Appendix C

Cumulative influence of infrastructure on reindeer space use: fitting habitat selection models

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Abstract

In this document we fit habitat selection models to wild reindeer GPS data to assess if and how the impacts of multiple infrastructure affect mountain reindeer (*Rangifer tarandus*) habitat selection during summer. We describe the modeling approach and present the results and predictions from the fitted models. This document complements the description of materials and methods and the results presented in in the main text of Niebuhr et al. *Estimating the cumulative impacts and the zone of influence from multiple anthropogenic infrastructure on biodiversity.*

Contents

Introduction

In this document we describe the procedures to fit habitat selection models to wild reindeer GPS data and assess if and how the impacts of multiple infrastructure affect mountain reindeer (*Rangifer tarandus*) habitat selection during summer. We first briefly describe the study area, the GPS data handling, and the environmental variables used in the analysis. We then describe the calculation of the infrastructure-related covariates using both the measures of cumulative influence and the influence of the nearest feature. These measures quantify the zone of influence (ZoI) as well as how the influence varies with the distance to infrastructure. Then, we describe the structure of the statistical models and the fitting procedures and present the results in details. We explore qualitatively the interpretation of both influence measures in single-infrastructure models, and then estimate the magnitude of the impacts and the ZoI of each infrastructure in multi-infrastructure models, to finally assess the combined impacts of infrastructure on reindeer habitat selection.

Material and Methods

Study area

The study area was the Hardangervidda wild reindeer area in Southern Norway, where the largest remaining population of mountain reindeer is found (Fig. C1). During summer, the area is mainly used for tourism. Hardangervidda is a big plateau surrounded by large roads around its contour, which corresponds to the lower part of the area (Fig. C2). Towards the upper, central part, there are small access roads that link the large highways to tourist cabins and a multitude of private cottages, which are also connected by a network of trails (Fig. C2). The area has 26 large tourist cabins which are constantly visited by many tourists and 24 smaller public cabins. In contrast, 14154 private cottages are spread throughout Hardangervidda.

Due to their high density, most areas (90%) in Hardangervidda are closer than 3 km from any private cottage and 5 km from the closest trail (Table C1). In contrast, more than 50% of the areas are farther than 13 km from large tourist cabins and 10 km from small tourist cabins. There are also many areas far from roads towards the central part of the Hardangervidda (Table C1).

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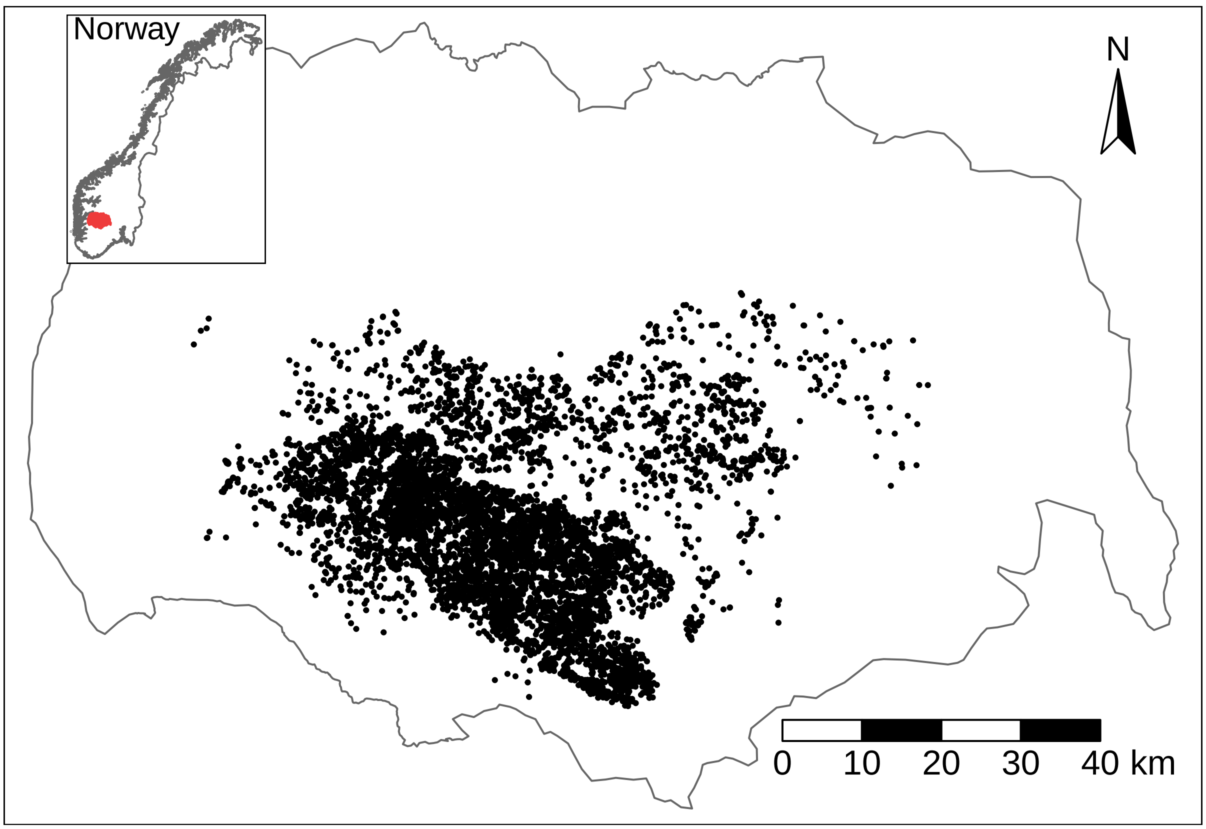

Figure C1: Hardangervidda reindeer area in Southern Norway and reindeer GPS locations used in this study.

Reindeer GPS data

Fourty-eight female reindeer were captured and monitored between 2001 and 2010. Reindeer were immobilized from helicopter (see details in Evans et al., 2013) and equipped with GPS collars with drop-off system. To regularize the fix rate among collars, we used 1 reindeer position every 6 hours, summing up a total of 7478 positions for all individuals. We analyzed only the data from July, selected here as a month representative of the summer, to avoid including reindeer positions during either the end of the calving season or during rut and autumn migration. For detailed data cleaning and preparation procedures, please see Panzacchi et al. (2015).

To perform habitat selection analyses, for each used GPS location we created a set of 9 locations available but not used by reindeer, spread uniformly within this wild reindeer area (Fig. C1). The combination of use and available locations was then annotated with environmental spatial data to assess the effects of the different infrastructure on reindeer space use.

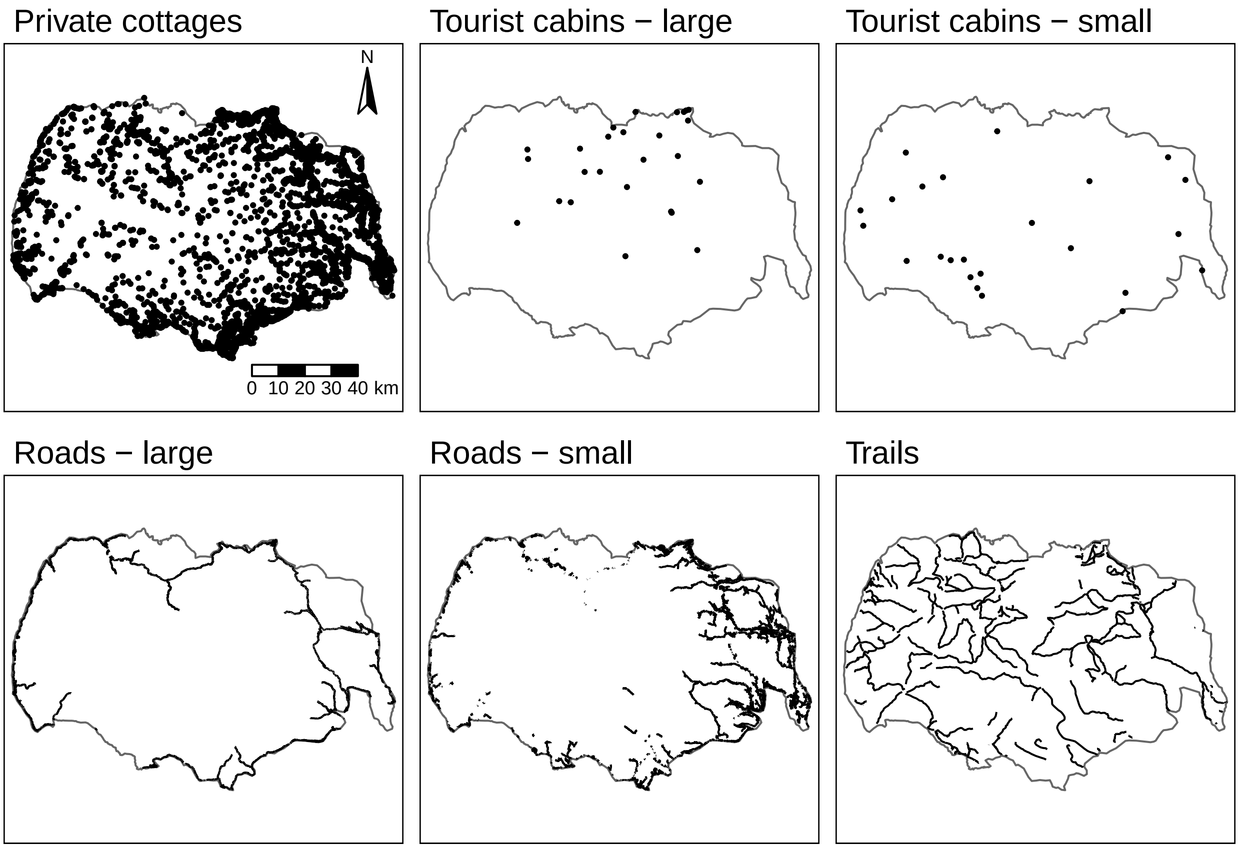

Figure C2: Main anthropogenic infrastructure in the Hardangervidda reindeer area, used to illustrate the landscape context. Only private cottages and large tourist cabins were included in the analysis.

Table C1: Quantiles of the Euclidean distance from each 100 m-side cell in the Hardangervidda reindeer area to the nearest feature (in meters), for the main anthropogenic infrastructure present in the study area.

Infrastructure	0%	10%	25%	50%	75%	90%	100%
Private cottages	0	316	671	1265	2102	3178	7580
Large tourist cabins	0	4115	7117	13180	22496	29461	45393
Small tourist cabins	0	3833	6537	10308	14223	18065	31752
Large roads	0	906	2816	7235	14454	20873	29362
Small roads	0	316	1273	3970	9405	15180	26249
Trails	0	283	762	1709	3228	5124	11309

Environmental covariates

The locations of most types of infrastructure in Hardangervidda are correlated. Roads occur mostly in the lower parts of the area – and are correlated with elevation and terrain ruggedness – while other infrastructure occur closely together (e.g. small roads and cabins). For this reason, and for illustration purposes, in the analyses presented here we considered only the effects of private cottages and large tourist cabins. The spatial data sources and details are described in Panzacchi et al. (2015).

First, the vector representation for each kind of infrastructure was rasterized using a grid of 100 m resolution for an extent which included a buffer of 50 km around the study area; the buffer was used to avoid edge effects in the influence measures' calculation. Then, both the influence of the nearest feature and the cumulative influence measures were calculated. Since the infrastructure considered here (cottages and cabins) are represented as points, the input for influence calculation was the count of features within each grid cell.

Influence measures were calculated considering different influence functions (threshold, linear, Gaussian, and exponential decays; Fig. 1 in the main text), for a set of (irregularly distributed) zones of influence, from 100 m to 20 km. This allowed us to assess whether habitat selection is affected by either the cumulative influence or the influence of the nearest feature, while estimating the ZoI and accounting for the shape of the influence of the features of the different types of infrastructure within the ZoI. All influence functions were considered to have value 1 at the origin (where the infrastructure are located) and vary according to the different shapes (Fig. 1A in the main text). For the threshold and linear decay functions, the ZoI was defined as the distance at which the influence decreases to zero. For the Gaussian and exponential decay functions, which asymptotically approach zero, the ZoI was defined as the distance at which the functions reach 0.05.

To account for bio-climatic variation in reindeer space use, we also included as covariates land cover and 4 principal components (PCA axes) from a large principal component analysis performed in Norway to understand patterns of bio-climatic-geographical variation across the country (Bakkestuen et al., 2008). We used the NORUT land cover map (Johansen, 2009) with 30 m resolution and 25 vegetation classes, which we further grouped for modeling purposes (see the final classes in Table C3). The four bio-climatic principal components represent gradients of (1) PC1 - continentality, (2) PC2 - altitude, (3) PC3 - terrain ruggedness, and (4) PC4 - solar radiation, and account for 75 - 85% of the bio-climatic variation in Norway, representing the major environmental gradients in the study area (Panzacchi et al., 2015). Prior to the analyses, the continuous variables (all but land cover) were standardized to mean 0 and standard deviation 1.

Habitat selection modeling

Reindeer habitat selection was modeled through habitat selection functions (HSF, eq. 1 in the main text) considering the additive effect of the covariates described above. We included a quadratic term for PC1 and PC2 to account for non-linear responses (Panzacchi et al., 2015). HSFs were fitted through binomial generalized linear models using the function `glm` in R (R Core Team, 2021), with weigth 1 for used locations and 5000 for available locations (as suggested in Fieberg et al., 2021).

The first step in the modeling approach was to fit HSFs considering one infrastructure type at a time in a procedure of variable selection (Burnham & Anderson, 2002), to infer which influence measures and zones of influence better explained habitat selection, while also checking for correlations among the predictors (an approach similar to Laforge et al., 2015, and Huais, 2018). These models included land cover and the bio-climatic PCAs, in addition to either the cumulative influence or the influence of the nearest feature of a single infrastructure type. Given that the influence measures could assume 2 representations (cumulative, nearest) and follow 4 different functions (threshold, linear, Gaussian, exponential decay) with 8 distinct ZoI values (100 m, 250 m, 500 m, 1 km, 2.5 km, 5 km, 10 km, 20 km), for each infrastructure type we fitted 64 HSFs. Additionally, we also fitted HSFs considering the log-distance to the nearest feature, which is a predictor commonly used in statistical models to assess the impacts of anthropogenic infrastructure on biodiversity (e.g. Torres et al., 2016; Polfus et al., 2011). Single-infrastructure HSFs were fit with the `multifit` approach in R (Huais, 2018). HSFs were compared though the Akaike information criterion (AIC), and for each infrastructure type the 15 influence measures that better explained habitat selection (lower AIC) were chosen to be included in the multi-infrastructure HSF (see below).

We considered variables to be correlated if the Pearson correlation coefficient between their values was higher than 0.6, and excluded models in which any of the infrastructure influence measures was correlated with the bio-climatic variables.

In the single-infrastructure HSFs, we also assessed the estimated coefficients related to the infrastructure influence variables (β's in Eq. 1 of the main text). Even though the coefficient values were not a criterion for selecting the most parsimonious influence variables, they are important to indicate consistency in the influence measures across the scales. If the coefficient changes signs as the ZoI increases, representing a shift from avoidance to selection, this might be a warning to be careful in the evaluation of the most plausible ZoI. Since the continuous covariates were standardized for model fitting, their model coefficients were rescaled back them to the original covariate range, for interpretation purposes and prediction.

We fitted multi-infrastructure HSFs by combining the best influence measures for each infrastructure. Since not necessarily the best influence function and ZoI for single-infrastructure models will remain as the most likely in multi-infrastructure models, we selected the 15 best covariates for each infrastructure and fitted all possible combinations between them. For models in which the infrastructure covariates were correlated, and excluded those variables with higher Variance Inflation Factor (VIF, which measures how much the variance of an estimated regression coefficient is increased because of collinearity; Kutner, 2005). In total, we fitted $15^2 = 225$ multi-infrastructure HSFs, which were also compared through AIC.

To quantify the impacts of infrastructure, for the most likely model we used eq. 2 of the main text and multiplied the magnitude of the impacts – the coefficients of the fitted model – by the influence measures included the model. We then estimated habitat suitability by predicting the HSF (eq. 1 in the main text) over the space and rescaling the predicted values to the interval [0, 1].

Results

Single-infrastructure HSF

We start by describing how much support the different influence measures presented in explaining reindeer habitat selection in the single-infrastructure models. By doing so, we aim at showing qualitatively what the different influence measures represent and how one would interpret them within an ecological context.

Private cottages

For private cottages, the most parsimonious HSF included the cumulative influence with Gaussian decay and ZoI = 10 km, but the support for the cumulative influence with the same ZoI of 10 km but other functions was also relatively high (low relative difference in AIC, Fig. C3A). Overall, the models including cumulative influence measures (regardless of the influence function and in great part of the ZoI) performed much better than the ones including the influence of the nearest private cottage (Fig. C3A), what shows a strong evidence that the impacts of multiple private cottages on reindeer habitat selection accumulate. The coefficients were consistently negative across ZoI values (Fig. C3B), which indicates the ZoI values with minimum AIC presented in the x axis of the Fig. C3A are also consistent.

We also go beyond the simple statistical variable selection and interpret the most parsimonious models considering the influence of the nearest feature. In this case, regardless of the influence function, the ZoI varies from 500 m to 1000 m (Fig. C3A). Combining the results, we can say that, if we consider the closest private cottage only, reindeer generally avoid being closer than 1 km from any cottage, but since many areas have a high density of cottages (Fig. C2, Table C1), they respond to the combined impact of individual cottages at a larger extent - a zone of influence of 10 km. This might also be related to how the cottages are used. Tourists who stay in a cottage hardly walk farther than a few kilometers from it, since they must return to the cottage in the end of the day. Then, the ZoI of a single cottage is shorter. However, in areas where many private cottages are clustered, there is a much wider area used by tourists and the ZoI of this combined cluster of cottages is higher.

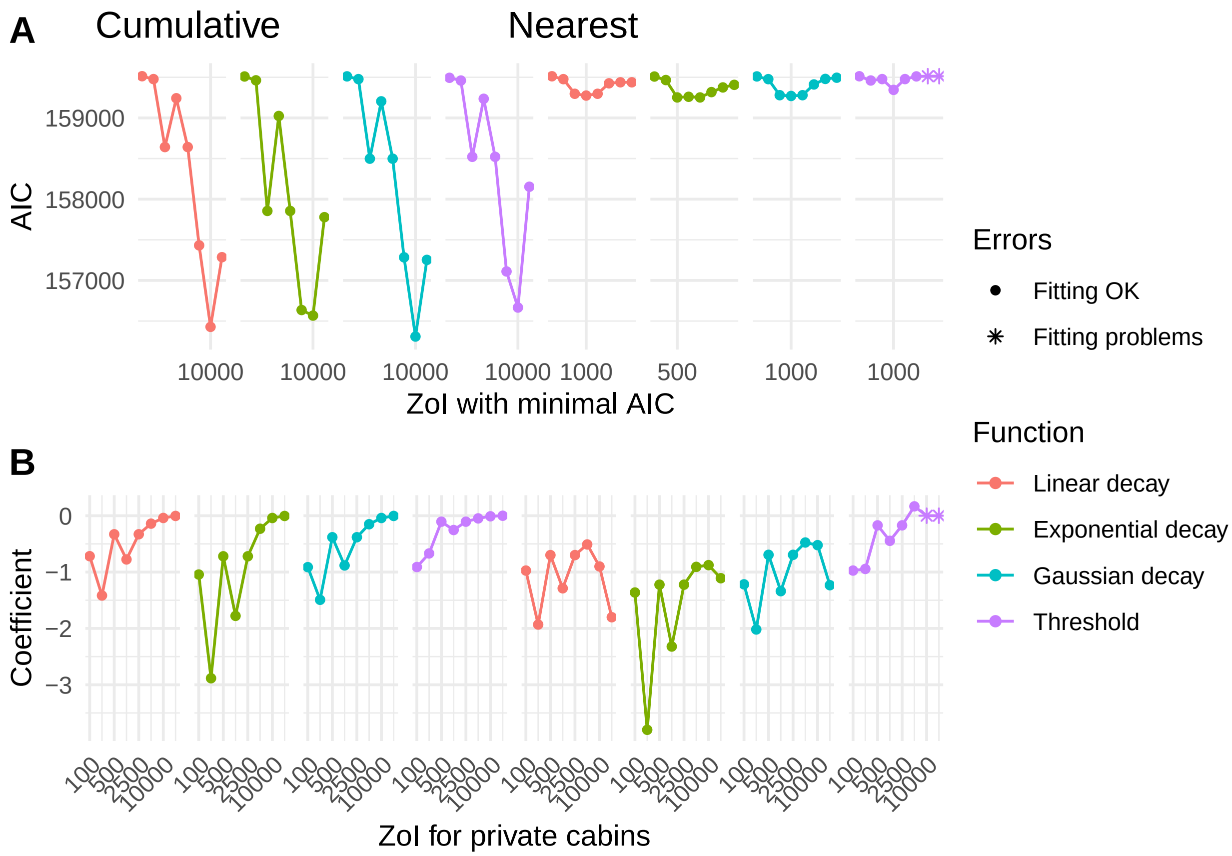

Figure C3: Model AIC (A) and coefficients (B) estimated for the influence of private cottages in models including only this type of infrastructure. The plots show the AIC and the coefficients (scaled back to the original range of the covariates) of the cumulative influence and influence of the nearest feature for different influence shapes and ZoI values (see the x axis in B for some of the candidate ZoI values, in meters, which varied from 100 m to 20 km). The x axis in A shows the ZoI at which the AIC was minimal for each type and function of the influence measure. Scales marked with '*' represent errors in the model fitting (e.g. threshold influnece of the nearest feature for ZoI = 10 km or 20 km, when the variable is constant = 1 over the whole study area).

Large tourist cabins

In the single-infrastructure models, there was also evidence of cumulative impacts of large tourist cabins with a 20 km zone of influence (Fig. C4). The most supported influence variable was the cumulative influence with exponential decay shape and ZoI of 20 km. This ZoI value was selected regardless of the influence function, and even for the influence of the nearest feature the most common ZoI was 20 km (see the x axis in Fig. C4A).

The closer correspondence between the selected ZoI of cumulative influence and nearest influence measures, in comparison to the private cottages, might be due to several factors. First, tourist cabins are present at a much lower density in Hardangervidda, with high median Euclidean distance to the closest cabin (Fig. C2 and Table C1). As a consequence, there is not so much difference between what the cumulative and nearest influences represent (as for the private cottages), since the influence function of each feature only start to accumulate for larger ZoIs. Therefore, the ZoI corresponding to smaller AIC is closer between models including cumulative and nearest influence measures. This is in accordance with the demonstrations from Appendix B, where we showed that, for landscapes with sparse distribution of features and small ZoI, $\phi_{nearest}$ and ϕ_{cum} are highly correlated. Second, large tourist cabins are used very differently by tourists than private cottages. Each cabin is visited by a large load of tourists at a time, which consequently use a much higher area around the cabins, compared to single private cottage. As a consequence, the ZoI of large tourist cabins tend to be higher.

As for private cottages, in the models with tourist cabins the coefficients were also consistently negative, representing reindeer avoidance to public tourist cabins.

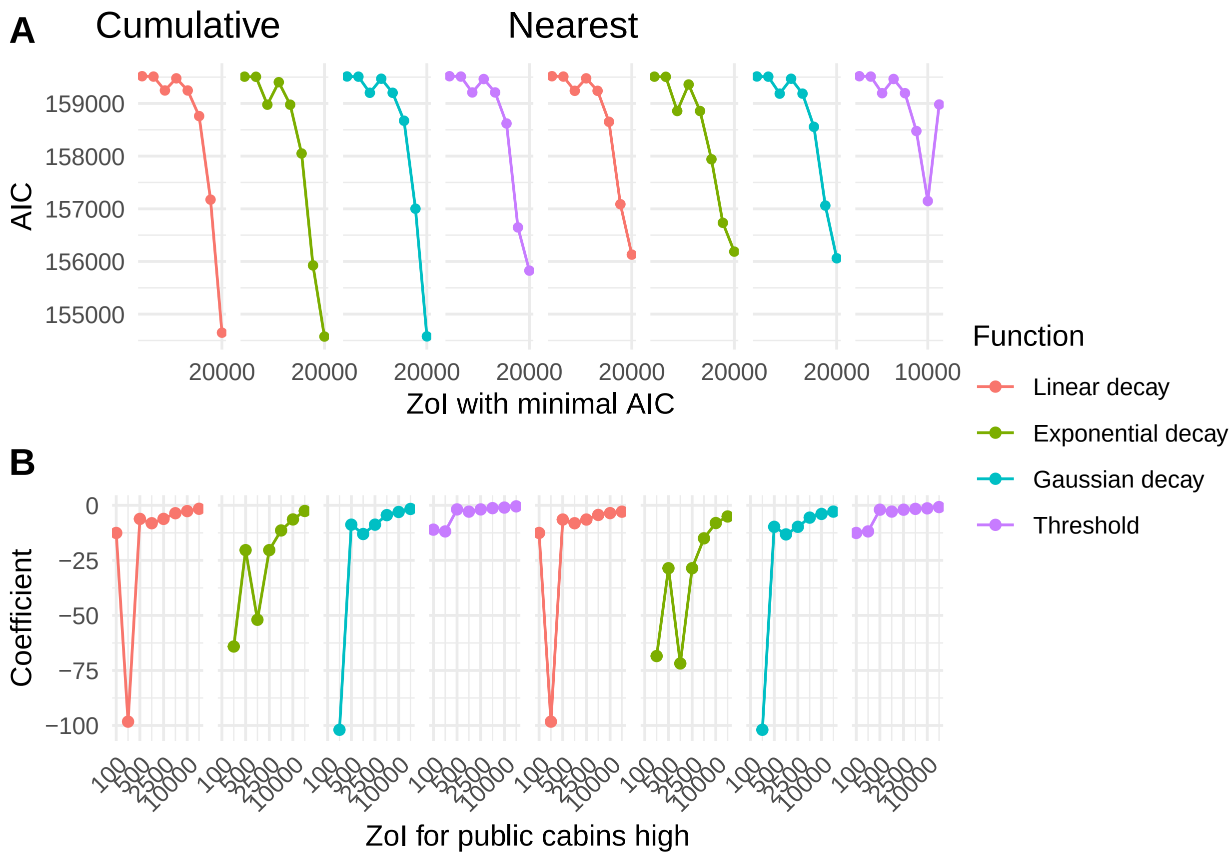

Figure C4: Model AIC (A) and coefficients (B) estimated for the influence of large tourist cabins in models including only this type of infrastructure. The plots show the AIC and the coefficients (scaled back to the original range of the covariates) of the cumulative influence and influence of the nearest feature for different influence shapes and ZoI values (see the x axis in B for some of the candidate ZoI values, in meters, which varied from 100 m to 20 km). The x axis in A shows the ZoI at which the AIC was minimal for each type and function of the influence measure.

Multi-infrastructure HSF

The most parsimonious multi-infrastructure model included the cumulative influence of private cottages with threshold decay and ZoI = 10 km and the cumulative influence of multiple tourist cabins with exponential decay and ZoI = 20 km ($\Delta AIC = 26.9$ from the second-ranked model, $wAIC = 1$; Table C2). Notice that, as parameterized here, for the tourist cabins an exponential decay with ZoI of 20 km means that the influence of cabins decrease to half of its maximum value at ca. 5 km from the infrastructure (exponential half life is ~ $ZoI/4$ here). The most plausible model with a covariate for the influence of the nearest feature was ranked 26$^{\text{th}}$ in the model selection ($\Delta AIC = 921$), and the most likely model including the log-distance to the nearest feature was ranked 44$^{\text{th}}$ ($\Delta AIC = 1197$; Table C2). This presents a strong support for the cumulative impacts of both private cottages and tourist cabins on reindeer habitat selection in Hardangervidda.

Table C2: Infrastructure variables included in the most parsimonious models. For each model we show the type of influence ("cumulative", "nearest"), the influence function ("exponential decay", "gaussian decay", "threshold", "Bartlett or linear decay"), and the ZoI (in km) for that covariate included in the model. For each model we also present the AIC, the difference in AIC to the most likely model (dAIC), and the AIC weight. The last lines show the most plausible model which included any variable with the influence of the nearest feature and the log-distance to the nearest feature (in this case, for tourist cabins). Models also included bio-climatic variables and land cover (see Table C3).

Rank	Private cottages	Large tourist cabins	AIC	dAIC	wAIC
1	cumulative, threshold, 10	cumulative, exp decay, 20	152167	0	1
2	cumulative, exp decay, 10	cumulative, exp decay, 20	152194	26.9	<0.001
3	cumulative, Gauss, 10	cumulative, exp decay, 20	152212	45.7	<0.001
4	cumulative, exp decay, 20	cumulative, exp decay, 20	152247	80.1	<0.001
5	cumulative, Gauss, 20	cumulative, exp decay, 20	152280	112.7	<0.001
26	cumulative, Gauss, 20	nearest, bartlett, 20	153088	921.3	<0.001
44	cumulative, exp decay, 10	nearest, log nearest, NA	153364	1197.4	<0.001

Looking closely to the most plausible multi-infrastructure HSF (after rescaling the coefficients back to the original range of variation of the infrastructure influence predictors), we see both infrastructure are avoided by reindeer. Their influence vary differently across space since their influence functions and ZoI differ – a threshold function with 10 km ZoI for private cottages and an exponential decay with 20 km ZoI for tourist cabins –, but also because the estimated magnitude of the impact of a single private cottage ($\beta_{\text{private cottage}} = -0.0081$) was much smaller than that of a single tourist cabin ($\beta_{\text{tourist cabin}} = -2.654$; Table C3, Fig. C6A). However, since private cottages occur at much higher densities, in some areas their overall impact is higher than that of tourist cabins (Fig. C6, Fig. 4 in the main text). Comparing an area with only 1 cottage in a 10 km radius with an area with only 1 tourist cabins in a 20 km radius, and assuming all other conditions are similar, the impact – measured here as the product between the magnitude of the impact and the influence covariate (eq. 4 from the main text) – is much smaller for private cottages (Fig. C6A). In contrast, if we take the areas with higher influence in Hardangervidda – where the number of private cottages sum to 2664 and the (exponentially weighted) number of tourist cabins sum to 5 – the impact of private cottages agglomerates is higher than that of tourist cabins (Fig. C6C). Following the HSF coefficient interpretation from Fieberg et al. (2021), and considering that all other conditions are kept similar, a reindeer avoids an area 14.43 ($exp(330 \cdot 0.0081) = 14.43$) times more strongly than another area with 330 less private cottages in a radius of 10 km. That is approximately the same difference in avoidance a reindeer presents among two areas that differ in 1 tourist cabin in a radius of 20 km ($exp(1 \cdot 2.654) = 14.21$).

Table C3: Magnitude of the impact (model coefficients) of the most parsimonious model of space use for reindeer, including private cottages and tourist cabins. The table show the coefficient estimates (scaled back to the scale of variation of the original data), their standard error (SE, in the standardized scale of the variables), and the significance (p). "pc" are the bio-climatic principal components and "poly" are the coefficients of a quadratic function of pc.

Covariate	Estimate	SE	p
(Intercept)	-15.3081	0.16	< 0.0001
private cottages (cumulative, threshold, 10km)	-0.0081	0.13	< 0.0001
tourist cabins (cumulative, exponential, 20km)	-2.65438	0.04	< 0.0001
exposed ridges	0.20948	0.14	0.1343
grass ridges	0.99185	0.13	< 0.0001
heather ridges	0.99219	0.13	< 0.0001
lichen	1.22547	0.17	< 0.0001
heather	1.04047	0.13	< 0.0001
heathland	0.93174	0.13	< 0.0001
meadows	0.97105	0.15	< 0.0001
early snowbed	0.61526	0.13	< 0.0001
late snowbed	0.43487	0.13	0.0012
bog	0.97646	0.15	< 0.0001
glacier	-0.43692	0.32	0.1732
other	-3.07193	37.62	0.9349
water	-1.6334	0.2	< 0.0001
poly(pc1, 2)1	323.5927	10.23	< 0.0001
poly(pc1, 2)2	-253.8435	10.81	< 0.0001
poly(pc2, 2)1	-611.40893	38.54	< 0.0001
poly(pc2, 2)2	-204.9332	22.97	< 0.0001
pc3	27.73861	23.91	0.246
pc4	-77.24946	24.02	0.0013

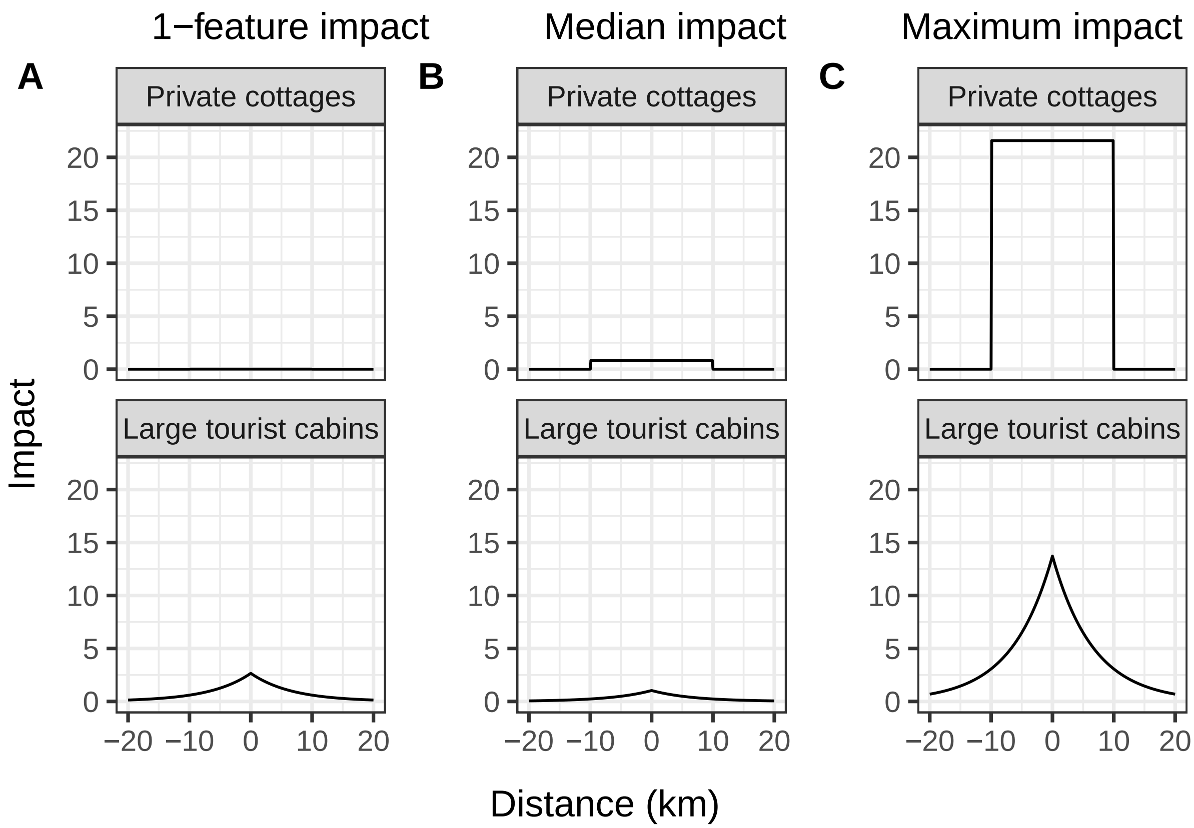

Figure C5: Impact of private cottages and tourist cabins considering (A) only 1 feature, (B) the median number of features (103 for private cottages, 0.38 for tourist cabins), and (C) the maximum number of each type of feature (2664 for cottages, 5 for cabins), given their respective influence functions and ZoI. The impact presented here is the multiplication between the magnitude of the impact (the model coefficients) and the cumulative influence variable (eq. 4 in the main text). The impact of only one private cottage is negligible (A). At their median values, the impacts of private and public cabins are comparable (B), while at their maximum the cumulative impact of private cottages might be higher than that of tourist cabins (C).

When cumulative impacts of infrastructure are predicted in space by multiplying the magnitude of the impacts by the cumulative influence measures, we see how the relative impact of private cottages and large tourist cabins change across space (see Fig. 4 in the main text). Since reindeer avoided high densities of both infrastructure types at relatively large extents, areas of high habitat suitability for reindeer correspond to those in which the cumulative influence of both infrastructure is low – what matches with the locations used by reindeer, indicated through the GPS data.

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