

Effects of spatial scale and sample size in GPS-based species distribution models: are the best models trivial for red deer management?

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Abstract Species distribution models (SDMs) are popular in conservation and management of a wide array of taxa. Often parameterized with coarse GIS-based environmental maps, they perform well in macro-ecological settings but it is debated if the models can predict distribution within broadly suitable “known” habitats of interest to local managers. We parameterized SDMs with GIS-derived environmental variables and location data from 82 GPS-collared female red deer (*Cervus elaphus*) from two study areas in Norway. Candidate GLM models were fitted to address the effect of spatial scale (landscape vs. home range), sample size, and transferability between study areas, with respect to predictability (AUC) and explained variance

(Generalized R^2 and deviance). The landscape level SDM captured variation in deer distribution well and performed best on all diagnostic measures of model quality, caused mainly by a trivial effect of avoidance of non-habitat (barren mountains). The home range level SDMs were far less predictable and explained comparatively little variation in space use. Landscape scale models stabilized at the low sample size of 5–10 individuals and were highly transferable between study areas implying a low degree of individual variation in habitat selection at this scale. It is important to have realistic expectations of SDMs derived from digital elevation models and coarse habitat maps. They do perform well in highlighting potential habitat on a landscape scale, but often miss nuances necessary to predict more fine-scaled distribution of wildlife populations. Currently, there seems to be a trade-off between model quality and usefulness in local management.

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Introduction

Species distribution models (SDMs) are important tools within many disciplines of ecology (Guisan and Thuiller 2005; Hirzel and Le Lay 2008; Elith and Leathwick 2009). A main reason for the general popularity of SDMs is that their geographically extrapolated outputs—habitat suitability maps—are continuous in space. This is a desirable format for managers and conservation practitioners compared to survey data which are discrete and often spatially biased and therefore less easy to comprehend (Andelman and Willig 2002; Wilson et al. 2005; Austin 2007). Yet, precisely because maps based on SDMs are extrapolations,

they vary in quality and are sensitive to modeling choices (Wilson et al. 2005; Johnson and Gillingham 2008).

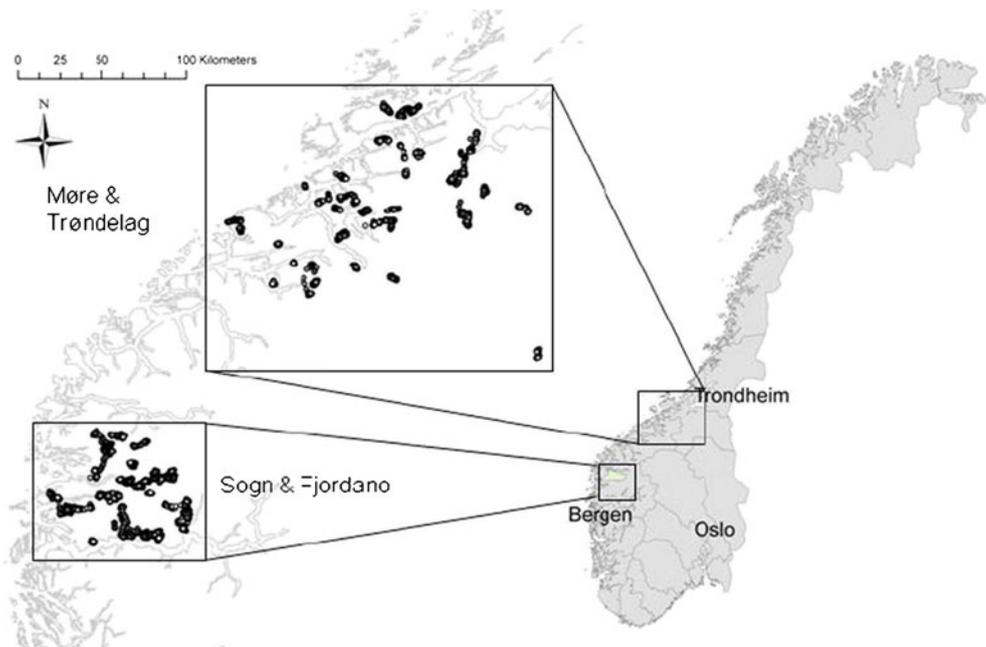
The most used SDM is the generalized linear model (GLM; McCullagh and Nelder 1989) because of a strong statistical foundation and the fact that it performs well in predicting species distribution (Austin 2002; Elith and Graham 2009) and local variation in relative density (Manly 2002; Johnson et al. 2006). As any other SDM, GLMs are inherently sensitive to which areas are considered available but unused. Although much attention has been devoted to at which scale pseudo-absences should be sampled (Pearce and Boyce 2006), this issue remains unsettled. Some studies have selected absences far from used locations in order to reduce the amount of false absences (e.g., Austin 2007). This results in statistically well-performing models but may have a negative side effect of being simplistic often predicting a too large distribution of a species (van der Wal et al. 2009; Lobo et al. 2010). In individual-based studies of mobile animals, it is most common to sample availability at two distinct scales—on landscape level (study area) and within home ranges (Johnson 1980; Manly 2002). In such studies, random sampling with replacement is advocated (Johnson et al. 2006) leading to more false negatives (occupied areas predicted to be empty) and models explaining less deviance (Lobo et al. 2010), but with the potential of more accurate fine-scaled predictions in distribution (van der Wal et al. 2009). From the perspective of local management, selection of scale may be important because the aim is often to predict variation in distribution and density of a species within broadly suitable “known” habitat types (e.g., forest for a forest-dwelling species). We investigate here if this is

best obtained by sampling pseudo-absences at the within-home range scale where trivial non-habitat (e.g., barren mountain for a forest dwelling species) is excluded.

Sample size has been found to have a large effect on predictive ability of the SDMs (Pearce and Ferrier 2000; Stockwell and Peterson 2002; Wisz et al. 2008). For SDMs of large mammals and birds, individual-based relocation data sampled through GPS telemetry (Dettki et al. 2003; Koehler et al. 2008; Johnson and Gillingham 2008) are increasingly often used. Due to logistic and financial constraints, it is still common to mark a limited number of individuals but in return receiving a very large number of locations per individual (D’Eon and Serrouya 2005; Hebblewhite and Haydon 2010). Thus, while the sample size across individuals by far exceeds what is considered critical in earlier studies (Wisz et al. 2008), the locations are correlated and derived from a limited number of individuals (Dettki et al. 2003; Koehler et al. 2008). This is worrying because individual variation in habitat selection is often pronounced (Gustine et al. 2006), and models parameterized for each individual may differ substantially from global models (using data from all individuals; Gillingham and Parker 2008). It may thus be expected that SDMs derived from data of few individuals will be highly sensitive to variation in individual behavior as well as the geographical range of included individuals.

In this study, we parameterize SDMs using GLM based on data from 82 GPS-collared female red deer (*Cervus elaphus*) in two areas (Sogn og Fjordane, $n=52$ and Møre og Romsdal and Sør-Trøndelag, $n=30$; Fig. 1) on the west coast of Norway along with environmental data derived from GIS maps. Firstly, we investigate how model quality

Fig. 1 The two study areas in Sogn og Fjordane (6,524 km²; excluding water) and Møre og Romsdal and Sør-Trøndelag (17,155 km²). Points are locations of 82 GPS-collared female red deer ($n=52$ in Sogn og Fjordane and 30 in Møre og Romsdal and Sør-Trøndelag)



changes from the landscape to the home range (henceforth abbreviated HR) scale along a gradient where progressively less non-habitat is included. Secondly, we analyze the effect of individual variation in habitat selection and estimate how many marked individuals are needed in order to get stable SDMs at landscape and HR level. Finally, we investigate the generality of our SDM by validating our model in a second region 250 km distant.

Materials and methods

Study area

The two study areas are located on the Norwegian west coast in the counties Sogn og Fjordane (decimal degrees=N 61.10–61.79; E 4.93–6.82) and Møre og Romsdal and Sør-Trøndelag (N 62.15–63.59; E 6.82–10.69). The study areas are situated in boreonemoral to middle boreal zone (Abrahamsen et al. 1977). Natural forests consist of deciduous forest (dominated by birch *Betula* sp. and alder *Alnus incana*) and pine forest (*Pinus sylvestris*), together with juniper (*Juniperus communis*), bilberry (*Vaccinium myrtillus*), and heather (*Calluna vulgaris*). Norway spruce (*Picea abies*) has been planted throughout the area and occurs in dense stands with little ground vegetation. Agricultural areas are situated on flatter and more fertile grounds in valley bottoms and consist of pastures and meadows for grass production (dominated by timothy *Phleum pratense* and meadow fescue *Festuca pratensis*). The topography is characterized by steep hills and mountains intersected by forest covered valleys, streams, and fiords.

The study areas are situated in the core area for red deer in Norway. The red deer populations in this region have increased approximately 6-fold over the last decades (Statistics Norway 2010), and the area can be viewed as saturated with deer in terms that there are no large unused areas or colonization fronts. Annual harvest (10 September–most often 15 November) takes place in all municipalities in the study areas. Red deer in this area show negative density-dependent effects on body weight (Mysterud et al. 2001), age at first reproduction (Langvatn et al. 2004), and dispersal (Loe et al. 2009).

The majority of female red deer migrate seasonally between small winter (coast; low elevation) and summer (inland; higher elevation) ranges that are separated by up to 70 km (Albon and Langvatn 1992). The mean size of the summer home ranges (95% LoCoH) used in this study is 302 ha (SE=575). Most individuals move from winter to summer range in April–May and return in September–November. Spring migration is nutritionally driven and coincides with plant green-up (Pettorelli et al. 2005). Deer

summer ranges are expected to be in high-elevation areas to prolong the access to protein-rich plants in an early phenological state (Albon and Langvatn 1992; Pettorelli et al. 2005), but red deer strongly avoid barren mountains (most often starting at elevations above ca. 7–800 m a.s.l. in the inland summer ranges of red deer, Godvik et al. 2009). Elevation above this limit is termed non-habitat in the following.

Red deer GPS data

The data on red deer derive from 82 adult (2 years and older) female red deer marked with GPS (Global Positioning System) collars (Televelt, Lindsberg, Sweden). All animals were captured by darting at winter feeding sites baited with hay from January to April 2005–2008, following a protocol approved by The Norwegian Animal Research Authority. All the collars were programmed to record a position once every hour. Here, we include only summer data (totaling more than 150,000 locations across individuals) delimited as dates from 1st June to 15th August. Biologically, this means the period when all individuals are in their summer range, when most adult females give birth to a calf and well before rutting activities start (Loe et al. 2005). Calving status of the marked red deer females was unknown.

Extreme outlying locations are likely GPS errors and were deleted based on speed rules and the cosine of the angle associated with the outgoing and incoming move according to the protocol of Bjørneraas et al. (2010). Deleted points compose ca. 0.5% of all locations. Data obtained with GPS are expected to vary with respect to location errors and fix-success rates (proportion of time-outs) due to failure to obtain a fix, e.g., under dense cover (D'Eon 2003; D'Eon and Delaparte 2005; Frair et al. 2004). To quantify these sources of error, we put out the same type of collars as used for the red deer on test sites in the study area. The test sites were stratified according to factors expected to influence on fix rate, including habitat openness, slope, and aspect (Godvik et al. 2009). The median location error for our GPS collars was 12 m (upper 95% CI=23 m) which is low compared to the expected accuracy of the GIS maps. GPS collars worn by red deer in this study achieved an average fix rate of 91% (range 77–98%). Based on the data from test sites, we modeled the probability to obtain a fix with different combinations of habitat characteristics (Godvik et al. 2009). We found that fixes were most often lost at sites with dense tree cover and low sky visibility. This model was in turn used to parameterize a map of probability to obtain a fix in all pixels within the study area. To counteract habitat bias in the RSF model, we replaced missing locations with new simulated locations in an iterative process where the

probability to retain a sampled location is inversely related to the probability of obtaining a fix in that pixel (Frair et al. 2004; Godvik et al. 2009). In practice, this procedure adds a simulated “used” location for every missing GPS fix primarily in locations with low probability to get a fix.

Environmental GIS variables

All environmental variables were derived from Geographic Information System (GIS) maps, primarily using ArcGIS 9.3 (ESRI, USA). Habitat types were derived from digital land resource vector maps provided by the Norwegian Forest and Landscape Institute, with a scale 1:5,000. Following Godvik et al. (2009), habitat types were simplified into the four functional groups: (1) pasture (farmland), (2) productive forest, (3) unproductive forest, and (4) other (consisting primarily of empty polygons dominated by barren mountains because the habitat was classified by forest engineers). Since use of pasture depends on local availability of pasture (i.e., a functional response; Godvik et al. 2009), the local availability of pasture was calculated as the proportion of pasture within a circle with a radius of 1,087 m resembling the same area as the mean size of a summer HR. Roads were represented in a separate vector layer (scale 1:50,000) which was used to calculate the shortest linear distance (in meters) to road for all pixels in the map. From a Digital Elevation Model (DEM) elevation (in meters), slope (in degrees) and aspect (in radians) were derived. Aspect was converted to a continuous variable of “northness” [ranging from 1 (north) to -1 (south)] by using the cosine function of aspect. All map layers were rasterized with a resolution of 100 m.

Statistical analyses

Generalized linear models The analytical approach consisted of fitting generalized linear models (GLMs) with a use-availability design (Guisan and Zimmermann 2000; Manly 2002; Johnson and Gillingham 2008). The response variable is binomially distributed and consists of used points (the red deer GPS points; coded 1) and randomly sampled available points (coded 0; see below for procedure). Candidate predictor variables in the models include all abovementioned environmental variables including second-order terms for continuous variables. The interaction between pasture availability and pasture use was implemented as the interaction between the boolean variable “habitat=pasture” and the arcsine-square root-transformed proportion of pastures within a circle with radius 1,087 m (Godvik et al. 2009). Candidate models of varying complexity were subjected to model selection based on AIC (Burnham and Anderson 1998). Parameter estimates of the best model (lowest AIC) are provided. The

best models also form the basis for extrapolations into habitat suitability maps by applying the GLM equation on each pixel in the multi-layered raster map. The map will then display the relative probability of detecting a female red deer in summer in each pixel of the map. Mean values for availability and use for all environmental variables are provided in Table S1 in the electronic supplementary material.

Measures of model quality It is recommended to use several diagnostics when comparing models (Elith and Graham 2009). All diagnostics consist of variations of selecting training sets of data and evaluating them based on retained calibration sets. Here we use the area under the ROC curve (AUC), Cohen’s kappa, and k -fold cross-validation as recommended for GLM models (Manel et al. 2001; Boyce et al. 2002). Kappa must be higher than 0.4 for a model to be classified as performing well (Berg et al. 2004). We used two measures to quantify how much variability of the data was explained by the model. Firstly, we used the generalized R^2 (Zheng and Agresti 2000) which will always fall between 0 and 1 and is recommended when using binomially distributed data. The other measure we used was the deviance (Lobo et al. 2010). In addition, we calculated partial deviance to highlight the variability explained by each parameter in the model. Finally, we refer to model complexity as the number of parameters retained in the best model.

Investigating the scale of availability We define the availability scale as the type of physical areas the randomly selected points (also termed pseudo-absences; van der Wal et al. 2009) are drawn from. To address the effect of the availability scale on model quality, pseudo-absences were sampled from four different types of areas. The available area on the *landscape scale* was defined as the minimum rectangle that encompassed all data points adding a buffer of 1 km in all directions (thus synonymous with study area). This resulted in a 6,524 km² area in Sogn og Fjordane and 17,155 km² in Møre og Romsdal and Sør-Trøndelag (excluding water). In landscape analyses excluding non-habitat, all areas above 800 m a.s.l. were excluded. At the *HR scale*, two types of estimators were used. Minimum convex polygons (MCP) were chosen because they are frequently criticized as including too large of an area (White and Garrott 1990) and therefore providing a “coarse” HR scale. In contrast, local convex hull polygons (LoCoH) are better at excluding unused areas (Getz and Wilmsers 2004) and therefore represent the “fine” HR scale. For simplicity, we hereafter refer to the two landscape methods (including and excluding non-habitat) and the two different HR methods (MCP and LoCoH) as the four availability scales. For each individual and

availability scale, random locations were sampled proportional (1 to 1) to the number of used locations using Hawth’s tools (Beyer 2004) in ArcGIS 9.3. All GLMs and model quality tests were ran in (R Development Core Team 2010).

Effect of sample size and transferability between areas Effect of sample size of individuals on model quality was based on the best landscape model (including non-habitat) and the best HR model (LoCoH). At each availability scale, one iteration consisted of the following steps. Firstly, nine individuals were randomly sampled and retained as validation data (Boyce et al. 2002). They were sampled with replacement due to the philosophy that they could represent strategies of other unsampled deer with identical habitat selection strategy. Secondly, the models were fitted with a progressively larger set of training data (range 2–35 individuals; also sampled with replacement) and tested on the same validation data. A second reason for sampling with replacement is that we would otherwise always end up with the same 35 individuals as sample size increased. As a consequence, the estimation of bootstrapped R^2 would converge toward the observed R^2 for all animals and the variance would decrease linearly towards zero. A new iteration started with random selection of nine new individuals for validation. Bootstrap confidence limits consist of the 2.5 and 97.5 percentiles of the iteratively derived quality estimates. When addressing the effect of the availability scale and sample size, only data from the Sogn og Fjordane study area are used. Regional model transferability was estimated by using individuals from the second study site Møre og Romsdal and Sør-Trøndelag (250 km distant) as validation data.

Correlation of maps Each habitat suitability map is a matrix of raster values (pixels). To calculate the Pearson correlation of map outputs at the landscape and the HR scale, we computed the Pearson correlation (or covariance)

between the columns of x and the columns of y matrices using the function `cor` in R.

Results

The availability scale at which pseudo-absences were sampled influenced only slightly which and how many variables were retained in the selected model. The model structure was identical for both HR scales and the landscape scale excluding non-habitat, but included a quadratic term for elevation at the landscape scale including non habitat (Table 1). Predictability of the models (AUC) and variance explained by the models (generalized R^2 and deviance) were high at the largest availability scale (landscape including non-habitat), but decreased to very low values at both HR scales (Table 1). Complexity of the selected model was slightly lower at the largest availability scale (five main effects) than at all the lower scales (six main effects and one interaction term; Table 1). Habitat (31–50% of explained deviance) and slope (25–45% of explained deviance) were the two main factors influencing red deer presence at the HR and landscape scales when excluding non-habitat. When including non-habitat at the landscape scale, this differed such that habitat (60% of explained deviance) and elevation (31% of explained deviance as a quadratic term) were the most important variables. The effect of elevation and slope was positive at the lowest availability scales indicating that red deer select steep, high elevation areas close to the tree line in the summer (Table 2). The inclusion of the second-order term for elevation at the landscape scale including non-habitat is presumably caused by the preference for moderately high elevations which are below the tree line, but avoidance of anything higher which is barren. All habitat types were selected over “other” (which is mainly barren ground below the 800 m a.s.l. threshold) and productive

Table 1 Effect of scale of availability on model complexity, number of parameters in the best model, predictability (AUC), and amount of variation explained (generalized R^2)

Level	Selected model	n parameters	AUC	Deviance explained (%)	Generalized R^2
Landscape—including non-habitat	Used~habitat+elevation+elevation ² +aspect+slope	5	0.786	23.7	0.525
Landscape—excluding non-habitat	Used~elevation+aspect+slope+habitat+pasture availability+ interaction pasture availability: pasture use+distance to road	7	0.698	9.04	0.345
HR MCP (large polygons)	Used~elevation+aspect+slope+habitat+pasture availability+ interaction pasture availability: pasture use+distance to road	7	0.562	1.03	0.119
HR LoCoH (smaller polygons)	Used~elevation+aspect+slope+habitat+pasture availability+ interaction pasture availability: pasture use+distance to road	7	0.587	1.6	0.148

Availability spans the four scales Landscape level including non-habitat (barren mountains), Landscape level excluding non-habitat, MCP (large polygons) HR level, and LoCoH (smaller polygons) HR level

forest was selected over unproductive forest. At the HR scale and the landscape scale excluding non-habitat, use of pasture depended on the local availability of pasture (the interaction term in Table 2). Extrapolated in space, landscape and HR models produced widely different habitat suitability maps (Fig. 2), correlated by only 43% on the landscape (excluding non-habitat) and HR (LoCoH) scale. The correlation of maps at the two HR scales MCP and LoCoH was high (82%).

At the landscape scale the means of all model quality measures stabilized at sample sizes down to only 5–10 individuals depending on the quality measure used (Fig. 3a). However, the bootstrap confidence limits around the mean continue to decrease with sample size even beyond the samples size of 10, in particular for generalized R^2 (Fig. 3a). The difference in model quality between the landscape and the HR scale was mainly additive, with an overall higher performance of landscape models over HR models irrespective of sample size (Fig. 3). At the HR scale, the models performed poorly and the quality measures failed to increase with increasing sample size (Fig. 3b). The low AUC values also indicated that selection is approaching random at the HR scale (values close to 0.5; Fig. 3b). The model parameterized in one area (Sogn og Fjordane) could be used in the other study area (Møre og Romsdal and Sør-Trøndelag) without any loss of predictive capacity both on the landscape (AUC=0.78 vs. 0.82) and the HR scales (MCP—AUC=0.562 vs. 0.610; LoCoH—AUC=0.587 vs. 0.596).

Discussion

GPS tagging of large mobile animals is viewed by managers as an important tool to gain insight of local variation in distribution and density. We provide insight into the effect of the scale of availability and sample size on SDMs parameterized with GPS data. Selecting pseudo-absences on a landscape scale including non-habitat yielded the models of best quality as judged from a pure statistical point of view. These summer models for female red deer were dominated by the effect of habitat (avoidance of barren mountains) and selection of high-elevation forested areas. These are selection gradients already well known to local red deer managers, yielding little new insight to them. With such coarse habitat maps, landscape models stabilized at a very low sample size of marked deer and were transferrable between regions suggesting that SDMs can be built based on data from few marked individuals and applied in neighboring similar landscapes.

The scale of availability was extremely important for all measures of model quality (Table 1). Only at the landscape scale, when including non-habitat, did the model perform adequately in terms of explained variance, deviance, and predictability. When sampling pseudo-absences from progressively larger areas, the proportion of points outside the fundamental niche of the species will increase. At one extreme end, when sampling absences on a global scale, SDMs will be dominated by large-scale climatic gradients (Hirzel and Le Lay 2008) and show an extremely good fit.

Table 2 Parameter estimates of the best SDM at the largest scale (landscape, including non-habitat) and smallest scale (HR, LoCoH)

	Estimate	SE	<i>z</i>	<i>P</i> value
Landscape—including non-habitat				
Intercept	−0.928	0.0180	−51.7	<0.001
Habitat (pasture—other)	0.671	0.0272	24.7	<0.001
Habitat (prod. forest—other)	1.04	0.0139	75.3	<0.001
Habitat (unprod. forest—other)	0.699	0.0158	44.4	<0.001
Elevation	0.00271	0.0000812	33.4	<0.001
Elevation ²	−0.00000586	0.0000000909	−64.5	<0.001
Aspect (continuous)	−0.0681	0.00773	−8.81	<0.001
Slope	0.0361	0.000500	72.2	<0.001
HR—LoCoH				
Intercept	−0.665	0.0177	−37.7	<0.001
Elevation	0.000101	0.0000296	3.41	<0.001
Aspect (continuous)	0.0443	0.00682	6.49	<0.001
Slope	0.00815	0.000422	19.3	<0.001
Habitat (pasture—other)	0.774	0.0456	17.0	<0.001
Habitat (prod. forest—other)	0.468	0.0124	37.8	<0.001
Habitat (unprod. forest—other)	0.270	0.0144	18.8	<0.001
Pasture availability	0.789	0.0830	9.51	<0.001
Interaction pasture availability×pasture use	−5.57	0.264	−21.1	<0.001
Distance to road	0.000167	0.00000572	29.2	<0.001

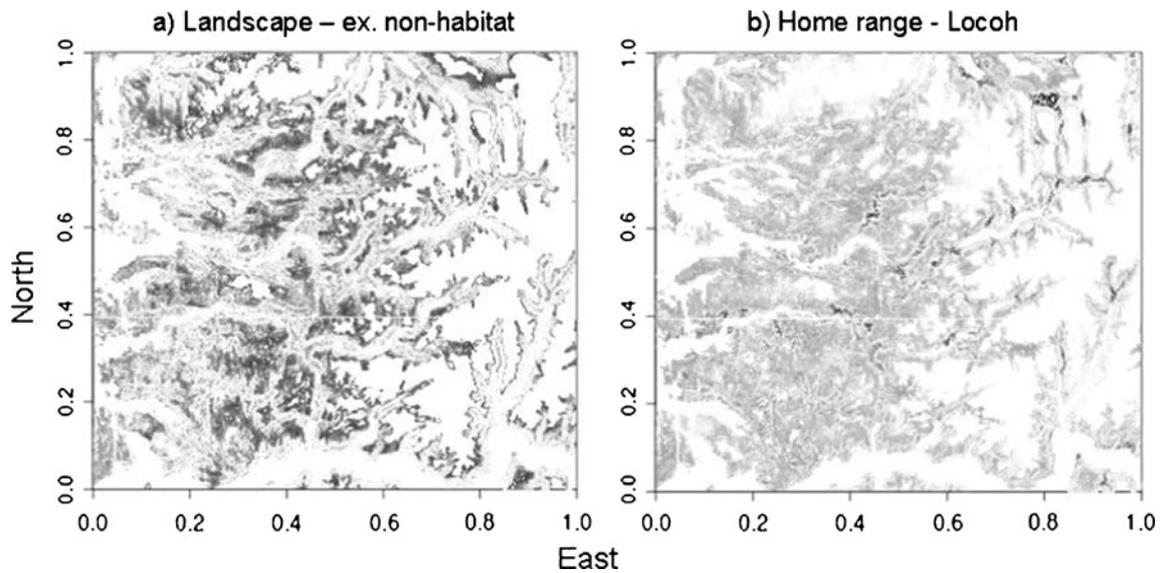
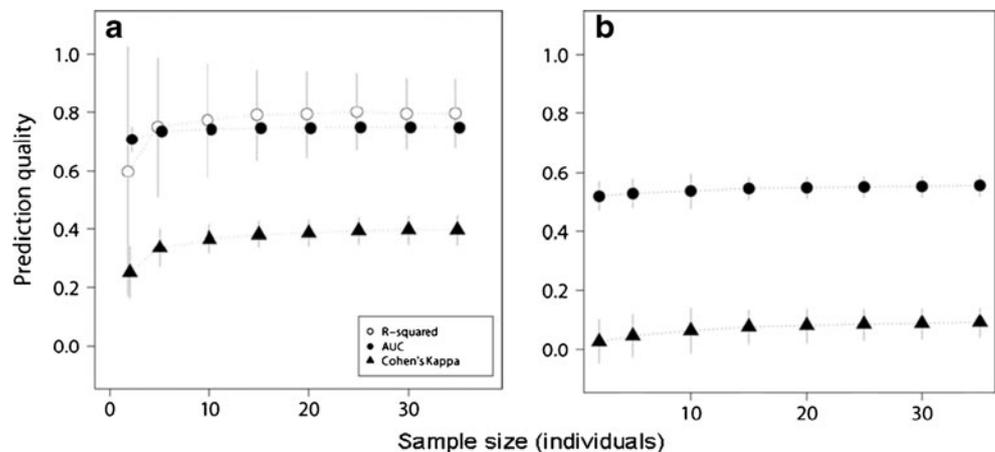


Fig. 2 Habitat suitability maps for female red deer in Sogn og Fjordane derived from logistic regression models at the **a** landscape level including non-habitat and at the **b** LoCoH HR level. Areas with *dark shading* have high probability of being used by red deer

This has been termed the “no elephants in the Arctic effect” (Lobo et al. 2010). The poor performance of models at a small scale likely occurs because most of the habitat selection is already done on larger scales (Boyce et al. 2003; D’Eon and Serrouya 2005), in particular with respect to the most fundamental variables such as elevation and habitat class (Rotenberry et al. 2002, 2006), which are typically the ones possible to derive from coarse GIS maps. Selection of the availability scale for sampling pseudo-absences depends on the research question (Boyce et al. 2003), and the availability scale of SDM will also vary depending on the management question to be asked. For delineating species distribution and large-scale variation in density, sampling of pseudo-absences should occur at the landscape scale and include non-habitat. At the same time, it is evident that important insight such as the functional response in selection of pasture (Godvik et al. 2009) only occurs in more complex models not overridden by “trivial”

effects (van der Wal et al. 2009), in our case red deer avoiding barren mountains. The landscape SDM including non-habitat stabilized at a very low sample size. Our results indicate that data from only a few individuals (<10) provide sufficient information about habitat suitable for red deer at the landscape level (Fig. 3a). Although larger sample size in general result in better models (Guisan et al. 2007), a small sample size can be used if individual variation in response to large-scale constraining factors is low (Rotenberry et al. 2002, 2006; Calenge et al. 2008). In our study, this implies that most individuals avoid barren mountain (Godvik et al. 2009) and migrate in spring to higher elevations close to the tree line (Albon and Langvatn 1992; D’Eon and Serrouya 2005). The reduced confidence limits even beyond 10 individuals point to a benefit of higher sample size in order to reduce the risk of heavy impact of parameter estimates by outlying individuals differing from the main-stream selection strategy. The quality of the HR scale SDMs failed

Fig. 3 Effect of sample size on three different measures of model predictability parameterized with data from Norwegian female red deer on **a** landscape scale including non-habitat and **b** HR LoCoH level



to increase with sample size (Fig. 3b). We interpret this as a very high degree of individual variation in selection at the HR scale, preventing prediction of selection of new individuals even from training sets of substantial sample size.

Our models were highly transferrable across regions located ca. 250 km apart. The landscapes in the two areas have comparable topographies and habitat types, and the deer selected similarly in both areas on both the landscape and the HR scale. Regional stability in models varies among species (Betts et al. 2006; Randin et al. 2006) and has been shown to be low for many species of plants (Randin et al. 2006). High transferability of models is primarily expected in species that respond strongly to large-scale limiting factors such as old-growth forest for the Northern spotted owl (*Strix occidentalis*) (Meyer et al. 1998).

Considering all of the ongoing large-scale marking with GPS collars, are managers and scientists wasting their efforts? Are 5–10 individuals and coarse GIS maps sufficient to parameterize landscape level SDMs, as indicated by the good test statistics? The statistically high predictability of SDMs at landscape scales can be misleading to wildlife managers, as the scale of resolution may be irrelevant to the problems they face. The manager is responsible for deciding harvest quotas for specific areas. Harvest quotas for red deer [as well as moose (*Alces alces*) and roe deer (*Capreolus capreolus*)] in Norway are set based on what can be broadly defined as suitable red deer habitat, termed “counting area”. Counting area is defined as the area of forest and bog under the tree line. The preference of forest and avoidance of mountains in the best landscape level SDM (Fig. 2a) produces a habitat suitability map very similar to the definition of counting area. This must be regarded as a rather trivial result to a manager, i.e., that “there are no red deer in the mountains”. For conservation of rare species with poorly known habitat requirements, this level of detail is likely sufficient, but not for abundant species where the main habitat is well known. There thus currently seems to be a trade-off between model quality and usefulness in local management.

Individual-based GPS data are excellent for deriving presence data of large mammals and birds. The constant refinement of remote sensing and GIS maps with a higher number of functionally important habitat classes (Johnson et al. 2004; Brambilla et al. 2009) is of paramount importance for development of more reliable fine-scaled SDMs. It remains to be seen whether further detail in GIS maps will provide the required level of detail to make more useful maps, or whether the inherent small-scale variation in food quality and quantity requires a different methodological approach. Habitat suitability maps have been

criticized for not being linked to fitness (Gaillard et al. 2010). Improved detail and maps and better classification of functional habitat classes may increase the power of habitat-fitness models turning habitat suitability maps into a concept of wider application.

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