of high-quality browse, the residuals of temperature, precipitation, snow depth (winter models only), hours of daylight and year (2007 vs. 2008). To allow the effect of each home range size determinant to change over time (i.e. within seasons), we also fitted an interaction between each covariate and hours of daylight. Collinearity between covariates was checked using Pearson's correlation (all values <0·3). We only included individuals in the analyses with at least two home range estimates (i.e. repeated measurements). This caused a reduction in the number of individuals included at longer time-scales.

Moose ID was fitted as a random intercept in all models to account for patterns in the residuals of the fixed effects occurring owing to repeated observations of the same individual (Pinheiro & Bates 2000; Börger *et al.* 2006). We used the Akaike Information Criterion (AIC) to evaluate whether the inclusion of a random effect was indeed necessary (Pinheiro & Bates 2000).

Table 2. Description of the covariates fitted as fixed effects in the linear mixed-effects models to explain variation in moose (N = 24) home range size. See Material and Methods for more details on data collection for each covariate

Parameter	Description
Age	The age (year) of each individual moose as determined from tooth annuli
Body mass	The January live mass (kg) of each individual moose as recorded during collaring. Note that age and body mass of adult females were not correlated
Calf at heel	Two-level factor indicating whether a female moose was accompanied by a calf (yes/no). Note that this covariate was included in the summer models only as all but one female moose was accompanied by a calf from the previous year during winter
Feeding station use	The proportion of time spent within 100 m of an artificial feeding station during each temporal scale (winter models only). Calculated by dividing the number of Global Positioning System (GPS) locations (hourly positions) within 100 m of a feeding station at a specific temporal scale by the total number of GPS locations at that scale
Browse density	The density of available moose browse (dry mass g ha^{-1}) in each home range. The 6 most abundant browse species in the study area were included in the calculations. Note that ground layer vegetation is not included
Browse quality	The proportion of high-quality moose browse available in each home range. Browse density was divided by the density of high-quality species
Temperature, rainfall and snow depth	The residual variation of each covariate after accounting for seasonal trends by regression (GAM) against Julian day. Note that the residuals of these three covariates were not correlated. Snow depth was included in the winter models only
Daylight	Mean number of daylight hours per temporal scale. Note that daylight was included in all two-way interactions to allow effects to change over time (during seasons)
Summer season	1 June till 15 September in both 2007 and 2008
Winter season	The period with snow depth exceeding 30 cm. As such winter in 2007 was 21 January till 8 April and in 2008, 4 January till 30 April
Year	Two-level factor (2007 vs. 2008)

Any residual dependence among observations that was not accounted for by the fixed or random effects was modelled using correlation structures for the within-group errors (Pinheiro & Bates 2000). We fitted either spatial or temporal correlation structures as it is (currently) not possible to fit both in the same model and evaluated which best fitted the data using AIC (Börger *et al.* 2006). Spatial correlation between home ranges was modelled using the harmonic mean of the home ranges, and temporal correlation was modelled by numbering consecutive home range estimates for each individual. We always used the 'corExp' function as this method provided the best fit based on AIC. Last, the models were checked for unequal variance structures (heteroscedasticity) of the within-group errors. We tested the fit of several available variance functions and evaluated model improvement by AIC (Pinheiro *et al.* 2009). In all cases where a variance function improved the model, we used the fitted values as the variance covariate using the 'varPower' function in the R library 'nlme'.

Once the distributional assumptions of the mixed model structure were fulfilled (Table S1, Supporting Information), model selection of the fixed effects was conducted by backward selection from the full model with F tests using P = 0·05 as the threshold for inclusion of predictor variables and interactions (Murtaugh 2009). To assess the amount of variation in the data explained by the final models and the random effects, we used a generalized R^2, which is calculated as the square of the correlation between the fitted values of the model and the observed values in the data (Zheng & Agresti 2000).

Results

We estimated a total of 6161 home ranges (3383 within summer and 2778 within winter). Both home range estimation methods produced qualitatively similar results (i.e. direction of relationships). We present the results obtained with the *k*-LoCoH method here (see Table S2 in Supporting Information for a summary using the fixed kernel home range estimator). Home range size varied greatly across spatiotemporal scales and was consistently larger during summer than winter (Fig. 1; Table S3, Supporting Information). Differences in home range size between years were minor and only occurred during summer at the monthly scale (50% isopleth) and during winter at the weekly scale (90% isopleth), with larger home ranges during 2008 than 2007 in both cases (Table 3). The fixed effects of the most parsimonious models explained between 37% and 80% of the observed variation in home range size, being greater for 90% home ranges (mean = 58%; range: 44–80%) than 50% home ranges (mean = 50%; range: 37–79%), and for monthly home ranges than daily home ranges (Table 3). Summary statistics of the final mixed-effects models predicting monthly, biweekly, weekly and daily home range sizes of moose are given in the Supporting Information (Tables S4–S7, respectively).

INDIVIDUAL-LEVEL DETERMINANTS

As expected (P. 1·1), we observed large individual variation in home range size (up to one order of magnitude or more) across all spatiotemporal scales (Table S3, Supporting Information). The proportion of variation explained by moose ID (i.e. R^2 of random effect) ranged between 0·12 and 0·46 across scales (Table S1, Supporting Information), being greater for
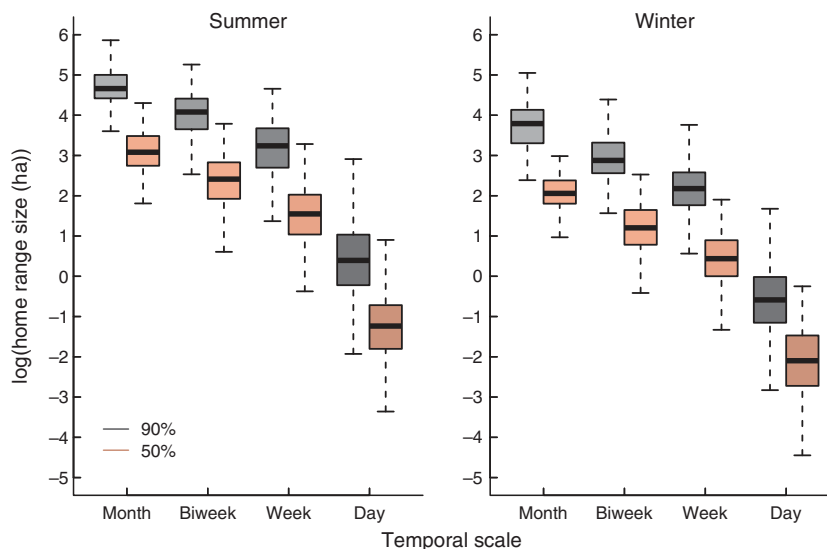
Fig. 1. Spatiotemporal variation of moose home range size during summer and winter in southern Norway. Box plots are given for 90% (black) and 50% (red) log-transformed *k*-LoCoH home range estimates (ha) from monthly to daily scales.

summer than winter, and for total home range area (90% isopleth) than core area (50% isopleth).

Body mass (log transformed) had a small positive effect on core home range size during winter only (P. 1·2; Table 3b; Fig. S2, Supporting Information), such that daily core home range size increased significantly with body mass (β = 0·92, SE = 0·40, $F_{1,22}$ = 5·92), while at the biweekly scale, heavier females increased their core area as winter progressed (interaction between body mass and daylight: β = 0·52, SE = 0·21, $F_{1,75}$ = 5·95).

As expected (P. 1·3), age did not appear to be an important variable affecting home range size across spatiotemporal scales.

Reproductive status (P. 1·4) was one of the most influential variables determining home range size during summer and was retained in all final models (Table 3a). As expected from P. 1·4$_b$, females with a calf at heel had smaller summer ranges than barren females, a pattern that was consistent across all scales. However, differences in home range size between females with and without a calf decreased over the course of summer (i.e. interaction between calf at heel and daylight) with similar range sizes in both groups in September (Fig. 2).

FORAGE CHARACTERISTICS

Browse density was included in most final models as a predictor of summer home range size. However, the expected decrease in home range size with increasing browse density (P. 2·1) was only observed at the daily scale (Table 3a; Fig. 3). At longer temporal scales, the effect was either positive throughout summer (e.g. biweekly scales) or changed through the season (i.e. interaction with daylight for weekly and monthly scales). For example, at the monthly scale in the beginning of summer (i.e. June), browse density negatively affected total home range size, but as summer progressed, the

relationship became increasingly positive (i.e. September in Fig. 3). During winter, browse quantity was retained in most final models of variation in home range size (Table 3b). Again, the relationship changed from negative at the start of winter to positive at the end of winter (e.g. monthly and weekly scales; Fig. S3, Supporting Information).

The proportion of high-quality browse (P. 2·2) was negatively correlated with summer home range size as expected but only at intermediate (i.e. weekly) to short (i.e. daily) temporal scales (Table 3; Fig. S4, Supporting Information). The effect was consistent throughout the season (i.e. no interaction effect with daylight). During winter, abundance of high-quality browse negatively affected home range size at most temporal scales with a stronger effect on core areas than on total home range size (Table 3; Fig. 4). However, at the monthly scale, the effect on core home range size changed from negative during the start and middle of winter to positive at the end of the season (i.e. April; Fig. 4).

Contrary to our expectation (P. 2·3), the proportion of time spent at feeding stations did not influence winter home range size at any spatiotemporal scale.

CLIMATIC DETERMINANTS

Variation in local climate during the study period (2007–2008) was similar to that observed over the last 30 years (Fig. S1, Supporting Information). Temperature (P. 3·1) affected moose home range size only at intermediate (biweekly scale during summer) and short (daily scale during summer and winter) temporal scales and affected total home range size more than core area size (Table 3). During summer, neither biweekly nor daily home range size decreased with temperature as predicted, but instead remained unaffected in the beginning of summer and increased with temperature in September (Fig. S5, Supporting Information).

Table 3. Overview of the *F* values and the direction of the relationship (+ for positive relationships and – for negative relationships) with home range size, of the fixed effects in the most parsimonious models determining moose home range size (ha) across spatiotemporal scales during summer (a) and winter (b) seasons. Analyses were performed on home ranges constructed with the *k*-LoCoH home range estimator. R^2 values show the amount of variation explained by the model (all fixed effects combined). *F* values in bold indicate $P < 0.05$. NR = Not retained in final model

Time-scale & fixed effects	90%*F*	+/−	50%*F*	+/−
(a) Summer				
Monthly scale				
Browse density	**4·56**	+	0·83	−
Calf at heel (yes)[a]	**8·48**	−	**23·76**	−
Daylight	0·63	+	0·02	−
Year (2008)[b]	NR		**5·57**	+
Browse density × Daylight	**12·86**	−	**9·01**	−
Calf at heel × Daylight	**10·92**	−	NR	
R^2	0·70		0·58	
Biweekly scale				
Browse density	**5·37**	+	**4·92**	+
Temperature	1·48	+	NR	
Calf at heel (yes)[a]	**6·08**	−	**11·13**	−
Daylight	0·02	−	0·92	+
Temperature × Daylight	**7·75**	−	NR	
Calf at heel × Daylight	**5·39**	−	**7·17**	−
R^2	0·61		0·53	
Weekly scale				
Browse density	**5·48**	+	**9·67**	+
Browse quality	NR		**6·56**	−
Calf at heel (yes)[a]	**6·62**	−	**10·86**	−
Daylight	1·45	+	1·39	+
Browse density × Daylight	**4·09**	−	NR	
Calf at heel × Daylight	NR		**5·44**	−
R^2	0·59		0·50	
Daily scale				
Browse density	**70·43**	−	**683·40**	−
Browse quality	**7·53**	−	**65·81**	−
Temperature	**4·55**	+	2·06	−
Precipitation	1·40	+	3·55	+
Calf at heel (yes)[a]	3·89	−	**5·19**	−
Daylight	**17·65**	+	**13·23**	+
Temperature × Daylight	**4·19**	−	**6·57**	−
Precipitation × Daylight	**4·76**	+	**8·32**	+
Calf at heel × Daylight	**8·33**	−	**6·94**	−
R^2	0·51		0·39	
(b) Winter				
Monthly scale				
Browse density	1·29	−	0·98	−
Browse quality	NR		1·93	−
Daylight	1·84	+	0·98	+
Browse density × Daylight	**8·05**	+	**7·94**	+
Browse quality × Daylight	NR		**5·34**	−
R^2	0·80		0·79	
Biweekly scale				
Browse density	**7·65**	−	**15·43**	−
Browse quality	**31·55**	−	**30·69**	−
Daylight	**4·88**	+	**4·56**	+
Body mass	NR		**4·92**	+
Body mass × Daylight	NR		**5·95**	+
R^2	0·50		0·37	
Weekly scale				
Browse density	NR		0·02	−
Browse quality	NR		**11·38**	−
Snow depth	**7·14**	−	NR	
Daylight	**18·74**	+	**8·77**	+
Year (2008)[c]	**9·04**	+	NR	

Table 3. (Continued)

Time-scale & fixed effects	90%*F*	+/−	50%*F*	+/−
Browse density × Daylight	NR		**4·13**	+
R^2	0·46		0·41	
Daily scale				
Browse density	**119·81**	−	**419·70**	−
Browse quality	**44·69**	−	**44·03**	−
Temperature	2·87	+	NR	
Snow depth	**8·12**	−	NR	
Daylight	**33·90**	+	**7·55**	+
Body mass	NR		**5·92**	+
Browse density × Daylight	**4·29**	+	NR	
Browse quality × Daylight	**4·48**	−	**4·26**	−
Temperature × Daylight	**11·06**	+	NR	
R^2	0·44		0·42	

[a]In reference to no calf at heel.
[b]In reference to 2007.
[c]In reference to 2007.
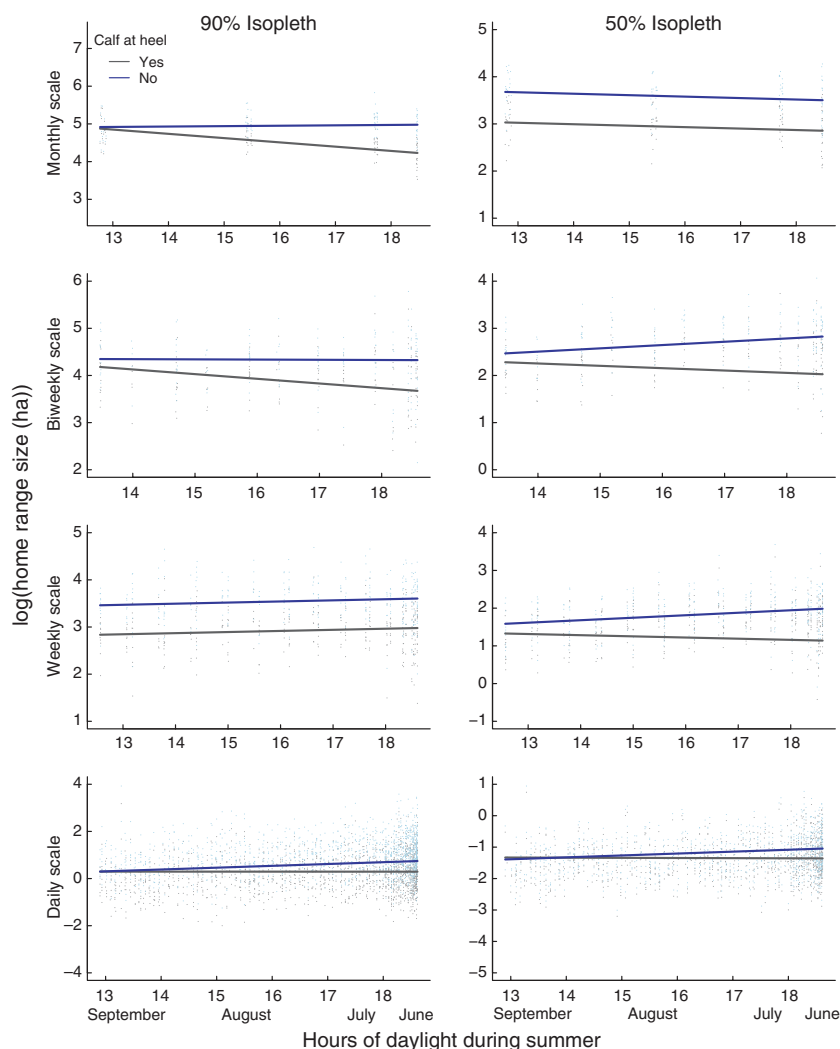
Fig. 2. Plot of predicted log-transformed home range sizes (ha) in relation to hours of daylight during summer for moose with a calf at heel (black) and for barren females (blue) in southern Norway. Home range size was calculated with the *k*-LoCoH home range estimator. Estimates are given for all spatial (90% and 50% isopleths) and temporal scales (daily to monthly). Predictions were made while keeping other variables constant at their mean value. Lines show predicted values, and points in corresponding colours are raw residuals.
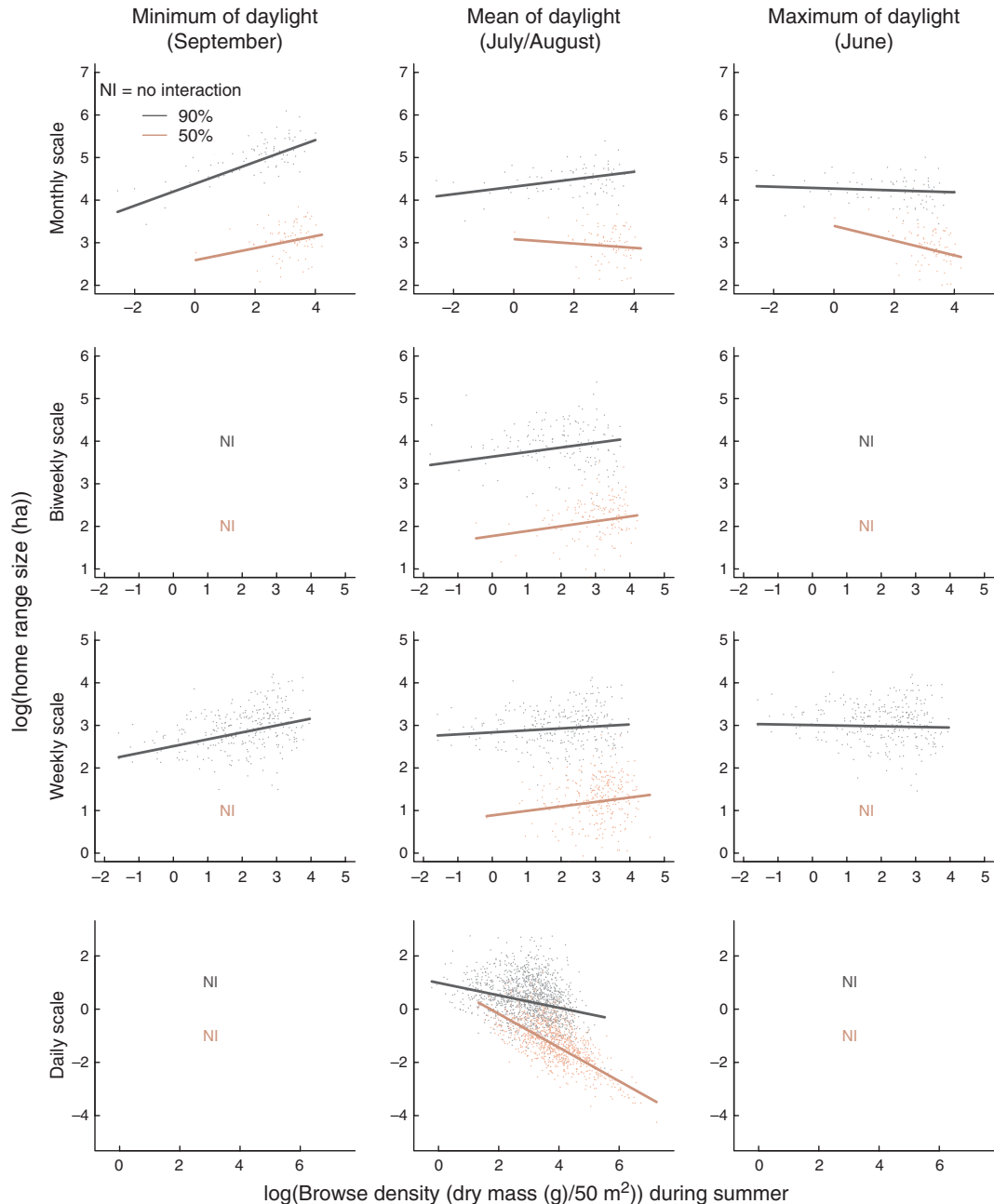
Fig. 3. Plot of predicted log-transformed summer home range sizes (ha) in relation to log-transformed browse density of moose in southern Norway. Home range size was calculated with the *k*-LoCoH home range estimator. Estimates are given for all temporal scales during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June, respectively. Predictions for overall browse density were made while keeping other variables constant at their mean value. Lines show predicted values for 90% (black) and 50% (red) isopleths, and points in corresponding colours are raw residuals. NI = no interaction with daylight (i.e. effect is consistent over time).

During winter, total home range size at the daily scale decreased with temperature as expected, but only in January. At the end of winter (April), daily ranges increased with temperature (Fig. S6, Supporting Information).

Snow depth (P. 3·2) negatively affected home range size as expected (Table 3b; Fig. 5), although this relationship was only evident at daily and weekly temporal scales for total home range size (90% isopleth).

Precipitation (P. 3·3) did not appear to be a major variable explaining variation in home range size. It affected home

range size only during summer at the daily scale (Table 3a) and the effect changed over time (Fig. S7, Supporting Information). In the beginning of summer, daily ranges (both total and core area) increased with precipitation while at the end of summer daily ranges decreased with increasing rainfall. Precipitation during winter (i.e. snow fall) was not retained in any of the final models.

Hours of daylight (P. 3·4) were a consistently important variable across all spatiotemporal scales (Table 3). As expected, home range size increased with hours of daylight
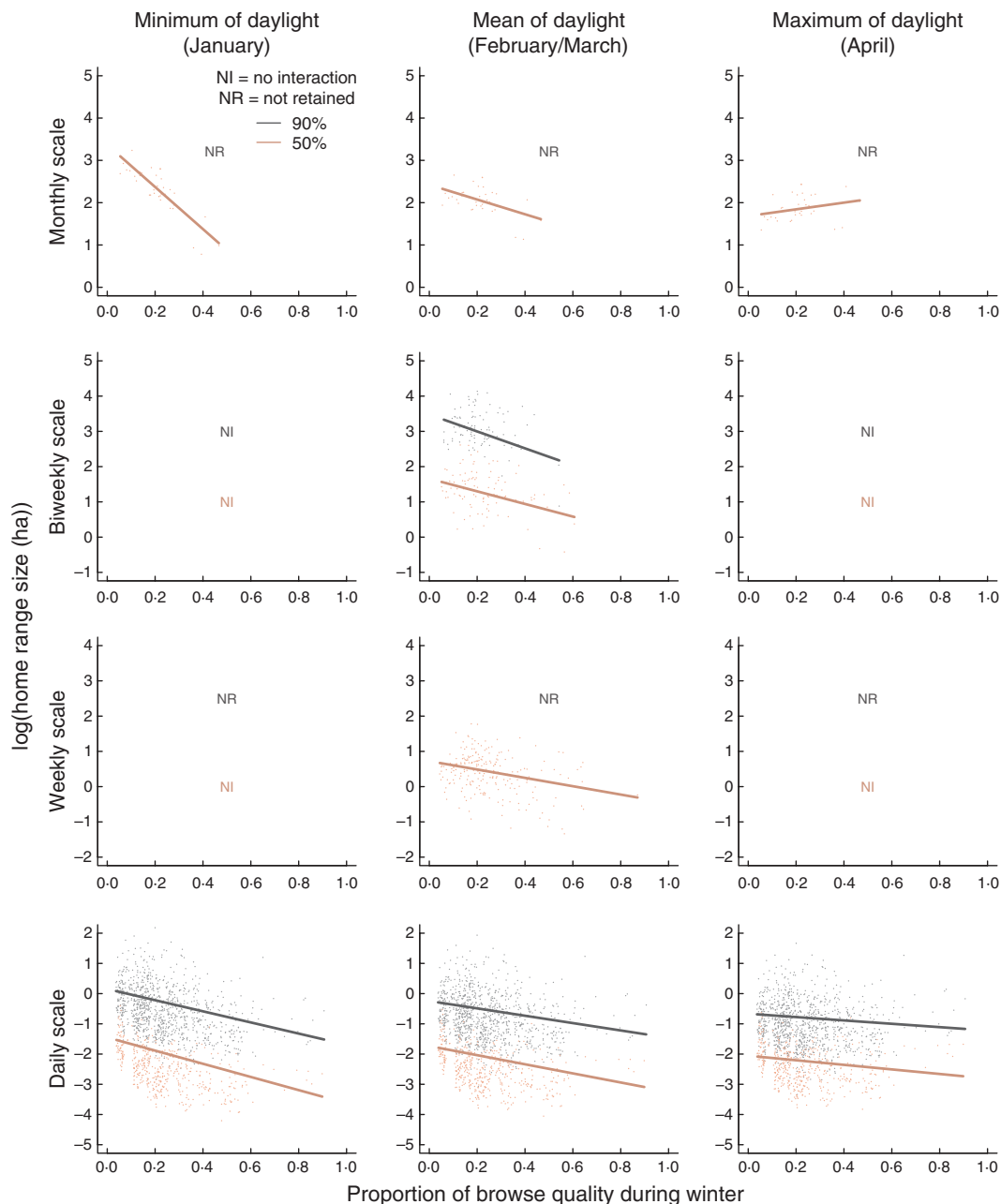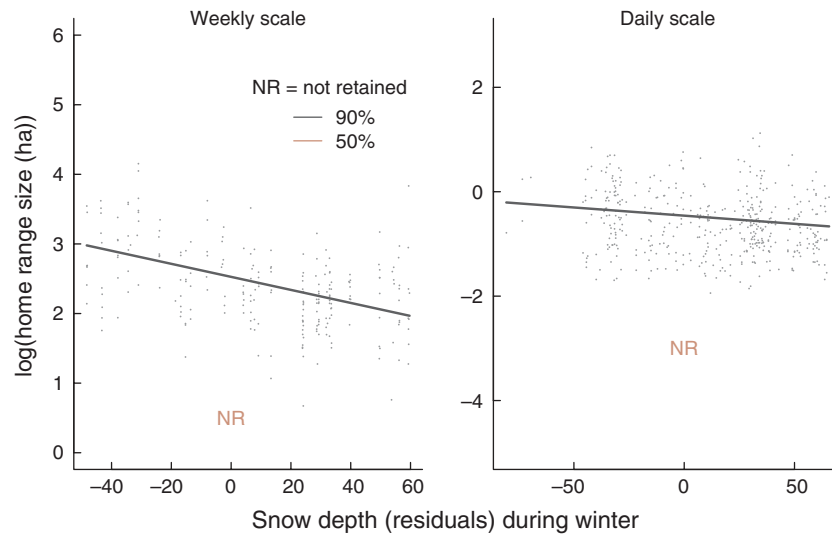
Fig. 4. Plot of predicted log-transformed winter home range sizes (ha) in relation to the proportion of browse quality of moose in southern Norway. Home range size was calculated with the *k*-LoCoH home range estimator. Estimates are given for monthly, biweekly, weekly and daily scales during winter, and for the minimum, mean and maximum value of daylight, corresponding to January, February/March and April, respectively. Predictions for the proportion of browse quality were made while keeping other variables constant at their mean value. Lines show predicted values for 90% (black) and 50% (red) isopleths, and points in corresponding colours are raw residuals. NI = no interaction with daylight (i.e. effect is consistent over time). NR = not retained in final models.

during winter (smallest and largest home ranges in January and April, respectively) and decreased with decreasing daylight during summer (smallest and largest home ranges during September and June, respectively).

Discussion

Most temperate ungulates are frequently confronted with spatiotemporal fluctuations in the availability and quality of food (Tufto, Andersen & Linnell 1996; Anderson *et al.* 2005; Hebblewhite, Merrill & McDermid 2008) and with climatic stochasticity (Saether 1997; Mysterud *et al.* 2001). However, concurrent analyses of the scale-dependent effect of both bottom-up processes and variability in local weather patterns on animal space use are rare (Börger *et al.* 2006). Bottom-up processes affect herbivores directly (Vucetich & Peterson 2004), and the way they exploit the variability of forage resources over time and space can have important effects on

Fig. 5. Plot of predicted log-transformed winter home range size (ha) of moose in southern Norway in relation to snow depth (cm) variability (measured as residuals see text for details). Home range size was calculated with the *k*-LoCoH home range estimator. Estimates (mean values) are given for weekly and daily scales during winter. Lines show predicted values for 90% isopleth, and points are raw residuals. Predictions for snow depth were made while keeping other variables constant at their mean value. Snow depth was not retained in the 50% isopleth model (NR).

their Darwinian fitness (McLoughlin *et al.* 2007). Simultaneously, variability in local weather patterns may affect species directly (Coulson *et al.* 2001), indirectly through trophic interactions among species (Mysterud *et al.* 2008) or both (Rivrud, Loe & Mysterud 2010). In addition, behavioural responses to forage variability and climate may vary considerably among individuals of the same species (Nicholson, Bowyer & Kie 1997; Dussault *et al.* 2005a; Börger *et al.* 2006).

This study is one of the first to assess the effect of multiple individual, forage and climatic determinants on spatial and temporal variation in home range size for a large browsing herbivore. Our results indicate that the relative effects of intrinsic and extrinsic determinants on variation in home range size differed within and between spatiotemporal scales (i.e. the mechanisms of home range size are scale dependent). Furthermore, we demonstrate that by including hours of daylight as an interaction in the models, we can reveal how behavioural responses to local climate and forage variability change within seasons. This makes it difficult to conclude whether intrinsic or extrinsic variables are the most important drivers in scaling of home range size. Instead, this study supports the notion that there is no single or most appropriate scale at which to study animal movement or activity (Börger *et al.* 2006; Rivrud, Loe & Mysterud 2010). Nevertheless, several important consistencies were evident across scales. For example, we observed great individual variation in home range size of moose irrespective of scale which is in agreement with previous findings (Stenhouse *et al.* 1995; Dussault *et al.* 2005a). In addition, the presence of a calf, variability in browse quantity and quality and hours of daylight appeared major determinants of home range size. In contrast, the effect of local climate on home range size appeared to be most pronounced at intermediate to short temporal scales,

which partly contrasts with findings for mixed feeders such as red deer (Rivrud, Loe & Mysterud 2010).

INDIVIDUAL-LEVEL DETERMINANTS

Differences between individuals (modelled by the random term moose ID; P. 1·1) explained more of the variance in home range size than individual-level attributes such as age or body mass (as expected from P. 1·2 and P. 1·3), as also found in roe deer (Tufto, Andersen & Linnell 1996; Saïd *et al.* 2005; Börger *et al.* 2006). This highlights the fact that individual variation in home range size is not fully captured by the factors age, body mass and reproductive status at the intraspecific level (but see Saïd *et al.* 2009 for an effect of age). This contrasts with findings from interspecific studies, typically spanning a wider range of body mass, in which body size is a major factor determining home range size (Lindstedt, Miller & Buskirk 1986; Carbone *et al.* 2005). Reproductive status nonetheless appeared to be a key individual-level factor determining summer home range size in moose. Contrary to findings for roe deer (Tufto, Andersen & Linnell 1996) in which lactating females had larger home ranges than barren females (P. 1·4$_a$), we found support for the reduced mobility argument (P. 1·4$_b$) whereby mobility of female moose in the period shortly after parturition is limited by the presence of a calf, but this constraint gradually decreases over time as offspring grow and become more mobile and independent (Grignolio *et al.* 2007; Long *et al.* 2009).

FORAGE CHARACTERISTICS

Given the importance of forage variability in the distribution and dynamics of herbivore populations (Tufto, Andersen & Linnell 1996; McLoughlin & Ferguson 2000; Relyea,

Lawrence & Demarais 2000; Anderson *et al.* 2005), it is not surprising that variation in quality and quantity of browse determines the location and size of moose home ranges within forested landscapes (Dussault *et al.* 2005a; Månsson *et al.* 2007; van Beest *et al.* 2010b). In our study, browse density explained a large part of the variance in home range size across all temporal scales (Fig. 3 and Fig. S3, Supporting Information). However, during summer, the expected decrease in home range size with increasing browse density (P. 2·1) was only observed at the daily scale (Fig. 3). At longer temporal scales, the effect gradually became positive towards the end of summer (i.e. September). Dussault *et al.* (2005a) found similar results for moose in Quebec and argued that during summer, when forage is abundant, the distribution of protective cover and human presence may become more important.

Another important aspect affecting herbivore space use is the temporal variation in nutritional quality of available forage as it matures the forage maturation hypothesis (Hebblewhite, Merrill & McDermid 2008). As forage abundance and density increase over summer, the nutritional quality decreases as fibres and tannins accumulate (Demment & van Soest 1985). Much of the evidence supporting the forage maturation hypothesis comes from studies on grass quality and the movement of grazing herbivores (Fryxell & Sinclair 1988; Wilmshurst *et al.* 1999; Hebblewhite, Merrill & McDermid 2008), but there is some indication that similar processes affect the quality of browse available to moose over summer (Hjeljord, Hovik & Pedersen 1990; Bo & Hjeljord 1991). Although we have no data to test this hypothesis, changes in the nutritional value of the available browse may have caused moose in our study area to periodically (i.e. over longer time-scales than 1 day) move in search of new patches of higher-quality browse in much the same way as is typically observed during periods of forage scarcity (e.g. during winter: Edenius 1991; van Beest *et al.* 2010b). Indeed, we found a positive effect of browse density on monthly and weekly home range size towards the end of winter (April; Fig. S3, Supporting Information). A reduction in high-quality browse during winter may cause moose to increase their movement in search of more abundant but lower-quality browse species (Edenius 1991), resulting in reduced overlap between monthly home ranges (van Beest *et al.* 2010b). Indeed, the proportion of high-quality browse species within home ranges was negatively correlated with home range size across all scales, as expected (P. 2·2), except at the monthly scale during winter when the effect gradually became positive towards the end of winter (April; Fig. 4). This result is consistent with previous findings on the effect of forage depletion on moose space use and, moreover, highlights that variance in home range size is largely a consequence of individuals tracking spatiotemporal changes in quantity and quality of food resources (Tufto, Andersen & Linnell 1996; McLoughlin & Ferguson 2000; Saïd *et al.* 2009).

We have previously shown that the use of supplementary feeding stations by moose can change foraging behaviour during winter (van Beest *et al.* 2010a). However, the propor-

tion of time spent in the vicinity of feeding stations was not retained in any of the final models of the current study, suggesting that the moose did not use supplementary feeding stations to a sufficient extent to affect home range size. The absence of such an effect may be related to the short (∼6 years) feeding history in our study area (van Beest *et al.* 2010a). Species with a higher reliance on artificial forage such as roe deer (Guillet, Bergstrom & Cederlund 1996) and white-tailed deer (Kilpatrick & Stober 2002) typically reduce home range size. In addition, the use of artificial feeding stations is related to climatic conditions, especially snow depth, as it reduces access to natural forage (Guillet, Bergstrom & Cederlund 1996). It is possible that snow depth during the two winters sampled in this study did not prevent moose from foraging on the preferred natural vegetation, which resulted in lower use of feeding stations than under more severe winter conditions. To further evaluate the effect of supplementary feeding stations on home range size, it is important to sample a wide range of climatic conditions over a longer time period than the 2 years presented here.

CLIMATIC DETERMINANTS

The focus on climatic effects on demography and population dynamics has augmented dramatically over recent years (Stenseth *et al.* 2002; Parmesan 2006; Grotan *et al.* 2009). By comparison, studies of behavioural responses to climate have lagged behind. For large herbivores, the few existing studies focus on intermediate feeders and grazers, such as red deer (Rivrud, Loe & Mysterud 2010) and reindeer (*Rangifer tarandus platyrhynchus* Vrolik: Stien *et al.* 2010), at the northern limits to their distributions.

The climatic conditions observed during our 2-year study period were typical of the long-term variability in the area (Fig. S1, Supporting Information). However, the effects of temperature and precipitation on variation in home range size were smaller than expected (P. 3·1 and P. 3·2.). Local climate affected moose home range size mainly at intermediate to short temporal scales (i.e. biweekly to daily scales; Table 3), suggesting that direct effects were more important than indirect effects. This contrasts with findings for red deer in which climate effects space use largely through indirect effects on plant growth and quality (Rivrud, Loe & Mysterud 2010). The greater indirect effects on intermediate feeders and grazers than browsing herbivores may arise from different climatic responses of grass and browse species. In addition, we found that temperature, snow depth and precipitation affected total home range size more than core home range size (Table 3) which agrees with the concept that peripheral home range areas are influenced more by climatic variability than the heavily used core areas (Börger *et al.* 2006).

We expected home range size to be negatively correlated with temperature across all scales (P. 3·1) because of the low upper critical temperature threshold of moose (Dussault *et al.* 2004), yet this was clearly not the case (Figs S5 & S6, Supporting Information). Daily ranges decreased in January

but increased with temperature in April. The interpretation of direct effects of temperature on animal space use during a season is complicated by changes in pelage insulation and snow depth (Kamler, Jedrzejewska & Jedrzejewski 2007; Rivrud, Loe & Mysterud 2010). The fact that moose did not reduce their home range as temperature increased despite ambient temperatures above their upper critical temperature threshold may indicate that moose at the southern limit of their distribution are more resilient to temperature than previously thought (Lowe, Patterson & Schaefer 2010) or that sufficient habitat with good thermal shelter was available for the risk of heat stress to be mitigated by habitat use (Dussault *et al*. 2004). However, as the European climate becomes warmer and wetter in the near future (Mysterud & Sæther in press), we can expect direct effects of climate on animal movement and activity to be augmented even at slight increases in temperature. Such effects may be most notable in animals adapted to cold environments.

Movement in deep snow is known to increase energy expenditure, and reduced activity when snow depth exceeds threshold levels is reported for a range of species (Schmidt 1993; Grignolio *et al*. 2004; Dussault *et al*. 2005b; Rivrud, Loe & Mysterud 2010). Indeed, snow depth was negatively correlated with moose home range size as expected (P. 3·3) but only at short temporal scales (weekly and daily; Fig. 5). In contrast, Rivrud, Loe & Mysterud (2010) reported that home range size of red deer was strongly affected by snow depth across all spatial temporal scales (from monthly to daily scales). Differences in body size and adaptation to deep snow between moose and red deer may explain why moose responded less strongly to snow depth over longer spatial scales. Furthermore, intermediate feeders and grazers may be more heavily affected by snow than browsers as access to their forage is restricted by snow.

Conclusion

Insight into the behavioural responses of large herbivores to climatic stochasticity and forage variability may facilitate the conservation and management of populations. Here, we show that variation in the home range size of a large browsing herbivore is scale dependent and results from the effects of several intrinsic and extrinsic determinants. Home range size varied most in response to changes in daylight within seasons, reproductive status and individual differences other than age and body mass. Forage variability affected home range size across most spatiotemporal scales, but the relationship varied over time as expected from changes in browse quantity and quality. Local climate directly influenced home range size of this large browser living at the southern limit of its distributional range, which contrasts with the indirect effect of climate on space use reported for mixed feeders at their northern distribution limit (Rivrud, Loe & Mysterud 2010). The importance and strength of direct climate effects on animal movement and activity at their southern distribution limit are likely to increase as global warming continues.

References

Anderson, D.P., Forester, J.D., Turner, M.G., Frair, J.L., Merrill, E.H., Fortin, D., Mao, J.S. & Boyce, M.S. (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*, **20**, 257–271.

Arnemo, J.M., Kreeger, T.J. & Soveri, T. (2003) Chemical immobilization of free-ranging moose. *Alces*, **39**, 243–253.

van Beest, F.M., Loe, L.E., Mysterud, A. & Milner, J.M. (2010a) Comparative space use and habitat selection of moose around feeding stations. *Journal of Wildlife Management*, **74**, 219–227.

van Beest, F.M., Mysterud, A., Loe, L.E. & Milner, J.M. (2010b) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology*, **79**, 910–922.

Bjørneraas, K., van Moorter, B., Rolandsen, C.M. & Herfindal, I. (2010) Screening GPS location data for errors using animal movement characteristics. *Journal of Wildlife Management*, **74**, 1361–1366.

Bo, S. & Hjeljord, O. (1991) Do continental moose ranges improve during cloudy summers. *Canadian Journal of Zoology*, **69**, 1875–1879.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. & Coulson, T. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist*, **168**, 471–485.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.

Calenge, C. (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005) How far do animals go? Determinants of day range in mammals. *American Naturalist*, **165**, 290–297.

Cederlund, G. & Sand, H. (1994) Home-range size in relation to age and sex in moose. *Journal of Mammalogy*, **75**, 1005–1012.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.

Demment, M.W. & van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, **125**, 641–672.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L. & Larochelle, J. (2004) Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience*, **11**, 321–328.

Dussault, C., Courtois, R., Ouellet, J.P. & Girard, I. (2005a) Space use of moose in relation to food availability. *Canadian Journal of Zoology*, **83**, 1431–1437.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L. & Jolicoeur, H. (2005b) Linking moose habitat selection to limiting factors. *Ecography*, **28**, 619–628.

Edenius, L. (1991) The effect of resource depletion on the feeding-behaviour of a browser – winter foraging by moose on Scots pine. *Journal of Applied Ecology*, **28**, 318–328.

Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, **3**, 237–241.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. (2007) LoCoH: nonparameteric Kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, **2**, e207.

Grignolio, S., Rossi, I., Bassano, B., Parrini, F. & Apollonio, M. (2004) Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. *Ethology Ecology and Evolution*, **16**, 255–264.

Grignolio, S., Rossi, I., Bertolotto, E., Bassano, B. & Apollonio, M. (2007) Influence of the kid on space use and habitat selection of female Alpine ibex. *Journal of Wildlife Management*, **71**, 713–719.

Grotan, V., Saether, B.E., Lillegard, M., Solberg, E.J. & Engen, S. (2009) Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose. *Oecologia*, **161**, 685–695.

Guillet, C., Bergstrom, R. & Cederlund, G. (1996) Size of winter home range of roe deer (*Capreolus capreolus*) in two forest areas with artificial feeding in Sweden. *Wildlife Biology*, **2**, 107–111.

Harestad, A.S. & Bunnell, F.L. (1979) Home range and body-weight – a reevaluation. *Ecology*, **60**, 389–402.

Hebblewhite, M., Merrill, E. & McDermid, G. (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, **78**, 141–166.

Hjeljord, O., Hovik, N. & Pedersen, H.B. (1990) Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Holarctic Ecology*, **13**, 281–292.

Kamler, J.F., Jedrzejewska, B. & Jedrzejewski, W. (2007) Factors affecting daily ranges of red deer Cervus elaphus in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, **52**, 113–118.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. (2001) Analysis of animal space use and movements. *Radio Tracking and Animal Populations* (eds J.J. Millspaugh & J.M. Marzluff), pp. 126–164, Academic Press, San Diego, California, USA.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B. & Loft, E.R. (2002) Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology*, **83**, 530–544.

Kilpatrick, H.J. & Stober, W.A. (2002) Effects of temporary bait sites on movements of suburban white-tailed deer. *Wildlife Society Bulletin*, **30**, 760–766.

Lavsund, S., Nygren, T. & Solberg, E.J. (2003) Status of moose populations and challenges to moose management in Fennoscandia. *Alces*, **39**, 109–130.

Lindstedt, S.L., Miller, B.J. & Buskirk, S.W. (1986) Home range, time, and body size in mammals. *Ecology*, **67**, 413–418.

Long, R.A., Kie, J.G., Bowyer, R.T. & Hurley, M.A. (2009) Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildlife Biology*, **15**, 288–298.

Lowe, S.J., Patterson, B.R. & Schaefer, J.A. (2010) Lack of behavioral responses of moose (Alces alces) to high ambient temperatures near the southern periphery of their range. *Canadian Journal of Zoology*, **88**, 1032–1041.

Luccarini, S., Mauri, L., Ciuti, S., Lamberti, P. & Apollonio, M. (2006) Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. *Ethology Ecology and Evolution*, **18**, 127–145.

Månsson, J., Andren, H., Pehrson, A. & Bergstrom, R. (2007) Moose browsing and forage availability: a scale-dependent relationship? *Canadian Journal of Zoology*, **85**, 372–380.

McLoughlin, P.D. & Ferguson, S.H. (2000) A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, **7**, 123–130.

McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Saïd, S. & Klein, F. (2007) Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192–3201.

van Moorter, B., Visscher, D., Benhamou, S., Borger, L., Boyce, M.S. & Gaillard, J.M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**, 641–652.

Muggeo, V.M.R. (2008) *Segmented Relationships in Regression Models, R Package Version 0.2-4*. R Foundation for Statistical Computing, Vienna, Austria.

Murtaugh, P.A. (2009) Performance of several variable-selection methods applied to real ecological data. *Ecology Letters*, **12**, 1061–1068.

Mysterud, A. & Sæther, B.E. (in press) Climate change and implications for the future distribution and management of ungulates in Europe. *Ungulate Management in Europe; Problems and Practices* (eds R. Putman, R. Andersen & M. Apollonio), Cambridge University Press, Cambridge, UK.

Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. & Steinheim, G. (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature*, **410**, 1096–1099.

Mysterud, A., Yoccoz, N.G., Langvatn, R., Pettorelli, N. & Stenseth, N.C. (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 2359–2368.

Nicholson, M.C., Bowyer, R.T. & Kie, J.G. (1997) Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammalogy*, **78**, 483–504.

Parker, K.L. (1988) Effects of heat, cold and rain on coastal black-tailed deer. *Canadian Journal of Zoology*, **66**, 2475–2483.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-Plus: Statistics and Computing*, Springer Verlag, New York, USA.

Pinheiro, J.C., Bates, D.M., DebRoy, S. & Sarkar, D. (2009) *nlme: Linear and Non-Linear Mixed Effects Models, R Package Version 3.1-96*. R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team (2009) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramanzin, M., Sturaro, E. & Zanon, D. (2007) Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Canadian Journal of Zoology*, **85**, 280–289.

Rivrud, I.M., Loe, L.E. & Mysterud, A. (2010) How does local weather predict red deer home range size at different temporal scales? *Journal of Animal Ecology*, **79**, 1280–1295.

Relyea, R.A., Lawrence, R.K. & Demarais, S. (2000) Home range of desert mule deer: Testing the body-size and habitat-productivity hypotheses. *Journal of Wildlife Management*, **64**, 146–153.

Rolandsen, C.M., Solberg, E.J., Heim, M., Holmstrom, F., Solem, M.I. & Saether, B.E. (2008) Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. *European Journal of Wildlife Research*, **54**, 6–14.

Saether, B.E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, **12**, 143–149.

Saïd, S., Gaillard, J.M., Duncan, P., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C. & Van Laere, G. (2005) Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology*, **267**, 301–308.

Saïd, S., Gaillard, J.M., Widmer, O., Debias, F., Bourgoin, G., Delorme, D. & Roux, C. (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, **118**, 1299–1306.

Schmidt, K. (1993) Winter ecology of nonmigratory Alpine Red deer. *Oecologia*, **95**, 226–233.

Schwede, G., Hendrichs, H. & McShea, W. (1993) Social and spatial-organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. *Animal Behaviour*, **45**, 1007–1017.

Spencer, S.R., Cameron, G.N. & Swihart, R.K. (1990) Operationally defining home range – temporal dependence exhibited by hispid cotton rats. *Ecology*, **71**, 1817–1822.

Stamps, J. (1995) Motor learning and the value of familiar space. *American Naturalist*, **146**, 41–58.

Stenhouse, G.B., Latour, P.B., Kutny, L., MacLean, N. & Glover, G. (1995) Productivity, survival, and movements of female moose in a low-density population, northwest territories, Canada. *Arctic*, **48**, 56–62.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.

Stien, A., Loe, L.E., Mysterud, A., Severinsen, T., Kohler, J. & Langvatn, R. (2010) Icing events trigger range displacement in a high-arctic ungulate. *Ecology*, **91**, 915–920.

Tufto, J., Andersen, R. & Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology*, **65**, 715–724.

Vucetich, J.A. & Peterson, R.O. (2004) The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 183–189.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999) Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, **77**, 1223–1232.

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton, USA.

Worton, B.J. (1987) A review of models of home range for animal movement. *Ecological Modelling*, **38**, 277–298.

Zheng, B. & Agresti, A. (2000) Summarizing the predictive power of a generalized linear model. *Statistics in Medicine*, **19**, 1771–1781.

Supporting Information

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

Fig. S1. Annual trends (mean ± SE) in precipitation, temperature and snow depth over the last 30 years in the study area in southern Norway. Grey box indicates the study period.

Fig. S2. Plot of predicted log-transformed home range sizes (ha) in relation to log-transformed body mass (kg) of moose in southern Norway.

Fig. S3. Plot of predicted log-transformed winter home range sizes (ha) in relation to log-transformed browse density of moose in southern Norway.

Fig. S4. Plot of predicted log-transformed summer home range sizes (ha) in relation to proportion of browse quality of moose in southern Norway.

Fig. S5. Plot of predicted log-transformed home range sizes (ha) of moose in southern Norway in relation to summer temperature (°C) variability.

Fig. S6. Plot of predicted log-transformed home range sizes (ha) of moose in southern Norway in relation to winter temperature (°C) variability.

Fig. S7. Plot of predicted log-transformed home range sizes (ha) of moose in southern Norway in relation to summer precipitation (mm) variability.

Table S1. Overview of the mixed-model structure for each spatiotemporal scale.

Table S2. Overview of the F values as estimated by the fixed kernel home range method.

Table S3. Summary statistics of adult female moose home range size (ha) across spatiotemporal scales.

Table S4. Summary of the mixed-effects models predicting monthly home range size.

Table S5. Summary of the mixed-effects models predicting biweekly home range size.

Table S6. Summary of the mixed-effects models predicting weekly home range size.

Table S7. Summary of the mixed-effects models predicting daily home range size.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.