RESEARCH ARTICLE

Learning from the past to predict the future: using archaeological findings and GPS data to quantify reindeer sensitivity to anthropogenic disturbance in Norway

**Manuela Panzacchi · Bram Van Moorter ·
Per Jordhøy · Olav Strand**

Abstract Norwegian wild reindeer *Rangifer tarandus tarandus* are divided into 23 virtually isolated populations, primarily due to the abandonment of traditional migration and movement corridors caused by the development of infrastructures. By conducting a nation-wide, interdisciplinary pre-post study on a temporal scale spanning centuries, we modelled current reindeer movements with respect to archaeological findings to quantify long-term changes in area use related to anthropogenic disturbance. The location of 3,113 pitfall traps and hunting blinds, built 600–2000 years ago and used until 350–400 years ago, testified the location of traditional movement corridors. Current movement routes were delineated using Brownian Bridge Movement Models based on 147 reindeer GPS-monitored during 10 years. Using Path Analysis we quantified direct, indirect and total effects of different infrastructures within multiple scales (1, 5, and 10 km-radius buffers) on the current probability of use of ancient movement corridors. Tourist cabins and roads had the strongest long-term direct effects at most scales: 1 tourist cabin and 1 km

road within a 1 km-radius buffer would lead, respectively, to complete area abandonment, and to a 46 % decrease in the probability of use. Power lines and private cabins had significant indirect effects on area use through their effect on roads, while hiking trails and, in particular, hydroelectric dams had highly variable effects, not significant at a nation-wide scale. Finally, we provide a flexible tool to estimate the potential long-term direct and cumulative effects of different types of infrastructures at the desired spatial scale to be used for the development of future sustainable land management plans.

Introduction

In a world inhabited by 7 billion people and in which the development of infrastructures is closely tracking population growth, understanding the impact of human activities on wildlife is of paramount importance for the conservation and management of landscapes and biodiversity. Notwithstanding the rapidly increasing amount of studies on the effects of anthropogenic disturbance, a comprehensive approach to quantify wild species' spatial responses to different types of infrastructures has not yet been developed. Research focus has shifted from early

M. Panzacchi (✉) · B. Van Moorter ·
P. Jordhøy · O. Strand
Norwegian Institute for Nature Research, Tungasletta-2,
7485 Trondheim, Norway
e-mail: manuela.panzacchi@nina.no

studies documenting short-term behavioural or physiological reactions towards more comprehensive long-term approaches investigating the species' changes in space use at the landscape scale (Underhill and Angold 2000), ultimately aiming at linking individual responses to population processes (Mallord et al. 2007; Sorensen et al. 2008; Gaillard et al. 2010). The most recent studies investigate disturbance effects by measuring to which extent anthropogenic factors influence habitat selection (Johnson et al. 2005; Aarts et al. 2008; Polfus et al. 2011). However, in heavily human-dominated environments barriers and constraints to movements can limit animals' accessibility to preferred habitat, thus biasing the estimation of the degree of avoidance of infrastructures using habitat selection studies (Van Horne 1983; Gill et al. 2001; Panzacchi et al. 2012). More robust results can be derived from pre-post development studies, where the species' response is measured before and after the development (Joly et al. 2006) or the removal of a given infrastructure (Nellemann et al. 2010). However, such approach is virtually always adopted in case-specific studies, and therefore the conclusions cannot be easily extrapolated to different environmental settings. To overcome the above-mentioned weaknesses we suggest using a pre-post development approach on a spatial and temporal scale wide enough to allow detecting in a probabilistic way major changes in the species' spatial behaviour imputable to the development of infrastructures. In other words, we suggest digging into the past to understand the present and aid the development of future sustainable land management plans. We adopted such approach to quantify the impact of the development of infrastructures on the use of traditional migration corridors by Norwegian wild mountain reindeer, the last remaining population in Europe.

Norwegian wild reindeer were historically grouped into two–three large populations undertaking a seemingly complex network of seasonal migrations along traditional movement corridors connecting adjacent mountain systems (Skogland 1986). Reindeer live in large herds (up to thousands of animals) moving across Norwegian mountains, and are well known for their tendency to avoid humans and human infrastructures (e.g. Vistnes and Nellemann 2008). Largely due to the development of infrastructures during the industrial revolution, reindeer abandoned several of the traditional migration routes, and are now divided into more than 20 sub-populations, which still occupy the original distribution range, but which are virtually isolated from each other; available data suggests that the fragmentation process is still ongoing (e.g. Strand et al. 2010, Panzacchi et al. 2012). Evidence for negative effects of transportation and other infrastructures on *Rangifer* space use has been provided in numerous cases (Skogland 1986; Nellemann et al. 2000, 2001; Vistnes et al. 2004; Vors and Boyce 2009; Polfus et al. 2011), but the quantification of such effects has been as sought-after as controversial. The results vary remarkably from avoidance of infrastructures to no-effects due to a combination of different ecological conditions among populations and inconsistencies in methodological approaches and scale of investigation among studies (reviewed by Vistnes and Nellemann 2008). Indeed, herds may differ in their local responses to disturbance depending on their population density, habitat availability, on their degree of wildness, or on the strength of the motivation to use a given area, and the quantification of the effect of infrastructures may vary with the wide range of methodologies adopted, ranging from aerial or ground surveys, to pellet counts, telemetry data, or proxies of deer abundances such as lichen measurements (Reimers and Colman 2003). Even the most advanced approaches such as resource selection functions or niche factor analyses based on telemetry data are limited in their ability to quantify the effect of different types of infrastructures due to the issues of spatial collinearity among anthropogenic disturbance factors (Rhodes et al. 2009), or to the influence of natural or artificial barriers on habitat availability (Gill et al. 2001; Matthiopoulos 2003; Polfus et al. 2011).
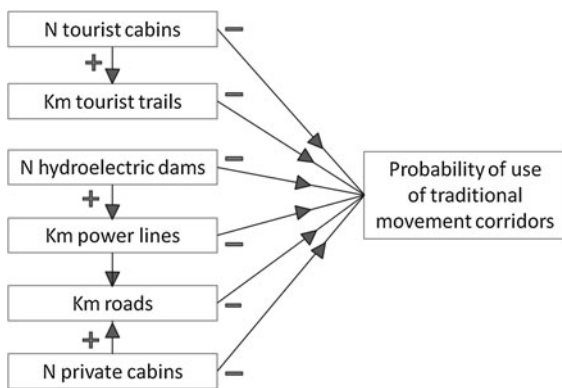
We adopted a nation-wide pre-post development approach on a temporal scale spanning centuries to quantify changes in the probability of use of traditional movement corridors, after the development of infrastructures. During the Viking Period and early Middle Age reindeer have been hunted using large-scale pitfalls, systems of fences which led animals into traps or lakes, and caches of stone to hide archers. About 8,000 remains of such trapping systems have been found across the reindeer distribution range in south Norway and testify the location of important traditional movement corridors for large numbers of animals. By comparing such historical data with data from 147 GPS-monitored reindeer inhabiting the largest remaining populations, we had the unique

opportunity to relate changes in the probability of use of traditional movement corridors to the development of infrastructures, which occurred in Norway mostly during the past 100 years (UNEP 2011). In particular, we tested for the hypothesis that the probability that GPS-monitored reindeer still use traditional movement corridors is negatively affected by the type and amount of infrastructures that have been built in the surrounding areas largely during the industrial revolution. As different types of anthropogenic infrastructures tend to be spatially correlated, we also aimed at disentangling their potentially correlated effects by quantifying direct and indirect effects of each type of infrastructure on the long-term probability of area use by reindeer, as illustrated in Fig. 1.

Methods

Study area

Norwegian wild mountain reindeer inhabit the mountain areas of southern Norway (5–12°E, 58–63°N), and are now divided into 23 more or less isolated sub-populations ranging from ca. 50 to ca. 8,000 individuals each, for a total of ca 35,000 reindeer. We studied six of the largest populations,

divided in different wild reindeer management areas called: Snøhetta, Rondane North, Nordfjella, Hardangervidda, Setesdal Austhei, Setesdal Ryfylke (Fig. 2). The areas span a wide range of environmental characteristics, but for the most part are located above the tree line, and are influenced by a pronounced east–west gradient, with the western part subjected to oceanic climatic influences characterized by abundant rain and snow precipitation, and the eastern part experiencing continental climatic influences (Bakkestuen et al. 2008). Traditional reindeer migrations occurred, and still partly occur, between more continental areas in winter and the more oceanic areas in summer. During the last 100 years Norwegian mountains have been increasingly altered by human activities known to have a potential impact on reindeer space use (Vistnes and Nellemann, for a review): within the study area (35,995 km^2) lay 188 hydroelectric dams, 9070 km of power lines, 10635 km roads, 7850 km of tourist trails, 299 tourist cabins, and 42,925 private cabins.

Historic data: pitfalls and hunting blinds

In addition to spears, bows and arrows, reindeer have been hunted in a variety of ways down the ages, not least using pitfalls and systems of fences positioned along migration or movement corridors which led the animals into traps, off precipices, or into lakes and rivers (Blehr 1987). During the course of 20 years we found and collected the location of 7,733 archaeological findings related to hunting and trapping infrastructure of large herbivores in the mountains of Southern Norway (Fig. 3). Each finding was mapped using GPS, and a standard procedure was used to record relevant parameters among which the type (pitfall traps, hunting blinds, meat storage places, burials etc.) and their targeted species (e.g. reindeer, moose *Alces alces*, red deer *Cervus elaphus*). Carbon-dating analyses on a few pitfall traps indicated that these were built between ca. 600 and 2000 years ago, and it has been estimated that some of these structures have been in use, during snow free periods, along migration or movement corridors until about 350–400 years ago. For detailed information on sub-samples of these data see Jordhøy and al (2005) and Jordhøy (2008). For our analyses we selected those pitfalls traps and hunting blinds (n = 3,113) used for reindeer or reindeer and moose which fell within the
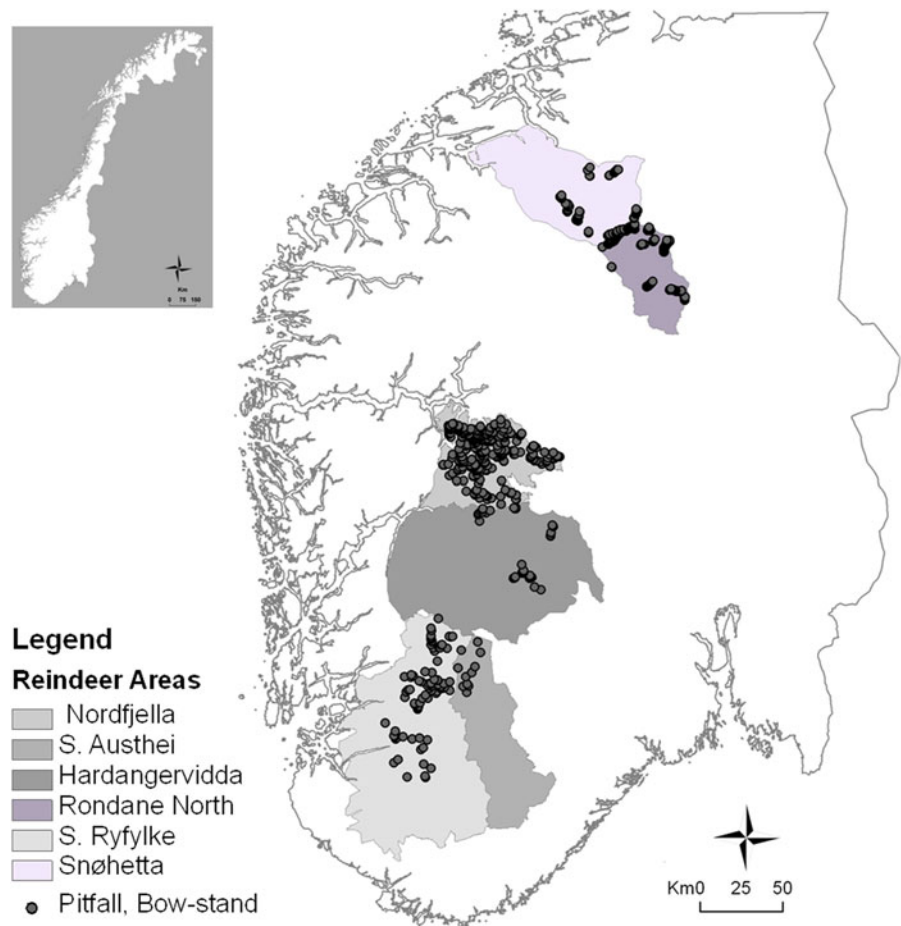

Fig. 1 Hypotheses tested: the probability that GPS monitored reindeer still use traditional movement corridors (i.e. the area within a buffer of 1, 5 or 10 km surrounding each pitfall trap and hunting blind) is negatively affected by the type and amount of infrastructures that have been built in the same area. As the presence of some infrastructures (e.g. tourist cabins) positively affects the presence of other infrastructures (e.g. tourist trails), we quantified both direct and indirect effects of infrastructures on the probability of use of ancient migration corridors

Fig. 2 Location of the six wild reindeer areas in which we have GPS-monitored reindeer in Southern Norway, and location of the pitfall traps and hunting blinds within those areas

Legend
Reindeer Areas
- Nordfjella
- S. Austhei
- Hardangervidda
- Rondane North
- S. Ryfylke
- Snøhetta
- Pitfall, Bow-stand

Fig. 3 Typical pitfall with stone walls designed for reindeer trapping in the Dovre mountain range, Norway. The *rows* of stone fences radiating from the pitfall were intended to direct the reindeer towards the trap. The pitfall surface was covered with thin branches and natural vegetation (*Photo* Per Jordhøy)

boundaries of the 6 reindeer areas for which we have GPS telemetry data indicating the present space use of reindeer.

Reindeer GPS data

Starting from 2001, 147 female reindeer were immobilized from helicopter, anesthetized using a mix of Salopine and Ketalar, equipped with animal-borne GPS devices with drop-off systems, and awakened using the antidote Narketan. For each individual we selected 1 GPS location every 3 h during the period July 1st–October 15th, as this was the period when the pitfall traps and hunting blinds were in use due to lack of snow-covered ground. A few animals had to be removed from the analyses due to lack of data in the specified period, and the final dataset was composed of 112 reindeer: 14 in Setesdal Ryfylke (study period 2006–2010), 9 in Setesdal Austhei (2007–2010), 45 in Hardangervidda (2001–2010), 17 in Nordfjella (2007–2010), 18 in Snøhetta (2009–2010) and 9 in Rondane North (2009–2010). Outlying locations were identified and removed using the script provided in Bjørneraas et al. (2010). Data processing and all

analyses were performed using the software R.11.1 (2010).

Analyses

We tested for the effect of different types of infrastructure on the probability of present use, P(use), of ancient movement corridors by reindeer by: (1) identifying areas currently used by reindeer; (2) classifying each pitfall trap or hunting blind as "located/not located in an area currently used by reindeer"; (3) constructing multi-scale buffers around each pitfall trap or hunting blind and quantifying infrastructures within each buffer; (4) investigating the relationship between P(use) and the presence of infrastructures within each buffer.

To identify areas currently used/not used by reindeer, for each individual and each year we built a Brownian bridge movement model (BBMM, Horne et al. 2007) using the function *kernelbb* in the R package *AdehabitatHR* (Calenge 2006). The BBMM estimates the utilization distribution of an animal using the Brownian Bridge approach of the kernel method for autocorrelated relocations. Hence, this approach allows calculating P(use) along the movement route of a given individual by accounting for location errors and for the uncertainty of the movement trajectory (Sawyer et al. 2009). The BBMM is dependent on time-specific location data, the distribution of location errors σ_2^2 and the Brownian motion variance parameter σ_1^2; following Horne et al. (2007) we assumed a σ_2^2 of 25, and we used an optimization procedure to estimate the maximum likelihood estimation of the parameter σ_1^2 using the function *Liker* (Calenge 2006). The large amount of individuals with GPS collars and years, together with the strong herding behaviour of reindeer, scientific studies (e.g. Skogland, 1986) and local information from reindeer managers, ensure that the results are representative of the species' present space use. By intersecting the 99 % contours of the BBMM with the layers representing pitfalls and hunting blinds using ArcMap, we classified each historic hunting structure as "located in areas still used" or "no-longer used by reindeer". This is the binary dependent variable we explained using: the length of roads, of the major

power lines, and of the major hiking trails from the Norwegian Trekking Association (DNT 2012), and the number of Norwegian Tourist Cabins (DNT 2012) private cabins, and hydroelectric dams. These variables were calculated within buffers of 1, 5, and 10 km radius built around each ancient hunting structure. Due to spatial dependency among some anthropogenic infrastructures, we tested for both direct and indirect effects of each type of infrastructure on P(use) of ancient movement corridors by using path analysis (Meyers et al. 2006), which is a special case of structural equation modelling allowing to examine the directed dependencies among a set of variables. Path analysis is often referred to as "causal modelling" as it allows to quantify hypothetical causal links (represented by arrows generating a path) among variables. In Fig. 1 we illustrate the path of causal relationships assumed in our model: the number of tourist cabins is assumed to have both a direct, negative effect on P(use), and a negative indirect effect on P(use) through a positive effect on the abundance of tourist trails, which depart from each cabin. Similarly, hydroelectric dams are expected to influence P(use) directly and indirectly through the network of power lines radiating from them, and through the roads required to grant access to power lines and dams, as well as to private cabins. Among the different approaches for the parameterization of paths (Meyers et al. 2006) we chose ordinary regression analysis, which uses one multiple regression equation for each endogenous variable (i.e. each variable for which we expect a causal relationship, or where an arrow arrives—Fig. 1); hence, each endogenous variable would be the dependent variable in a separate regression. The resulting slopes can be used as path coefficients to calculate direct, indirect and total effects of each variable on P(use) (Meyers et al. 2006). Given a variable A, which has both a direct effect on C but also an indirect effect on C through its effect on B, the path would be: $A \rightarrow C$, $B \rightarrow C$ and $A \rightarrow B$. The direct effect of A on C is the beta coefficient β_1 from the regression:

$$C = \beta_0 + \beta_1 \times A + \beta_2 \times B + \varepsilon \qquad (1)$$

The indirect effect of A on C is obtained by multiplying the effect of A on B (β_3 from Eq. 2) by the effect of B on C (β_2 from eq. 1):

$$B = \beta_0 + \beta_3 \times A + \varepsilon \qquad (2)$$

Thus, the total effect of A on C is the sum of its direct and indirect effects:

$$\text{Total effect of } A = \beta_1 + \beta_2 \times \beta_3 \qquad (3)$$

While the 95 % confidence interval, CI, for the direct effects are the CI of the corresponding β coefficients, for the indirect effects we used a normal approximation as described by MacKinnon et al. (2007), implemented in the *RMediation* package for R (Tofighi and MacKinnon 2011). Using regression coefficients we calculated the percentage decrease in P(use) related to the presence of infrastructures (Table 1) as:

$$\text{Decrease in P(use)} = -(1 - \exp(\beta)) \times 100 \qquad (4)$$

Note that the variable unit (Table 1) may not be very meaningful at each given spatial scale (for example, a manager might want to know the effect of the construction of 10 km of road in a 10 km radius buffer); however, by using the flowing formula the reader can easily calculate the percentage decrease in P(use) by using the desired and most meaningful unit in his own study context:

$$\text{Decrease in P(use)} = -(1 - \exp(\beta \times n)) \times 100 \qquad (5)$$

where n is a multiple of the variable unit indicated in Table 1. It is also possible to calculate the percentage decrease in P(use) due to the cumulative effect of two (or more) different types of infrastructures by summing up their direct effects using the formula:

$$\text{Decrease in P(use)} = -\big(1 - \exp\big((\beta_D \times n) + (\beta_E \times n)\big)\big) \times 100 \qquad (6)$$

where β_D and β_E are the beta coefficients of the direct effects of the infrastructures D and E. As large trapping systems were often built in key movement corridors, the locations of pitfall traps and hunting blinds are highly spatially autocorrelated (Fig. 4, Fig. A1). To avoid pseudoreplication and spatial autocorrelation, we built a grid with 10×10 km cells and extracted randomly 1 pitfall or hunting blind per cell (i.e. we removed all but one pitfall per square); each analysis was performed adopting a 1,000 times bootstrapping procedure on such subsamples.

Results

Movement model

The BBMM well described reindeer movement data and allowed us to obtain a close representation of the area actually used by each reindeer along its trajectory. The Brownian motion variance σ_1^2, which is the parameter controls the width of the bridge connecting successive relocations (the larger this values, the larger the bridge), was 8.7 m^2 (SE = 0.2). By overlaying the 99 % contours of the BBMM we obtained a close representation of the area actually used by each reindeer along its trajectory, and to label each ancient hunting structure as "located in areas still used by reindeer" ($n = 606$) or as "located in areas no longer used" ($n = 4185$; see Fig. 4 for details, and Fig A1 in Appendix for a nation-wide overview).

Effect of infrastructures on the probability of area use by reindeer

Hereafter, we present the results of the path analysis, which we used to investigate direct and indirect relationships between the present probability of reindeer use of areas surrounding ancient hunting structures and the type and amount of infrastructure built therein. In particular, in Table 2 we present the parameters of all the expected direct relationships illustrated in Fig. 1; to ease the reading of Table 2, we also visualize all significant results in Fig. 5, in a format mirroring the hypotheses presented in Fig. 1. In Table 1 we provide the direct, indirect and total effects of each variable on P(use). In the following we briefly summarize the main results for the units chosen by the authors, and we also illustrate examples of how the reader can recalculate the results using their own preferred units or by calculating the cumulative effect of different types of infrastructures, using Eqs. 1–6.

The most striking results (Fig. 5) is that at the smallest scale (1 km radius buffer) tourist cabins have a strong direct negative effect on reindeer P(use) of traditional movement corridors, as the presence of only 1 cabin is responsible for the complete area abandonment, i.e. 100 % decrease in P(use) (Table 1). The presence of tourist cabins is highly significant also at the largest scale (10 km), 1 cabin being responsible for a 34 % decrease in P(use). However, at such large

Table 1 Parameter estimates (with lower and upper CI; * = p < 0.05) for the direct (Dir.), indirect (Indir.) and total (Tot) effects of each disturbance variable (within 1, 5, and 10 km-radius buffers built around each historic hunting structure) on the current probability of use of traditional movement corridors

Variable	Unit	Effect	1-km radius buffer				5 km-radius buffer			
			Estim.	Upper and lower CI		P(use) (%)	Estim.	Upper and lower CI		P(use) (%)
Roads	1 km	Dir.	−0.61	−11.85	−0.08*	−46	−0.07	−0.13	−0.03*	−7
		Tot	−0.61	−11.85	−0.08*	−46	−0.07	−0.13	−0.03*	−7
Power lines	1 km	Dir.	−0.49	−81.93	0.17	−39	0.00	−0.05	0.04	0
		Indir.	−0.49	−5.47	4.38	−39	−0.06	−0.11	−0.02*	−6
		Tot	−0.99	−87.40	4.55	−63	−0.06	−0.16	0.03	−6
Trails	1 km	Dir.	−0.02	−0.40	0.29	−2	−0.01	−0.07	0.03	−1
		Tot	−0.02	−0.40	0.29	−2	−0.01	−0.07	0.03	−1
Tourist cabins	n = 1	Dir.	−17.66	−32.82	−15.36*	−100	−0.38	−1.54	0.46	−32
		Indir.	−0.05	−0.80	0.69	−5	−0.08	−0.38	0.19	−7
		Tot	−17.71	−33.62	−14.67*	−100	−0.46	−1.91	0.65	−37
Private cabins	n = 10	Dir.	0.56	−1.75	2.83	76	0.00	−0.08	0.06	0
		Indir.	−0.30	−3.71	2.91	−26	−0.04	−0.07	−0.01*	−4
		Tot	0.26	−5.46	5.75	30	0.04	−0.15	0.05	−4
Dams	n = 1	Dir.	0.29	−0.99	1.31	34	0.30	−0.13	0.69	35
		Indir.	0.03	−12.12	12.28	3	−0.12	−0.40	0.10	−11
		Tot	0.32	−13.11	13.59	38	0.18	−0.53	0.79	19

Variable	Unit	Effect	10 km-radius buffer			
			Estim.	Upper and lower CI		P(use) (%)
Roads	1 km	Dir.	−0.03	−0.05	−0.02*	−3
		Tot	−0.03	−0.05	−0.02*	−3
Power lines	1 km	Dir.	0.01	−0.01	0.03	1
		Indir.	−0.03	−0.04	−0.01*	−3
		Tot	−0.02	−0.05	0.02	−2
Trails	1 km	Dir.	0.00	−0.01	0.01	0
		Tot	0.00	−0.01	0.01	0
Tourist cabins	n = 1	Dir.	−0.41	−0.81	−0.13*	−34
		Indir.	−0.01	−0.10	0.08	−1
		Tot	−0.42	−0.91	−0.05*	−34
Private cabins	n = 10	Dir.	0.00	−0.02	0.02	0
		Indir.	−0.02	−0.04	−0.01*	−2
		Tot	−0.02	−0.05	0.01	−2
Dams	n = 1	Dir.	0.00	−0.19	0.19	0
		Indir.	−0.03	−0.12	0.06	−3
		Tot	−0.03	−0.30	0.25	−3

For each variable the reader can calculate the percentage P(use) using the desired unit (e.g. 10 km roads instead of 1) using the formula—$(1 − \exp(\text{parameter estimate} \times n)) \times 100$, where n is a multiple of the variable unit (see Methods Sect.). In addition, it is possible to calculate the additive value of different variables (e.g. roads + power lines): the estimate and the CI of the new variable would be given by the sum of their respective parameter estimates and CI for the direct effects, and its P(use) would be calculated as described above

Fig. 4 Illustration of the approach to determine whether ancient movement corridors are still currently used by reindeer. Pitfall traps and hunting blinds are still in use if they fall within the contours of the outputs of the 99 % BBMMs calculated for each GPS monitored reindeer during the period July-mid October. For graphical reasons, we present here only two study areas (Snøhetta *left*; Rondane *right*), but a full overview of all areas is presented in the online Appendix I. Note the line of no longer used pitfalls between the two areas, close to a highway and a railway
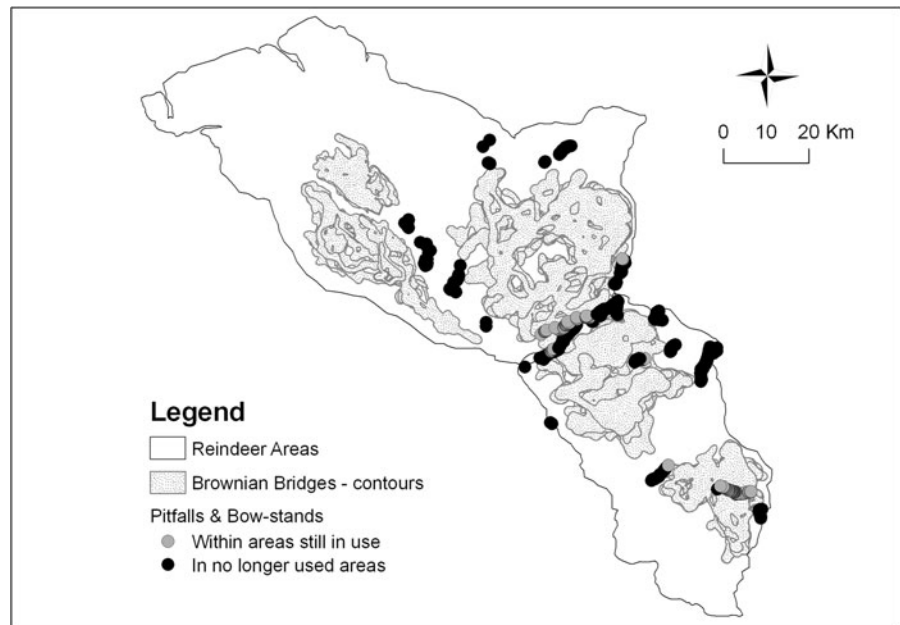
scale it might be more useful to calculate the effect of, for example, 2 tourist cabins, and this could be easily done using Eq. 5: while the effect of 1 cabin is—$(1 - \exp(-0.42)) = -35$ %, the effect of 2 cabins would be—$(1 - \exp(-0.42 \times 2)) = -57$ %. The presence of roads is highly significant at all investigated spatial scales: the presence of 1 km of road within a 1 km-radius buffer would decrease P(use) of 46 % while, for example, 10 km of roads within a 10 km buffer radius would decrease P(use) of 25 %. Using Eq. 6 the reader can also calculate cumulative effects of infrastructures; for example, 1 tourist cabin and 10 km road within a 10 km buffer would decrease P(use) of 51 %. While the effect of roads and tourist cabins is direct, power lines and private cabins have indirect effects on P(use)—through their effect on roads—at 5 and 10 km spatial scales; at the smallest scales their effect is extremely variable and, hence, it is not significant. A high range in CI was also detected at all spatial scales for hiking trails and dams which, as a consequence, had no overall significant effect on P(use) of ancient movement corridors.

Discussion

We had the unique opportunity to conduct a nation-wide pre-post study on a temporal scale spanning

centuries to test for the hypothesis that the development of human infrastructures, which occurred mostly during the industrial revolution, caused a reduction in reindeer probability of use of traditional movement corridors. In addition, as reindeer follow well-established traditional migration and movement corridors (Harris et al. 2009), and the only major change that occurred in Norwegian mountain ecosystems has been the construction of roads, trails, power lines, cabins and dams, we were able to quantify the direct and indirect effect of each type of infrastructure on the probability of area use by reindeer.

In support of our hypotheses (Fig. 1), four out of the six infrastructures investigated had a significant negative effect, either direct or indirect, on reindeer use of traditional movement corridors. The main patterns were consistent across scales, although at increasingly larger buffers the effect sizes decreased, while the precision of the estimate improved due to the reduction of the noise associated to local ecological settings. The most striking effect was caused by tourist cabins, as the presence of one cabin within a 1 km radius led to a 100 % probability of abandonment of the movement corridor. In the study areas lay 299 tourist cabins connected by a network of 7,850 km of marked trails; most cabins have lodgings and can host up to a hundred guests, while others are popular eating places or rest-stops. Although a negative impact of tourist
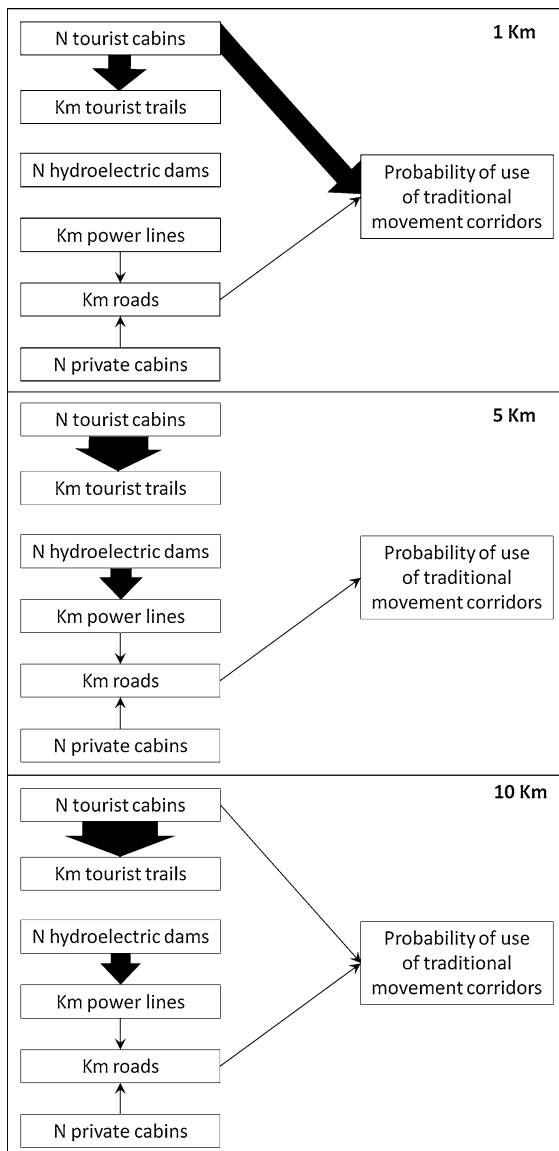
Table 2 Beta coefficients, SD, CI and *p* value for all direct relationships tested in Fig. 1

Scale	Dependent variable	Independent variable	Beta	SD	*p*	Lower CI	Upper CI
1 km	P(use)	Roads	−0.611	10.494	0.015	−11.846	−0.079
	P(use)	Power lines	−0.495	24.122	0.076	−81.928	0.168
	P(use)	Tourist trails	−0.024	0.177	0.439	−0.399	0.287
	P(use)	Tourist cabins	−17.659	5.548	0.000	−32.819	−15.363
	P(use)	Private cabins	0.564	1.193	0.085	−1.751	2.835
	P(use)	Dams	0.294	0.569	0.275	−0.988	1.310
	Power lines	Dams	−0.030	0.238	0.444	−0.438	0.487
	Roads	Power lines	0.805	0.159	0.000	0.458	1.104
	Roads	Private cabins	0.497	0.172	0.000	0.373	1.122
	Tourist trails	Tourist cabins	2.066	0.510	0.001	1.075	3.004
5 km	P(use)	Roads	−0.070	0.025	0.000	−0.128	−0.028
	P(use)	Power lines	−0.001	0.023	0.488	−0.047	0.043
	P(use)	Tourist trails	−0.015	0.025	0.271	−0.067	0.033
	P(use)	Tourist cabins	−0.384	0.524	0.204	−1.535	0.455
	P(use)	Private cabins	0.000	0.039	0.497	−0.083	0.059
	P(use)	Dams	0.297	0.202	0.077	−0.130	0.687
	Power lines	Dams	2.004	0.886	0.020	0.115	3.596
	Roads	Power lines	0.855	0.156	0.000	0.516	1.137
	Roads	Private cabins	0.521	0.080	0.000	0.380	0.692
	Tourist trails	Tourist cabins	5.158	1.651	0.000	3.398	9.711
10 km	P(use)	Roads	−0.029	0.008	0.000	−0.047	−0.017
	P(use)	Power lines	0.011	0.009	0.121	−0.007	0.029
	P(use)	Tourist trails	−0.001	0.007	0.416	−0.015	0.011
	P(use)	Tourist cabins	−0.410	0.168	0.004	−0.806	−0.130
	P(use)	Private cabins	0.004	0.010	0.305	−0.017	0.021
	P(use)	Dams	−0.004	0.095	0.481	−0.186	0.190
	Power lines	Dams	1.755	0.721	0.011	0.149	3.015
	Roads	Power lines	0.929	0.125	0.000	0.653	1.156
	Roads	Private cabins	0.770	0.085	0.000	0.626	0.960
	Tourist trails	Tourist cabins	6.677	1.174	0.000	4.666	9.149

The units of the dependent and independent variables are the same as in Table 1

resorts on reindeer space use is well-documented, the estimation of the effect size and of the zone of influence is controversial and varies greatly among case studies depending on the type and size of the tourist resort and associated infrastructures, on the season, sex, and on the methodological approach (Helle and Särkelä 1993; Nellemann et al. 2000, 2010; Vistnes et al. 2001; Vistnes and Nellemann 2008; Reimers and Colman 2009 for review). The large temporal and spatial scale of our study allowed us to highlight in a probabilistic way a marked long-term reindeer spatial response to tourist cabins, and the

analytical approach we adopted allowed us to disentangle the effects of correlated sources of disturbance such as hiking trails. Trails had highly variable impacts especially at smaller scales and, consequently, no overall long-term effects on the probability of use of movement corridors could be detected. Note, however, that the lack of a nation-wide response to trails does not necessarily imply a lack of response to hikers. On the contrary, wild reindeer and caribou are well known for decreasing their foraging time and fleeing in response to hikers approaching on foot or skis (Duchesne et al. 2000; Reimers et al. 2006; Strand

Fig. 5 Overview of the results of the direct hypotheses tested in Fig. 2. Only significant results ($p < 0.5$) are illustrated with an *arrow*, whose width is proportional to the effect size; see Table 2 for numerical details

and population responses of reindeer to varying degrees of intensity of use of trails.

Although several case studies documented avoidance of roads and of other linear features often associated to roads such as power lines (Nellemann et al. 2001; Dyer et al. 2002; Polfus et al. 2011), in other cases no avoidance could be detected (Vistnes and Nellemann 2001; Reimers et al. 2007; Reimers and Colman 2009). The probabilistic approach we adopted allowed us to detect a significant, direct, long-term, negative effect of roads on reindeer use of traditional movement corridors at all spatial scales (see Courbin et al. 2009; Leblond et al. 2011). For example, the presence of a 1 km of road within a 1-km radius buffer would nearly halve the probability of use of traditional movement corridors. Available information suggests that reindeer tolerance thresholds to disturbance have to be adjusted to the local ecological settings determining the strength of their motivation to use a given movement corridor, and to the position of the infrastructure with respect to the core part of the seasonally preferred habitat (see Reimers and Colman 2009). Indeed, while reindeer in Norway more readily avoided roads located in marginal parts of their ranges (Dahle et al. 2008), they continued crossing a road intersecting their traditional migration route, although trajectory analyses highlighted a markedly altered spatial behavior and suggest that, should the disturbance increase, the migration route may be abandoned (Panzacchi et al. 2012).

The majority of mountain roads either provide access to other infrastructures such as power lines and hydroelectric dams, or lead to private cabins, which are often clustered forming large recreational areas. Accordingly, at large spatial scales we detected significant negative effects of power lines and private cabins, but only subordinated to those of roads. Note the high confidence intervals associated with the total effect of power lines and private cabins at fine spatial scales, implying that their impact can vary from complete area abandonment to no changes in the use of corridors, likely due, once more, to local ecological settings such as the size of the infrastructure and reindeer need to continue moving along the corridor. Our results help understanding the previously detected marked local differences in the effect of power lines on reindeer space use (Reimers et al. 2007 and ref. therein). Dense power line networks originate from hydropower stations, whose piecemeal development

et al. 2010), though our approach was not designed to highlight such short-term responses. Most important, the long-term consequences of hiking likely depend on the amount of hikers and on their space use patterns (Reimers et al. 2006 and references therein; Reimers and Colman 2009), in combination with the amount of available refuge habitat for reindeer. As such data were not available at a nation-wide scale, we recommend future studies to focus on the long-term spatial

has flourished in the last century in Norwegian mountains. Several studies have reported a negative effect of dams and associated infrastructures on reindeer space use and migration, though the most marked effects have been reported during the construction phase (Mahoney and Schaefer 2002; Nellemann et al. 2003). Our results do not highlight any significant effect of dams on reindeer space use on a nation-wide scale, though the particularly high confidence intervals indicate marked local variations. Note that in several cases valleys containing ancient hunting structures have been flooded due to the construction of a dam: while in such cases the probability of area use is likely close to zero, if the dam was constructed on a marginal part of the surrounding area P(use) can be much higher. In accordance to previous studies, the cumulative effects of the piecemeal development of infrastructures associated to dams can have significant effects on reindeer space use (Nellemann et al. 2003; Sorensen et al. 2008).

The analytical approach we adopted allowed us to isolated direct, indirect and total effects of each type of infrastructure while minimizing problems typically arising when studying the effects of anthropogenic disturbance. The pre-post disturbance approach on such wide spatio-temporal scale allowed us to avoid the confounding effect of barriers to movements on the estimated coefficients of selection/avoidance obtained using resource selection functions or niche factor analyses. Path analysis allowed us to minimize problems related to spatial dependencies among different types of infrastructures by taking such correlations directly into account, and by disentangling direct and indirect effects (Graham 2003). In addition, the model is simple and flexible, as the coefficients can be re-calculated by the reader to obtain estimates for the desired variable unit at the spatial scale of interest (Eq. 5), or for cumulative effects of different types of infrastructures (Eq. 6).

The most obvious limit of our approach is that it requires a massive amount of data, though this would promote interdisciplinary collaboration and, thus, a more comprehensive understanding of the species' ecology. Secondly, as pathways in path analyses represent the hypotheses and cannot be statistically tested for directionality, pitfalls may arise in very complex systems in which the causal mechanisms among variables are poorly known and in which the suspected causes may be highly intercorrelated

(Petraitis et al. 1996). Finally, although it is well known that changes in migration patterns and area use can be density dependent (Farnell 2009), we have no information on reindeer density during the time during which the traps were in use. However, Skogland (1986) documented the definitive abandonment of one the most important Norwegian migration routes due to the construction of a road and railway, irrespective of density fluctuations.

The importance of migration for species inhabiting the highly seasonal circumpolar environment is such that some caribou populations perform the longest overland movements in the world (Bergman et al. 2000). Following the expansion of human activities we are facing an unprecedented abandonment of migration routes worldwide, often leading to population declines due to the inadequate year-round carrying capacity of one single seasonal range (Wilcove and Wikelski 2008; Harris et al. 2009). In Norway, although most migration routes connecting adjacent mountain ranges have been abandoned, we did not detect the population crashes observed elsewhere, as herd sizes are largely regulated by hunting quota based on availability of winter forage (Strand et al. 2012). However, the inability to migrate is well known to decrease access to high quality food, increase the risk of population crashes due to density dependence (Fryxell and Sinclair 1988; Ferguson and Messier 2000), and to increase population vulnerability to predation (Hebblewhite and Merrill 2007) and stochastic events, particularly at higher latitudes (Robinson et al. 2009). So far, in Norway herds year-round confined to sub-optimal, snowy winter areas seem to have been more often decimated by avalanches (e.g. Nellemann et al. 2010) and subjected to icing events, while those confined to sub-optimal summer areas might be more vulnerable to insect harassment (Reimers 1995; Hagemoen and Reimers 2002). Not only the loss of migration, but also the habitat loss associated with the avoidance of disturbance can have negative consequences for population dynamics through an increase in the energetic expenditure in antipredator behavior (Frid and Dill 2002), and through an increase in the strength of density-dependent processes (Sorensen et al. 2008). Although the long-term consequences of these processes are difficult to predict, note that they might become clear only after they have caused substantial effects on population viability (Berger et al. 2008; Sorensen et al. 2008).

Considering the ongoing climatic change and human encroachment in reindeer habitat it is of fundamental importance to be aware of the specific consequences of the piecemeal construction of new infrastructures to aid the formulation of sustainable land development plans. By using information from the past and the present we quantified direct, indirect, and total effects of different types of infrastructures on reindeer probability of use of traditional movement corridors. Furthermore, we provide stakeholders with a simple and flexible tool to predict a preliminary minimum estimate of the long-term effects of different types and combinations of infrastructures at the desired unit (e.g. number of cabins, km of roads etc.) and spatial scale (1, 5, 10 km), thus aiding the development of sustainable land management plans.

References

Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160

Bakkestuen V, Erikstad L, Halvorsen R (2008) Step-less models for regional biogeoclimatic variation in Norway. J Biogeogr 35:1906–1922

Berger J, Young JK, Berger KM (2008) Protecting migration corridors: Challenges and optimism for Mongolian saiga. PLoS Biol 6(7). doi:10.1371/journal.pbio.0060165

Bergman CM, Schaefer JA, Luttich SN (2000) Caribou movement as a correlated random walk. Oecologia 123(3): 364–374

Bjørneraas K, Herfindal I, Solberg EJ, Sæther B-E, van Moorter B, Rolandsen CM (2010) Screening GPS location data for errors using animal movement characteristics. J Wildl Manag 74(6):1261–1366

Blehr O (1987) The need for ethnographical analogies in the study of prehistoric caribou/wild reindeer hunting: A case study from Sumtangen, Norway. In: Burenhult G, Carlsson A, Hyenstrand Å et al (eds) Theoretical approaches to artefacts, settlement and society. BAR International Series, Oxford, pp 87–93

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

Courbin N, Fortin D, Dussault C, Courtois R (2009) Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. Landscape Ecol 24(10):1375–1388

Dahle B, Reimers E, Colman JE (2008) Reindeer (*Rangifer tarandus*) avoidance of a highway as revealed by lichen measurements. Eur J Wildl Res 54(1):27–35

DNT (2012) Norwegian Trekking Association. http://www.turist foreningen.no/english. Accessed Jan 2012

Duchesne M, Côté SD, Barrette C (2000) Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biol Conserv 96(3):311–317

Dyer SJ, O'Neill JP, Wasel SM, Boutin S (2002) Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Can J Zool 80(5):839–845

Farnell R (2009) Three decades of caribou recovery programs in Yukon: a paradigm shift in wildlife management. MRC-09-01. Department of Environment, Government of Yukon, Whitehorse. 18s

Ferguson MAD, Messier F (2000) Mass emigration of arctic tundra caribou from a traditional winter range: population dynamics and physical condition. J Wildl Manag 64: 168–178

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol 6:11

Fryxell J, Sinclair A (1988) Causes and consequences of migration by large herbivores. Trends Ecol Evol 3(9):237–241

Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. Phil Trans R Soc B 365:2255–2265

Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbance. Biol Conserv 97(2):265–268

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815

Hagemoen RI, Reimers E (2002) Reindeer summer activity pattern in relation to weather and insect harassment. J Anim Ecol 71(5):883–892

Harris G, Thirgood S, Hopcraft JG (2009) Global decline in aggregated migrations of large terrestrial mammals. Endanger Species Res 7(1):55–76

Hebblewhite M, Merrill EH (2007) Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377–387

Helle T, Särkelä M (1993) The effects of outdoor recreation on range use by semi-domesticated reindeer. Scand J For Res 8:1–4

Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363

Johnson CJ, Boyce MS, Case RL, Cluff HD, Gau RJ, Gunn A, Mulders R (2005) Cumulative effects of human developments on arctic wildlife. Wildl Monogr 160:1–36

Joly K, Nellemann C, Vistnes I (2006) A reevaluation of caribou distribution near an oilfield road on Alaska's north slope. Wildl Soc B 34(3):870–873

Jordhøy P (2008) Ancient wild reindeer pitfall trapping systems as indicators for former migration patterns and habitat use in the Dovre region, southern Norway. Rangifer 28(1):79–87

Jordhøy P, Binns KS, Støren SA (2005) Ancient wild reindeer hunting and trapping practices as indicators for former

migration patterns, hunting organization and use of resources in the Dovre region. NINA Report 19, 72 pp

Leblond M, Frair J, Fortin D (2011) Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landscape Ecol 26(10):1433–1446

MacKinnon DP, Fritz MS, Williams J, Lockwood CM (2007) Distribution of the product confidence limits for the indirect effect: program PRODCLIN. Behav Res Methods 39:384–389

Mahoney SP, Schaefer JA (2002) Hydroelectric development and the disruption of migration in caribou. Biol Conserv 107(2):147–153

Mallord JW, Dolman PM, Brown AF, Sutherland WJ (2007) Linking recreational disturbance to population size in a ground-nesting passerine. J Appl Ecol 44:185–195

Matthiopoulos J (2003) The use of space by animals as a function of accessibility and preference. Ecol Model 159:239–268

Meyers LS, Gamst G, Guarino AJ (2006) Applied multivariate research: design and interpretation. Sage publication Inc., Thousand Oaks 722 pp

Nellemann C, Jordhøy P, Støen O-G, Strand O (2000) Cumulative impacts of tourist resorts on wild reindeer (Rangifer tarandus tarandus) during winter. Arctic 53(1):9–17

Nellemann C, Vistnes I, Jordhøy P (2001) Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biol Conserv 101(3):351–360

Nellemann C, Vistnes I, Jordhøy P, Strand O (2003) Progressive impact of piecemeal infrastructure development on wild reindeer. Biol Conserv 113(2):307–317

Nellemann C, Vistnes I, Jordhøy P, Støen O-G, Kaltenborn BP, Hanssen F, Helgesen R (2010) Effects of recreational cabins, trails and their removal for restoration of reindeer winter ranges. Restor Ecol 18(6):873–881

Panzacchi M, Van Moorter B, Strand O (2012) A road in the middle of one of the last wild reindeer migrations routes in Norway: crossing behaviour and threats to conservation in Rangifer, Special Issue (in press)

Petraitis PS, Dunham AE, Niewiarowski PH (1996) Inferring multiple causality: the limitations of path analysis. Funct Ecol 10:421–431

Polfus JL, Hebblewhite M, Heinemeyer K (2011) Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biol Conserv 144:2637–2646

R. 11.1, R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reimers E (1995) Rangifer population ecology: a scandinavian perspective. Rangifer 17(3):105–118

Reimers E, Colman JE (2003) Reindeer and caribou (Rangifer tarandus) response towards human activities. Rangifer, 26(2):55–71

Reimers E, Colman JE (2009) Reindeer and caribou (Rangifer tarandus) response towards human activities. Rangifer 26(2):55–71

Reimers E, Miller FL, Eftestøl S, Colman JE, Dahle B (2006) Flight by feral reindeer Rangifer tarandus tarandus in

response to a directly approaching human on foot or on skis. Wildl Biol 12(4):403–413

Reimers E, Dahle B, Eftestøl S et al (2007) Effects of a power line on migration and range use of wild reindeer. Biol Conserv 134(4):484–494

Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) GLMM applied to the spatial distribution of koalas in a fragmented landscape, mixed effects models and extensions in ecology with R. Springer, New York

Robinson A, Crick HQP, Learmonth JA, Maclean IMD, Thomas CD, Bairlein F, Forchhammer MC, Francis CM, Gill JA, Godley BJ, Harwood J, Hays GC, Huntley B, Hutson AM, Pierce GJ, Rehfisch MM, Sims DW, Vieira dos Santos MC, Sparks TH, Stroud D, Visser ME (2009) Travelling through a warming world: climate change and migratory species. Endang Species Res 7(2):101–113

Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009) Identifying and prioritizing ungulate migration routes for landscpe-level conservation. Ecol Appl 19:2016–2025

Skogland T (1986) Movements of tagged and radio-instrumented wild reindeer in relation to habitat alteration in the Snohetta region, Norway. Rangifer 1:267–272

Sorensen T, McLoughlin PD, Hervieux D, Dzu E, Nolan J, Wynes B, Boutin S (2008) Determining sustainable levels of cumulative effects for boreal caribou. J Wildl Manag 72(4):900–905

Strand O, Gundersen V, Panzacchi M, Andersen O, Falldorf T, Andersen R, Van Moorter B, Jordhøy P, Fangel K (2010) Human disturbance in wild reindeer range lands. NINA Report 551. 101 pp. ISBN: 978-82-426-2127-6

Strand O, Nilsen EB, Solberg EJ, Linnell JDC (2012) Can management regulate the population size of wild reindeer (Rangifer tarandus) through harvest? Can J Zool 90:163–171

Tofighi D, MacKinnon DP (2011) RMediation: an R package for mediation analysis confidence intervals. Behav Res Methods 43:692–700

Underhill JE, Angold PG (2000) Effects of roads on wildlife in an intensively modified landscape. Environ Rev 8(1):21–39

van Horne B (1983) Density as a misleading indicator of habitat quality. J Wildl Manag 47:893–901

Vistnes I, Nellemann C (2001) Avoidance of cabins, roads, and power lines by reindeer during calving. J Wildl Manag 65(4):915–925

Vistnes I, Nellemann C (2008) The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. Polar Biol 31(4):399–407

Vistnes I, Nellemann C, Jordhøy P et al (2001) Wild reindeer: impacts of progressive infrastructure development on distribution and range use. Polar Biol 24(7):531–537

Vistnes I, Nellemann C, Jordhøy P, Strand O (2004) Effects of infrastructure on migration and range use of wild reindeer. J Wildl Manag 68:101–108

Vors LS, Boyce MS (2009) Global declines of caribou and reindeer. Glob Chang Biol 15:2626–2633

Wilcove DS, Wikelski M (2008) Going, going, gone: is animal migration disappearing? PLoS Biol 6(7):e188