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Modeling Habitat Suitability for Moose in Coastal Northern Sweden: Empirical *vs* Process-oriented Approaches

Habitat models may provide viable tools for co-management of large ungulates and forest resources, yet their applicability has not been comprehensively evaluated in managed forest. We examined 2 inherently different approaches to model the relative winter habitat suitability for moose *(Alces alces)* in the coastal area of northern Sweden. An empirical approach based on GPS positions of 15 female moose was used to scrutinize the assumptions and functional mechanisms of a process-oriented, conceptual approach, based on published material on the species' preferences for habitat components related to food and cover. For both model approaches habitat was described using estimates of forest-stand characteristics based on satellite imagery. The empirical model also included variables relating to topographic properties of the landscape as well as distances to landscape features. The output from both models was a habitat suitability index (HSI) score, enabling the models to be compared with each other. The models showed different results, highlighting the need to include the spatially explicit distribution of environmental variables in future conceptual, process-oriented models.

INTRODUCTION

The moose (*Alces alces*) has a circumpolar distribution largely coinciding with the boreal forest biome. Of the 9 subspecies of moose distinguished, *A. alces alces* is indigenous to western Eurasia. In Fennoscandia, moose feed primarily on woody plants, particularly during winter when Scots pine (*Pinus sylvestris*), birch (*Betula pendula* and *B. pubescens*) and willows (*Salix* spp.) are staple food (1). Moose are charismatic animals with high aesthetic value, and, further, have high socioeconomic value as a game species (2). The post-World War II era has seen a dramatic increase in population numbers of moose in Fennoscandia, coinciding with the introduction of large-scale clearcutting practices. As a consequence, conflicts and problems have emerged in terms of elevated levels of traffic accidents and damage to forest regeneration. Moose is nowadays considered the major damage agent to commercially valuable woody plant species in Sweden (3), and of great concern for fulfilment of production goals in forestry. Combining large populations of ungulates such as the moose and sustainable forest management is thus a challenging task.

Natural-resource management should be served by efficient and accurate methods to quantify relationships between amounts and distribution of forest resources and their use by moose. Such knowledge would, for example, be useful as a tool for evaluating aspects other than timber production, e.g. species conservation, in harvest programs (4). To achieve this, management programs need to include the specific needs of animals. With respect to impact on habitat components like food and cover for ungulates, habitat models could be used for evaluating different forest scenarios. Incorporating habitat use by ungulates in these models would allow evaluation of damage risk due to browsing, which in turn, could be used to set targets for ungulate harvesting programs. Most habitat models are simplified representations of the real world focussing only on a fraction of the factors that determine fitness or population size of targeted species. More specifically, habitat models are practical operational tools based on assessment of physical and compositional attributes of the habitat (5). Habitat models thus estimate the suitability or capacity of targeted areas to provide the needs of a species.

Development of wildlife-habitat models is facilitated by increased availability and coverage of remote sensing data, e.g. satellite imagery, allowing detailed assessment of amounts and distribution of resources over large areas. Application of GPS-technique in animal habitat-use studies brings forward large amounts of positional data with unprecedented accuracy (6, 7). Together with new GIS-software, these improvements open up for rapid development of habitat models. Hitherto, little work has been carried

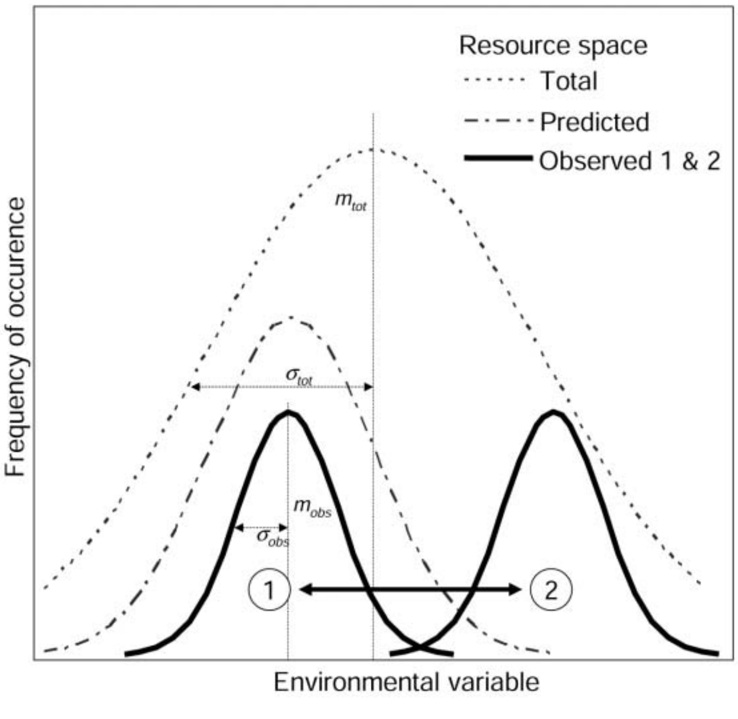

Fig. 1. The distribution of resources may differ between the resource space predicted by a process-oriented model and the observed resource space calculated by an empirical model. The relative position and shape of the observed resource space compared with the predicted resource space may indicate the use of the correct functions but low precision of the process-oriented model (observed resource space 1) or wrong or missing functions (observed resource space 2). Differences between the means of the total resource space in the landscape m_{tot} and the means of the observed resource space m_{obs} are used to calculate the marginality; differences of the standard deviations ($\sigma_{tot} \neq \sigma_{obs}$) allow calculation of specialization.

out on animal habitat modeling in managed forests in Fennoscandia (but see 8). Much work has been done in North America, but many of these models cannot directly be transferred to managed forests such as those found in Sweden since vegetation, climate, landownership, intensity and history of land management, etc. are different.

Concept of Resource Space

A habitat can be described as the resources and conditions present in an area that produce occupancy — including survival and reproduction — by a given organism. The habitat concept thus is organism-specific as it relates the presence of a species, population or individual (animal or plant) to an area's physical and biological characteristics (9). For each habitat resource variable we can define the total resource space in the landscape (Fig. 1). Most species are expected to be nonrandomly distributed in regard to related environmental variables, i.e. they show selection behavior (10). The distribution of habitat resources can be predicted using a process-oriented, conceptual model based on expert knowledge. This type of model can be seen as a mechanistic 'black box', where the specific physical, causal relations leading to the modeled, plausible processes, remain unspecified. Thus, we use the terms 'process-oriented' or 'conceptual model' as synonyms for terms such as 'theoretical' or 'mechanistic' models used by other authors (e.g. 11–13). The distribution described by such a model is defined as the 'predicted resource space' (Fig. 1). In contrast, with an empirical approach (14), the distribution of the species in the resource space is derived from observations of the species in the field. We refer to this distribution as the 'observed resource space' (Fig. 1).

The predicted resource distribution of a species should be as close as possible to the observed resource use when there are no restrictions in habitat accessibility. If this is the case, we expect to find the observed resource space for a variable entirely contained within the predicted resource space (observed resource space 1 in Fig. 1). This would mean that our conceptual model is predicting the correct functional processes. If, however, the observed resource space is located partly or entirely outside the predicted one (observed resource space 2 in Fig. 1), it would be an indication that the conceptual model is using the wrong or incomplete functional responses when describing the predicted resource space of the focal species. It is thus possible to use an empirical model to scrutinize the functional processes and model assumptions used in a related conceptual model.

A great deal of work has been devoted to analyzing interactions between forestry and moose in Fennoscandia. Whereas much has been done on the level of individual animals and plants, comparatively little work has been done on relating moose habitat use and forest resources at larger spatial scales (15, 16). The experiences from the work already carried out in Fennoscandia are crucial in the building of habitat models designed for managed forest. The aim of this paper is to examine 2 different approaches to model habitat suitability for winter habitat for moose based on expert knowledge on limiting habitat resources, and empirical data on habitat use by moose in managed forest. The primary objective is to outline and discuss the different modeling approaches with respect to scope, limitations and future prospects. We present an approach to scrutinize the assumptions and functional processes of a conceptual model based on the literature and on expert knowledge using a model based on empirical data. To achieve this we adopted a common standard in terms of a habitat suitability index (HSI; 17), i.e. the rating of a landscape's relative habitat quality, which is its capacity to ensure the persistence of an animal species.

MATERIAL AND METHODS

Study Area

The study was conducted in the coastal area of Västerbotten, Sweden (Fig. 2), near Umeå (64°12'N, 20°45'E [WGS 84]) in the middle boreal zone (18). Most (62%) of the study landscape (9077 km^2) consists of productive forest land (annual production > 1 m^3 ha^{-1}), followed by open mires and lakes (24%). The remaining vegetation cover types consist mainly of forest impediments, agricultural land and settlements. The dominating tree species are Scots pine and Norway spruce (*Picea abies*) with deciduous tree species such as aspen (*Populus tremula*), birch (*Betula* spp.), rowan (*Sorbus aucuparia*) and willows interspersed. The age of productive forest stands varies between 0 and 163 years, and the normal rotation period in this area is 80 – 100 years.

The field layer varies from dry *Vaccinium vitis-idea* and *Cladonia* spp. dominated stands to mesic *Vaccinium myrtillus* type stands. While on clearcuts, grasses such as *Deschampsia flexuosa* and *Calamagrostis purpurea* dominate, on mires both grasses of the family Poaceae, sedge (*Carex*

Fig. 2. The county of Västerbotten (hatched area) in Fennoscandia is shown with the study area (rectangle) and the Arctic circle (dashed line) indicated.

spp.) and woody plants such as willow and dwarf birch (*Betula nana*) are common. The elevation varies between 0 and 431 m a.s.l. Along the coast, the ground is covered by snow for 140 to 160 days yr^{-1} (19), with a median snow depth in January of ca 40 cm. In interior areas the snow-cover period is slightly longer (160-180 days) with a median snow depth of 50-60 cm (19). The moose density in the area varies between 0.4 and 1.2 individuals km^{-2} during the winter (Swedish Hunters' Association, pers. comm.).

Moose Data

Between 1995 and 1998, 15 female moose were equipped with GPS-collars (Lotek GPS_1000) scheduled for taking at least 1 position (fix) per hour. GPS fixes were corrected to better than 20 m by differential post-processing. This resulted in a total of 17 036 fixes, whereof 86% had a precision better than 20 m. Seventy percent of all fixes were taken during the winter season from December to May. In 1998, 6126 fixes were recorded whereof 98% with a precision better than 20 m.

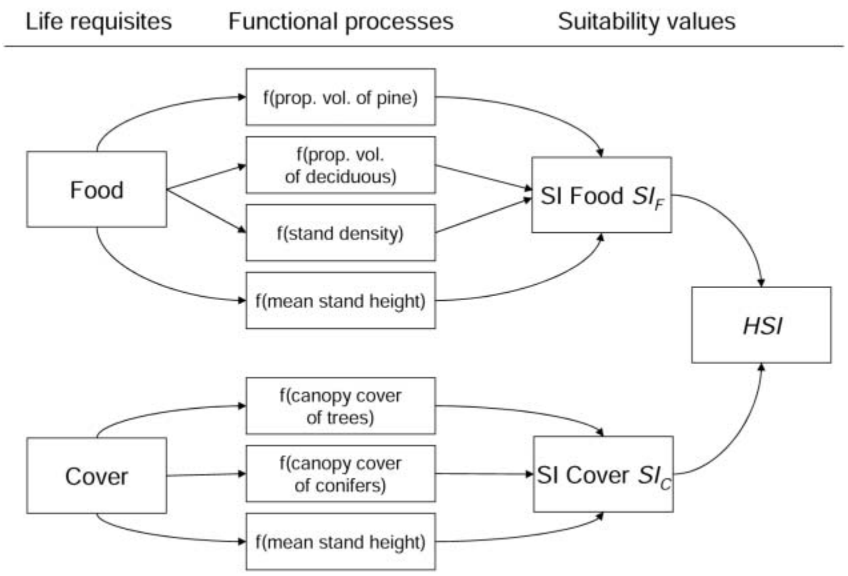

Fig. 3. A flow diagram describing the live requirements, the variables used in the functional processes of the conceptual, process-oriented model and combinational processes to calculate the habitat suitability index (HSI) for moose.

Vegetation and Geographical Data

The vegetation datasets based on forest-stand data (Tables 1 and 2) were obtained by processing Landsat TM satellite images from 1994, 1996, and 1998 together with data from the National Forest Inventory (NFI) using the *k*-Nearest–Neighbour (*k*NN) algorithm (20–22). The *k*NN estimation method is essentially an inverse-distance weighted average method, commonly used for spatial interpolation (23). Here, the forest variable values (Tables 1 and 2) are calculated as weighted averages of the *k* spectrally nearby samples. Such nearby samples are defined as the sample plots used within the NFI with shortest spectral distance to the pixel for which the variable is to be estimated. As spectral distance, Euclidean distance is used, and the weight is proportional to the inverse squared Euclidean distance. Thus, the interpolation is done in a spectral space defined by the 6 TM bands (22). For a more detailed description of this method, see also Nilsson et al. (24). As a result we obtained 3 raster data maps (cell size 25 x 25 m^2) for each year (1994, 1996, and 1998) and vegetation variable in Table 2 for the landscape.

The geographical datasets (Table 2) including distance measurements to geographical objects such as railroads or water surfaces were obtained from digital topographical maps (original scale 1:100 000) from the Swedish National Land Survey in Sweden. Calculation of altitude, slope and aspect were based on a digital elevation model (DEM) from the Swedish National Land Survey. The cell size in all raster data maps was 25 x 25 m^2.

Habitat Suitability Modeling

Approaches to assess wildlife-habitat relationships include empirical and process-based models (13). Empirical models analyze data on habitat use and habitat characteristics collected at specific sites. In contrast, process-oriented models aim at assessing plausible causal relationships or functional processes underlying habitat use, and therefore provide a more general conceptual framework for assessing wildlife-habitat relationships than empirical models.

For both modeling approaches, i.e. the conceptual and the empirical model, we used the habitat suitability index (HSI) to evaluate the aptness of the study area for moose. The HSI is used for assessing the suitability of an area for the species of interest as a function of several environmental variables, which most affect species presence, abundance and distribution (4). The relative measures of suitability prohibit exact population estimates and only allow areas to be compared to each other. HSI scores are on a standard scale between 0 and 1, where 0 indicates unsuitable habitat and 1 indicates optimum conditions and optimum quality and availability of resources.

Process-oriented Model

A process-oriented species-habitat model aims at modeling the relative suitability of an area for the focal species. It is using known or plausible causal relationships as the base for predictions of an area's relative quality. This approach can also be used to model habitat use or species distribution. It predicts the distribution of a species on the basis of environmental parameters that are believed to be the causal, driving forces for the distribution and abundance of the target species (13). Process-oriented HSI models are based on the assumption

Table 1. Vegetation variables used in process-oriented model in alphabetical order. The abbreviations indicated are used in Eq. 1-11 (Box 1). Only *k*NN estimates based on the Landsat TM satellite image from 1998 were used in the model.

Variable	Abbrev.
Canopy cover of all trees (%)	cct
Canopy cover of coniferous trees (%)	ccc
Mean stand height (m)	msh
Proportion stem volume of deciduous species (%)	pvd
Proportion stem volume of *Pinus sylvestris* (%)	pvp
Stand density (no. trees ha^{-1})	sde

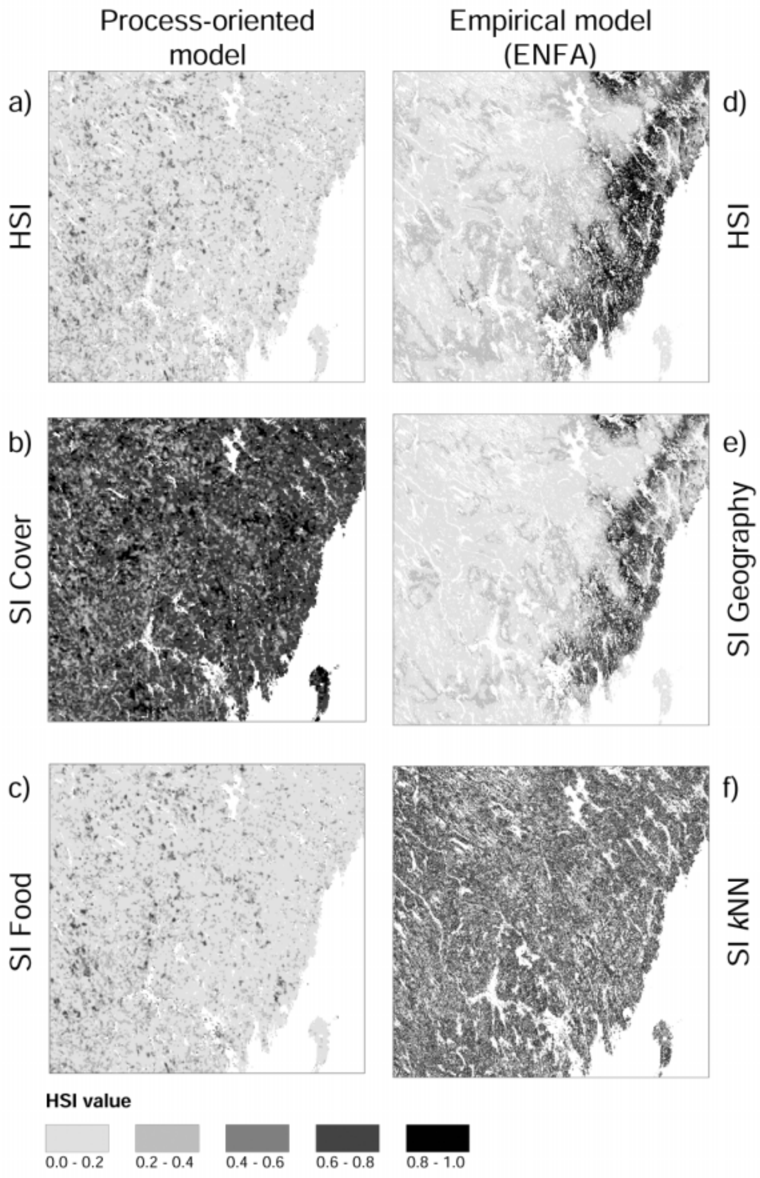

Fig. 4. The suitability index value maps are shown for both the process-oriented model (a-c) and the empirical model (ENFA results; d-f). While (a) and (d) show the resulting HSI map for each model, (b) and (c) show the intermediate suitability maps for food (SI Food) and cover (SI Cover) as calculated by the process-based model. For the calculation of (e) only geographical variables (DEM & Topo in Table 2) were used in the empirical model (ENFA), while for (f) only vegetation variables (*k*NN in Table 2) were used.

that a species will select and use areas that are best able to satisfy its life requisites, and thus greater use should occur in higher quality habitat (5). The fundamental components of such HSI models are the environmental variables (independent variables), the resulting habitat suitability values (dependent variables) and the classification functions or functional processes that link the two (25).

The process-oriented, conceptual HSI model for moose-habitat assessment presented in this paper builds on a habitat modeling framework described by Löfstrand et al. (26). Habitat is modeled as a function of variables (Table 1) known or perceived to be important components of the life requisites cover and food during winter (Fig. 3), using functions from Allen et al. (27) and Kurtilla et al. (8), respectively. Despite earlier mentioned potential difficulties to apply models developed in North America in Fennoscandia, we used functions from Allen et al. (27) for the calculation of suitability indices for cover in Fennoscandia, as the variables used in these functions (Fig. 3) are applicable to Swedish conditions. The calculated suitability indices for food and cover, SI_F and SI_C, were combined into the habitat suitability index (HSI). For a detailed description of the functional relationships, see Box 1.

Empirical Model

The second approach to predict winter habitat suitability for moose used an empirical model. Empirical models are often based on field observations in a specific area and thus usually sacrifice the generality of their predictions for the precision under realistic conditions (13). Hence, such a model is not expected to provide any information about the underlying ecological functions and mechanism or to describe in a realistic way the correlations between model parameters and predicted responses (28). However, it can be used to identify and rank the most important variables for the predicted responses. In this study, we use an empirical model based on the Ecological-Niche Factor Analysis (ENFA; 14). The method builds on the concept of the ecological niche, assuming that species are nonrandomly distributed regarding their physiological preferences. ENFA compares the distribution of independent environmental variables for a presence dataset, i.e. the locations where the species was observed, with the distribution of the same variables for the whole area. The method is basically a multivariate approach which does not require absence data of the focal species such as, e.g. logistic regression models do. Further, using ENFA spatial and nonspatial variables can be combined. A key feature of ENFA is that it summarizes, like a Principle Component Analysis, the environmental variables into a few, uncorrelated, but ecologically meaningful factors. Hirzel et al. (14) labelled the first factor reported by ENFA as the 'marginality' of the model species, i.e. the ecological distance between the species optimum and the global mean (Fig. 1). It represents the differences between the means of the global distribution m_{tot}, i.e. the total resource space, and the observed resource space m_{obs}. The following factors extracted by the method representing the specialization of the species, resemble the ratio of environmental variance in the habitat of the whole landscape and the observed positions of the species. It is calculated using differences of the standard deviations σ_{tot} and σ_{obs} to describe the species specialization. Based on the importance of the factors, a habitat map is calculated scaled to a suitability range between 0 and 1. For a detailed description of ENFA, the mathematical methods and their implementation in the software program Biomapper, see Hirzel et al. (14).

In this study, ENFA is based on presence data for moose in the landscape, i.e. the positions of moose as recorded by GPS-collars, *k*NN-derived forest-stand variables, distance measurements to different landscape features from topographical maps and a digital elevation model (DEM; Table 2). We used 3 different sets of ecological variables, thus producing 3 different habitat maps (Fig. 4d-f). The sets were composed of *i)* vegetation variables, i.e. forest data obtained from satellite and ancillary data using the *k*NN method (Fig. 4f); *ii)* geographical variables, i.e. data obtained from a DEM and topographical maps (Fig. 4e); and *iii)* a combination of both (Fig. 4d). As software implementation of ENFA the software package Biomapper (14) was used.

Table 2. Environmental variables used in the empirical model (ENFA) sorted after decreasing absolute value of the coefficients of the marginality factor. Positive values mean that moose prefer locations with higher values of the corresponding environmental variable than the average location in the study area. Coefficients of the next 4 most important specialization factors (23) are also given. The 5 factors explained together 54% of the total variation. For each variable the data source is indicated as either digital elevation model (DEM), digital topographical maps (Topo) or merged *k*NN estimate maps from 3 years (1994, 1996 and 1998; *k*NN).

Environmental variables	Marginality	Spec. 1	Spec. 2	Spec. 3	Spec. 4	Data source
Altitude	-0.657	-0.2	0.498	0.194	0.034	DEM
Distance to railroads (m)	0.504	0.293	0.542	-0.27	-0.007	Topo
Distance to roads 7-9 m wide (m)	-0.270	0.456	-0.056	0.026	-0.071	Topo
Distance to settlements (m)	-0.268	-0.06	0.303	-0.238	0.108	Topo
Slope	-0.265	-0.065	-0.347	-0.735	-0.009	DEM
Distance to streams (m)	-0.261	0.479	0.105	-0.156	-0.087	Topo
Distance to roads 5-7 m wide (m)	-0.102	0.535	-0.347	0.236	0.085	Topo
Distance to brooks (m)	-0.071	0.089	-0.146	0.057	0.001	Topo
Stem volume of Norway spruce (m^3)	-0.059	0.143	-0.170	0.014	-0.310	*k*NN
Distance to roads ≤ 5 m wide (m)	0.055	0.053	0.029	-0.052	0.020	Topo
Degree of stocking (%)	0.055	0.004	-0.033	-0.016	0.076	*k*NN
Distance to lakes and rivers (m)	-0.045	0.122	-0.072	-0.063	0.004	Topo
Stem volume of Scots pine(m^3)	0.029	0.099	-0.013	0.119	-0.268	*k*NN
Mean stem diameter (mm)	-0.028	0.002	-0.092	0.206	-0.449	*k*NN
Stem volume of other deciduous species (m^3)	-0.025	0.006	-0.009	0.018	-0.012	*k*NN
Stem volume of Lodgepole pine (m^3)	0.022	-0.006	0.021	-0.001	0.001	*k*NN
Stem volume of birch (m^3)	0.019	-0.2	-0.056	0.055	-0.117	*k*NN
Biomass of needles and branches (kg DW ha^{-1})	-0.017	-0.001	0.073	0.167	-0.065	*k*NN
Trunk biomass (kg DW ha^{-1})	-0.017	-0.286	0.119	-0.297	0.485	*k*NN
Stand age (years)	-0.016	0.034	0.111	-0.013	0.016	*k*NN
Aspect	0.013	0.022	-0.01	0.032	0.018	DEM
Mean stand height (m)	-0.001	0.025	-0.102	-0.152	0.578	*k*NN
Bark biomass (kg DW ha^{-1})	0.001	0.022	-0.006	0.032	-0.057	*k*NN

Dataset Preparation

In this study, we used positional data for moose over a period of 4 years (1995 – 1998) in the empirical model. We matched each year's positional data to the nearest vegetation dataset (Table 2) in time (1994, 1996, or 1998). The geographic datasets (DEM and Topo; Table 2) were regarded as constant over time. To be able to use the datasets for the 3 different years simultaniously in the empirical model, for each variable we artificially moved the 3 maps representing different years in space until they were adjacent to each other. We then merged the 3 'annual' maps to one artificial, single large map and used these new variable maps during the empirical model approach. After the resulting habitat maps were derived, only the parts of the maps corresponding to the map extent of the original 1998 maps were extracted for subsequent analysis. The habitat maps derived from the process-oriented model are based on vegetation datasets from 1998.

RESULTS AND DISCUSSION

When applying the process-oriented model to the study landscape, we found an almost uniform distribution of HSI pattern throughout the landscape with a small scale variation only (Fig. 4a). The same results were obtained for both the suitability index calculated for cover (SI_C; Fig. 4b) and the suitability index calculated for food (SI_F; Fig. 4c). However, the suitability index levels for food were generally lower than the levels for cover, resulting in a generally low total HSI due to the multiplicative combination of these 2 factors.

In comparison to the process-oriented model, the empirical model showed a distinct spatial pattern, with high values of HSI along the coast (Fig. 4d), while HSI values in the inland are generally lower. One explanation for this pattern may be found in the predicted preferences of moose to the additionally included environmental variables (Table 2). An analysis of the marginality values showed that moose location data were linked to low-altitude, flat areas close to larger roads and settlements, like those found in the coastal area. In contrast, moose seemed to avoid areas close to railroads and smaller roads. Ball and Dahlgren (29) found that browsing pressure on Scots pine was inversely related to distance to a major road in the area, suggesting that larger roads function as barriers for moose movement.

One of the most interesting findings in this study is the result of the ranking of the variables explaining moose habitat preferences from ENFA: of the first 10 most important variables only 1 forest vegetation variable (Stem volume of Norway spruce) was found, but first at the 9th position (Table 2). All prior, more important variables related moose habitat selection to spatially explicit features, suggesting that geographical factors had a decisive influence on habitat selection. When we used only vegetation variables in ENFA (Fig. 4f), the HSI values were spatially evenly distributed similar to the results of the process-oriented model (Fig. 4a), based on forest vegetation variables.

The generally higher level of HSI values in the empirical model may imply that the assumptions made for the process-oriented model were too conservative or incomplete. Judged by the empirical results, moose used habitat with lower quality or quantity of forest vegetation variables than predicted by the process-oriented model. A sensitivity analysis for the process-oriented model revealed that tree height > 5 m was a restricting resource, as only trees below this height were modeled as food. In contrast, suitability index values for cover were almost always high throughout the landscape (Fig. 4b), and thus did not represent a limiting factor in this model. However, the HSI values of both models are difficult to compare directly, using their absolute numbers, as the foundations of the models are different.

In many models, much emphasis is put on the assessment of vegetation distribution in the landscape to explain habitat suitability for moose (27, 30, 31). All of them are habitat suitability index (HSI) models or expert systems, describing the predicted resource space for moose in the landscape. These models have the potential to be of a general and mechanistic nature and can be extrapolated over a relatively wide spatial range. They therefore belong to the mechanistic or process-based group of models based on cause-relationships. Such a model is not judged primarily on predicted precision, but rather on the theoretical correctness of the predicted response (13, 32). One potential advantage with a process-based approach is that it is ecologically meaningful since the variables are selected based on habitat requirements of the species (33). The used variables represent conditional habitat factors with an explicit causal relationship. Furthermore, the process-based approach commonly uses a limited number of variables (33), which, if correctly identified, enables us to understand the effects of changes in the landscape to the model outcome. On the other hand, a drawback with process-based models is that they are cumbersome to parameterize, thereby potentially reducing their applicability as management tools (34). Further, validation of any HSI model requires demographic data which often are not available for most habitat models (35). Animals may be absent from the study area or one may lack data for particular areas.

A different approach pursued by wildlife managers, scientists and foresters is to monitor moose movement using GPS or conventional VHF transmitter techniques. This data can be analyzed to build an empirical model describing the actual movement or home-range size of moose. By this method, the observed resource space for moose in the landscape can be assessed. The empirical model usually represents a statistical model as defined by Guisan and Zimmermann (13), which means the predictive power is limited by the low ability to extrapolate. Thus, these models have a tendency to be static and site specific. On the other hand, this type of model is easier to evaluate from a habitat utilization perspective as one can use a different data set or boot-strapping techniques of the same data set used to construct the model in model evaluation (14).

As our results show, it is likely that the assumptions and functional processes behind the presented mechanistic HSI model for moose, based on expert knowledge, did not reflect the complexity of reality. In addition, the present process-oriented model neither included any geographical relationships describing the spatially explicit distribution of resources in the landscape nor did it account for the varying accessibility of resources to moose. The importance of including such spatially explicit resource distribution was also discussed by Allen et al. (27). Current process-oriented HSI models used in practical wildlife management have hitherto mainly focused on variables which are relatively simple to quantify with only few attempts to determine the spatial distribution of the resources (27, 30, 31). With the development of more sophisticated GIS analysis tools and the availability of geographical and vegetation data in digital form, the models used in wildlife management could be refined to include geographical factors in a spatially explicit way.

Based on the results from the empirical approach we hypothesize that moose is selecting its habitat on at least 2 different spatial scales (see also 36, 37). At the landscape level, geographical conditions such as altitude and distances to, e.g. railroads, large roads or settlements (Table 2) appear to be important for habitat selection. On a finer scale, e.g. the forest stand level, vegetation variables such as stem volumes of spruce and pine or the degree of stocking (Table 2) may influence local habitat selection. Scale-dependent food selection was reflected in patterns of moose browsing on aspen in the same area (38, 39). Scale-dependencies are also reflected in Figure 4d-f in combination with Table 2. For example, altitude seemed to be the single most important factor, separating the high HSI values along the coastal lowland from lower HSI values in the inland at a generally higher altitude.

Further, the process-oriented model may have been too conservative with reference to the functional relations of environmental variables. Habitats which were classified to low suitability values by this model were frequently used by moose resulting in higher HSI values in the empirical model (Fig. 4a *vs* Fig. 4f), especially along the coast (Fig. 4d). This can have 2 different causes. First, the assumptions of the process-oriented model are too strict, meaning that moose did explore a broader resource space than predicted, i.e. the observed resource space for a specific variable exceeds the predicted resource space. However, this may be a consequence of the emphasis of conceptual, process-oriented models on causal relationships rather than precision. Second, not all habitats may be equally accessible to moose, resulting in a higher actual usage of low quality-habitat than predicted by the mechanistic model (Fig. 4d). This may arise, e.g. from social behavior, as moose usually avoid aggregating. Some individuals may then be forced into low quality areas as high quality areas are occupied. Hence, this might be an example for a missing factor describing accessibility in the process-oriented model, which places the predicted resource space partly outside the observed resource space.

CONCLUSIONS

Habitat modeling may help to mitigate or resolve complex issues in co-management of large ungulates and forest resources. In this study we examined 2 approaches to model moose-forest-relationships. Our aim was not to perform a formal model evaluation of neither of both approaches, but used the empirical HSI model based on presence data of moose to explore the assumptions of a conceptual, process-oriented HSI model based on expert knowledge. We could show that the empirical approach can be used to set the assumptions of the process-oriented model in perspective using the concept of overlapping resource spaces.

The process-oriented model did not take spatially explicit features of landscape structure into account, but calculated habitat suitability based on stand-level vegetation estimations. The empirical model approach, however, ranked the importance of the surrounding landscape structure for moose movement and habitat selection higher than the vegetation distribution alone. To further improve the process-oriented HSI model, these findings suggest that it is necessary to include spatially explicit landscape structure and configuration variables in the model.

Conceptual, process-oriented models designed to steer browsing damage have thus to focus on a broader scale than single forest stand variables. Further research will be needed to construct the mechanistic functions which take the spatially explicit distribution and juxtaposition of resources for moose into account. Empirical data are important to fine-tune parameters of the functional processes to local conditions. Further, the scale dependency of different ecological and geographical variables for moose movement and habitat selection must be carefully evaluated. Future decision making systems for wildlife managers to control moose population density must thus be based on both forest stand scale variables as today, and new functions of spatially explicit landscape structure and resource distribution.

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Box 1.

Habitat is modelled as a function of variables (Table 1) known or perceived to be important components of the life requisites food and cover during winter (Fig. 3). A food suitability index, SI_F was calculated based on 4 variables (Fig. 3): proportion of pine (*pvp;* Eq. 1), proportion of deciduous trees (pvd; Eq. 2), stand density (*sde;* Eq. 4) and mean stand height (*msh*; Eq. 5) using the functions presented by Kurtilla et al. (8).

$(pvp \leq 0.45)$	$SI_{pvp} = 2 \times pvp + 0.1$	Eq. 1
$(pvp > 0.45)$	$SI_{pvp} = 1$	
$(pvd \leq 0.45)$	$SI_{pvp} = \frac{pvp}{0.9} + 0.5$	Eq. 2
$(pvd > 0.45)$	$SI_{pvd} = 1$	

For the food component the first 2 variables, *pvp* and *pvd* were given equal relative importance as they were combined to form a new suitability index for proportion of pine and deciduous species, SI_p (Eq. 3). As we assume that for a limited time one component can substitute the other, an additive approach was chosen.

$(SI_{pvp} + SI_{pvd} \leq 1.0)$	$SI_p = SI_{pvp} + SI_{pvd}$	Eq. 3
$(SI_{pvp} + SI_{pvd} > 1.0)$	$SI_p = 1$	
$(sde \leq 4000)$	$SI_{sde} = \frac{sde}{4000}$	Eq. 4
$(sde > 4000)$	$SI_{sde} = 1$	
$(msh \leq 2.5)$	$SI_{msh} = 0.4 \times msh$	Eq. 5
$(2.5 < msh \leq 4.0)$	$SI_{msh} = 1$	
$(4.0 < msh \leq 5.0)$	$SI_{msh} = -msh + 5.0$	
$(msh > 5.0)$	$SI_{msh} = 0$	

In the overall food suitability index, SI_F, (Eq. 6) the 3 *SI* components for proportion of pine and deciduous trees SI_p, stand density SI_{sde}, and mean stand height SI_{msh} all received equal relative importance (i.e. 1/3). The 3 model components are regarded obligate, thus, the multiplicative approach of the geometric means is used which means that SI_F equals 0 if one of the indices equals 0.

$$SI_F = \sqrt[3]{SI_p \times SI_{sde} \times SI_{msh}} \qquad \text{Eq.6}$$

A cover suitability index, SI_C was calculated in a similar way as the SI_F and was based on three variables (Fig. 3; (27)): canopy cover of all trees (*cct*; Eq. 7), canopy cover of coniferous trees (*ccc*; Eq. 8) and mean stand height (*msh*; Eq. 9).

$(cct \leq 75)$	$SI_{cct} = \frac{cct}{75}$	Eq. 7
$(cct > 75)$	$SI_{cct} = 1$	
$(ccc \leq 60)$	$SI_{ccc} = 0.015 \times ccc + 0.1$	Eq. 8
$(ccc > 60)$	$SI_{ccc} = 1$	
$(msh \leq 3.0)$	$SI_{msh} = \frac{msh}{30} + 0.1$	Eq. 9
$(3.0 < {}_{msh} \leq 10.6)$	$SI_{msh} = \frac{msh}{9.5} - 0.116$	
$(msh > 10.6)$	$SI_{msh} = 1$	

In the overall cover suitability index SI_C (Eq. 10) the 3 components all received equal relative importance (i.e. 1/3). The 3 model components are regarded obligate the same way as for the food index thus the multiplicative approach of the geometric means is used which means that SI_C equals 0 if one of the cover indices equals 0.

$$SI_C = \sqrt[3]{SI_{cct} \times SI_{ccc} \times SI_{msh}} \qquad \text{Eq. 10}$$

Prior to combining the 2 indices SI_F and SI_C into a composite index of overall habitat suitability HSI, we averaged pixel values within a circular moving window which equalled the size of a daily home range of moose in this region. The size of this circle was set to 32 ha (H. Dettki, unpubl. data). As for moose in the study area food SI_F was considered the most important factor for winter habitat, SI_F received the weight 0.9 compared to 0.1 for cover, SI_C. Both food and cover are perceived as requirements of habitat and a multiplicative approach was used when combining both indices. The HSI is thus calculated as a weighted geometric mean of the pixel-level indices SI_F and SI_C.

$$HSI = (SI_F)^{0.9} \times (SI_c)^{0.1} \qquad \text{Eq. 11}$$

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