



Rangifer within areas of human influence: understanding effects in relation to spatiotemporal scales

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Abstract

Depending on the spatial scale, fluctuations in the area use of social, migratory herbivores may be related to changes in population size, season, predation, climatic variation, different types of disturbance, and random animal movement. We present a review and case study highlighting how study design limitations and publication bias have influenced our current knowledge on effects of human disturbance on *Rangifer* spp. Our case study illustrates how yearly variation may lead to false conclusions about the effects of infrastructure. From 58 analyses presented in 52 reviewed papers, we found that 14 analyses had study designs comparing area use before and after construction of infrastructure, 24 included spatial time series of > 6 years, 21 included spatiotemporal variation in their analyses, and only six contained both static and dynamic habitat variables. Categorizing the 58 analyses into 404 specific outcomes, we found that 64% of the authors focused their conclusions on negative effects and 14% focused on mixed effects but emphasized on negative effects of human activities and infrastructure, while only 53% of the outcomes actually showed negative effects, 34% no effects and 13% positive effects. Our review shows that only one study had a before–after–control–impact (BACI) design, and a majority of publications do not include before–after (BA) designs (76%), have not included spatiotemporal variation (64%), and do not evaluate the effects of spatial fluctuations on *Rangifer* area use at long enough time intervals (only 8 studies had > 10 years data). Although *Rangifer* is vulnerable to human disturbances, we have showed how the effects of infrastructure differ among studies and highlight the need for study designs that integrate and account for spatiotemporal variation in future studies, for a better understanding of *Rangifer* (or wildlife) area use in relation to anthropogenic effects.

Keywords Area use · Confounding factors · Human disturbance · Publication bias · *Rangifer tarandus* · Spatiotemporal scale

Introduction

Animals move, constantly making habitat selections based on resources, threats and disturbances that interact, vary over time and are unevenly distributed within their home ranges (Börger et al. 2008), while terrestrial mammals in particular

show restrictions in movement globally due to increased anthropogenic footprint and other environmental interacting factors (Tucker et al. 2018). Understanding the effects of humans and human disturbances on area use may be complex, and appropriate scaling is a focal point in questions relating to anthropogenic effects on wildlife (Johnson et al. 2005; Polfus et al. 2011; Boulanger et al. 2012; Johnson and Russell 2014; Long et al. 2015; Northrup et al. 2016). Multi-scale resource selection modelling is used to identify factors that limit species distributions across scales of space and time (DeCesare et al. 2012), but results from such models are necessarily scale specific, as different behavioural responses appear within different spatial scales (e.g. Boyce 2006). In order to draw inferences relevant for management decision and legal constructs for critical habitats (DeCesare et al. 2012), there is a need to emphasize “the scales that matter” depending on animal resource selection and

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avoidance responses in a heterogeneous landscape (Hobbs 2003). Furthermore, it is becoming increasingly apparent how temporal scale is of the essence when evaluating the effects on wildlife area use from environmental and human activity and infrastructure changes at larger geographical scales (e.g. Long et al. 2015; Northrup et al. 2016; Skarin and Alam 2017).

Rangifer, with its large population ranges, circumpolar distribution, and potential vulnerability to human disturbance, is a model species for questions relating to human activity and infrastructure and scaling effects (e.g. Bergerud et al. 1984; Wolfe et al. 2000; Vistnes and Nellemann 2008a; Skarin and Åhman 2014). Most *Rangifer* populations live in groups that may constitute hundreds or ten thousands of animals, constantly on the move within or between seasonal pastures (Skogland 1989; Bergerud et al. 2008), and within habitats of varying pasture characteristics, human influence and risk of predation. Populations of *Rangifer* utilize areas ranging in size from about 200 to 8000 km² in Southern Norway to several hundred thousands of km² in North-America and Russia (Klein 1994). Living in large groups necessitates expansive ranges, and an increase in population size is often followed by an expansion of the population's range (Reimers et al. 2007; Bergerud et al. 2008). Movements within large ranges allow for a dynamic utilization of pastures, as well as avoidance of areas with increased predation risk or human infrastructure. When navigating in a so-called "landscape of fear" (Allen et al. 2014; Lone et al. 2014), decisions are trade-offs between optimizing resource availability and reducing the risk of life-threatening encounters with predators, including humans. Since reindeer and caribou are dynamic in their area use and move over long distances in response to changing environmental factors (Courtois et al. 2003; Taillon et al. 2012), we cannot properly address how environmental factors affect area use unless studying populations at the appropriate spatiotemporal scale.

A possible effect of human disturbance and infrastructure on *Rangifer* may be abandonment or reduced use of large surrounding areas (avoidance or aversion), resulting in a loss or less use of available pastures and overuse of remaining pastures. When such effects appear in analyses of *Rangifer* area use, it needs interpretation in a spatiotemporal context. As suggested by Vistnes and Nellemann (2008a) and Skarin and Åhman (2014), studies should incorporate regional scales, or possibly the home range level in order to capture large-scale effects of human disturbance. However, if changes are apparent at a regional scale (e.g. > 10 km), it becomes increasingly difficult to separate cause and effect, since spatiotemporal fluctuations in area use caused by other factors, like snow cover and grazing pressure (Gunn et al. 2009; Post et al. 2009), may occur at the same scale. Animal movement can be characterized as a combination of random walk and active selection (Fauchald and Tveraa 2003), but

it is not clear how the random component relates to variation or fluctuations in area use (Bartumeus et al. 2005; Pape and Löffler 2015a). Moreover, stochastic events like extreme weather (Loe et al. 2016) or predators (e.g. Reimers et al. 2012) could make a flock move away from preferred pastures at short time perspectives, while grazing pressure and resource availability may change area use over long time perspectives (Vowles et al. 2017). Thus, mechanisms driving avoidance responses towards human activity and infrastructure are difficult to measure and interpret (Theobald et al. 1997). Hence, dynamic area use at large spatiotemporal scales requires long-term studies and study designs controlling for natural fluctuations and confounding factors, like multiple years' worth of data before and after development (e.g. Colman et al. 2017; Smokorowski and Randall 2017). In this way, correct and robust interpretations can be made about results pertaining to effects of infrastructure and/or human activities (Bergerud et al. 1984; Reimers and Colman 2006).

We see large heterogeneity in findings from studies on large-scale responses of reindeer and caribou towards comparable anthropogenic factors like power lines, despite using fairly similar approaches and studying the same populations, e.g. the GPS study by Colman et al. (2015) showing no effects except during construction vs. the observation study by Nellemann et al. (2003) showing strong negative effects, both for the same wild reindeer population. Also opposite findings were the case in Reimers et al. (2007) showing no effect vs. Vistnes et al. (2004) showing strong negative effects on area use for wild reindeer, based on aerial photography and lichen grazing pressure. Possibly, reported responses can be largely different depending on landscape context and interacting ecological and disturbance factors (Panzacchi et al. 2013). It might also be a matter of the same population showing different responses at different times. Clearly, large-scaled negative effects of human disturbance necessitate studies including large areas, but when increasing the study area more interacting factors are included (e.g. predators, other human disturbances, different habitats, etc.). This increases the complexity of cause and effect relationships and the risk of making incorrect conclusions about large-scale effects unless being critical about limitations of the study design. While the importance of spatiotemporal scale has received attention in the literature (e.g. Vistnes and Nellemann 2008a; van Moorter et al. 2013; Skarin and Åhman 2014; Jørgensen et al. 2018), a main view for *Rangifer* seems to be that small spatial scale, behavioural or physiological studies fail to show disturbance effects suggesting the importance of large-scaled studies (Vistnes and Nellemann 2008a; Skarin and Åhman 2014). On the other hand, it is rarely emphasized how large spatial variation along the temporal scale may appear independent of impacts from human activity and infrastructure, and may affect results.

This signals a need for an in-depth review of the methodological approach in various studies related to anthropogenic effects on *Rangifer*.

In this paper, we review anthropogenic effect studies on area use of *Rangifer* from the last four decades. We evaluate study design and sampling techniques, focusing on how habitat and environmental variation along the spatiotemporal scale has been included and how such variation has been interpreted in relation to effects of infrastructure and human activity. In addition, we present a case study on area use from GPS-collared semi-domesticated reindeer in the Fosen peninsula in Norway in relation to fictive infrastructure within their habitat. Our aims were to evaluate (1) how different study designs limit analysis of effects from infrastructure, exemplified by the case study; (2) the importance and difficulty of including confounding variables in studies at large spatial scales; (3) how the temporal scale is included and discuss its importance in relation to dynamic area use of *Rangifer*, again exemplified by our case study; (4) how sampling techniques constrain our understanding of spatiotemporal area use; and (5) if the results and conclusions from published studies may be biased as a consequence of insufficient data or study designs and the selection of scientific publication processes. Our review is relevant for wildlife in general and especially transferable to other gregarious herbivores with large population ranges and in areas with increasing human use.

Reviewed literature

We examined scientific papers within the field of ecology and biological conservation quantifying effects of human development in relation to area use of *Rangifer* spp. (i.e. reindeer and caribou). During September 2017 and August 2018, we searched for papers in Web of Science and

Google Scholar, and also cited references within papers. We used diverse search terms to maximize the number of papers considered for review: avoidance, aversion, barrier, displacement, area use, space use and home range with the words anthropogenic, infrastructure, roads, power line, wind farm, resorts, trails, cabins, settlements and dams in combination with *Rangifer*, reindeer, and caribou.

We included all peer-reviewed papers that addressed avoidance effects from human development on *Rangifer* since 1983. We evaluated 79 papers, resulting in 52 papers for this review (Table 1). We excluded 27 papers that focused on direct disturbances, i.e. fright and flight studies, barrier studies and experiments, and also commentary papers. These excluded papers provide important insight and baseline information about mechanisms driving *Rangifer* behaviour and responses towards human activities and infrastructure, but did not directly investigate large-scale area use. We organized papers that met our criteria into one main table (Online Resource: Tables S1–S4), separating four sampling methods, i.e. GPS/VHF (Table S1), aerial survey (Table S2), visual animal observation (Table S3) and faeces counts and/or lichen measurements (Table S4), hereafter referred to as “type of studies”. We summarized the design of the study, type of human development, spatial scale (e.g. landscape, population home range, individual home range, and local disturbance area), temporal spatial variation in available area (e.g. annual home range, available area within 95% movement distance between locations), dynamic habitat variables [e.g. normalized vegetation index (NDVI), snow condition], static habitat variables (e.g. vegetation type, elevation), main results/conclusions, and specific outcomes (negative, no effects and positive effects in relation to disturbance factor per study period). Temporal spatial variation in the available area refers how the available area may change with time, independent of other factors included in the analyses. We

Table 1 Summary of number of studies and analyses reviewed by sub-species

Sub-species	Number of analysis by methods				
	All	GPS/VHF	Aerial survey	Visual animal observation	Field sign surveys (pellet/ lichen)
Arctic/Alpine caribou (AC)	15	5	8	2	0
Woodland caribou (WC)	19	13	1	1	1
Semi-domesticated reindeer (SR)	11	6	0	5	5
Wild reindeer (WR)	11	2	3	4	2
Both wild and semi-domesticated reindeer (SWR)	0	0	0	0	0
Total	58 ^a	26	12	12	8

A total of 79 studies were considered for the review, but 27 studies based on experimental/barrier, commentary/synthesis, methodological not related to avoidance effects, and flight/freight studies were excluded from the analysis

^aA total of 58 analyses from 52 studies because 6 of these studies included two of the four types of methods

also evaluated how the papers interpreted the effects in relation to spatiotemporal scale.

From the 52 papers reviewed, six (Boulanger et al. 2012; Helle et al. 2012; Colman et al. 2013, 2015; Serrouya et al. 2017; Tsegaye et al. 2017) included two of the four sampling methods, giving us a total of 58 sets of analyses (and results) in Online Resource 1. Twelve of the analyses were based on aerial counts, 12 were based on visual observation of animals from ground surveys, 26 were GPS/VHF studies, and 8 were based on field sign surveys (i.e. faeces counts or lichen measurements) as indirect indices of area use by *Rangifer*.

We also specified the temporal scale for each analysis; i.e. over how long time period the data spanned in the 58 analyses, and whether long-term change was tested, for instance by comparing the variation in area use before and after the construction of infrastructure. We divided the 58 analyses into separate human activities and infrastructure, seasonal, and scale-related “effect outcomes” (Table 2), and presented specific outcomes. For each outcome, we evaluated the type

of effect from human activities or infrastructure actually shown in the analyses (i.e. negative, none or positive), and whether static and dynamic habitat variables were accounted for (see also Online Resource 1). In order to set the scene for later presentation and discussion of our selection of *Rangifer*/infrastructure papers, we introduce the next part with analyses of our case study.

Case study: reindeer area use in relation to wind farms

The study area of 2320 km² (Fig. 1) is located in coastal climate at 64°10N, 10°50E, constituting low-alpine mountain ranges and birch-spruce dominated boreal forests at altitudes of 0–1000 m.a.s.l. in the Fosen North reindeer herding district in Nord-Trøndelag county, Norway. We studied spatial use of GPS-collared semi-domesticated reindeer, ranging from 10 to 32 individuals per year from

Table 2 Summary of reported effect outcomes within 52 reviewed studies (58 analyses)

Study	Factors	Negative effect	No effect	Positive effect	Total
GPS/VHF	Both static and dynamic	26	17	1	44
	Static	108	70	36	214
	Dynamic	0	0	0	0
	None	6	7	0	13
	Subtotal	140	94	37	271
	%	52	35	14	
Aerial survey	Both static and dynamic	3	1	0	4
	Static	16	8	6	30
	Dynamic	0	0	0	0
	None	25	7	4	36
	Subtotal	44	16	10	70
	%	63	23	14	
Visual animal observation	Both static and dynamic	0	0	0	0
	Static	13	10	2	25
	Dynamic	1	1	0	2
	None	4	2	0	6
	Subtotal	18	13	2	33
	%	55	39	6	
Field sign surveys (pellet-lichens)	Both static and dynamic	0	0	0	0
	Static	11	13	6	30
	Dynamic	0	0	0	0
	None	0	0	0	0
	Subtotal	11	13	6	30
	%	37	43	20	
All studies	Grand total	213	136	55	404
	%	53	34	13	

Each analysis is grouped into categories based on sampling technique for *Rangifer* area use, and based on types of habitat factors included in the analyses. Dynamic variables refer to spatial variables that vary during the study period (e.g. snow cover, NDVI); static variables refer to spatial habitat variables that are constant throughout the study period (e.g. vegetation type)

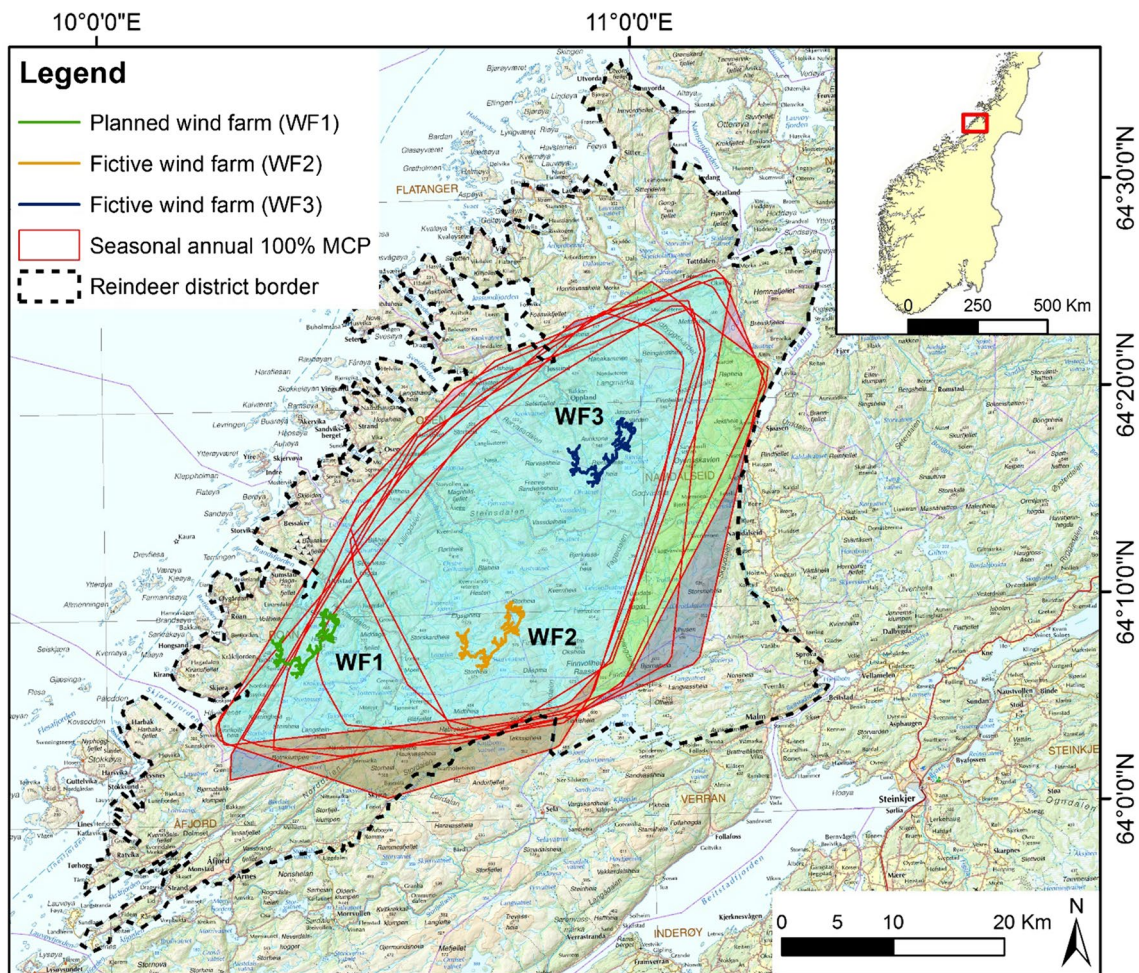


Fig. 1 Map of the Fosen domestic reindeer study area in Nord-Trøndelag County, Norway, depicting seasonal annual MCPs (minimum convex polygon) and planned and fictive wind farms (WFs)

a total herd averaging 900 reindeer for a period of 8 years. Animal location data were collected every 3-h throughout the study period.

As a case study, we defined three areas with wind farm (WF) development, i.e. WF1, WF2 and WF3 (Fig. 1). WF1 represents the location of a real wind farm where construction started in 2017/2018, after our GPS recordings (<https://www.statkraft.com/about-statkraft/Projects/norway/fosen>). The two other areas, representing fictive WFs or control areas (WF2 and WF3), were placed in landscapes with similar elevation and subalpine vegetation (i.e. similar habitats). None of the three areas were intersected by other major infrastructures like settlements or roads. We defined three study periods spanning 8 years: before (2009–2011), during (2012–2013) and after construction (2014–2016), imitating before–after (BA) designs. In relation to a before–after control–impact (BACI) design of anthropogenic effect studies, as defined in Kuvlesky et al. (2007) and Bartzke et al. (2014), WF3 and WF1, being

located in the outskirts of spring habitats, are more similar than WF2, which is located in more central spring habitats. By including multiple years for each period, we could also test variability in area use across years within and amongst the periods. Since the reindeer herdsman sometimes gather the animals as early as 24 June for calf marking and as late as February/March for slaughter, we only used data for the spring season for our analyses (1 April–20 June). This was done to minimize the effect of reindeer herding. The response variable was binomial (used/available) and consisted of reindeer GPS locations and an equal amount of randomly sampled positions within 100% seasonal MCP for all animals each year, representing available area for their seasonal annual population home range. To avoid overlap between the three study areas, we only included data within a 10 km zone from the WFs in the final analyses. As a result of this, we used 17,379 observations and 23,065 random points (WF1), 78,644 observations and

50,573 random points (WF2), and 34,540 observations and 51,798 random points (WF3) in the final analysis.

A main hypothesis of avoidance towards WFs was tested in three ways; (1) separately for each WF area in relation to distance and period, imitating three BA designs, (2) for each WF area in relation to distance and year to illustrate the effects across years, and (3) the three WFs interacted with distance and period to illustrate relative differences in effects among the WFs, imitating a BACI design. These three ways were chosen to clarify how different approaches can be useful depending on the choice of study design. Fixed effects included distance (m) to the nearest WF, period categorical at three levels: before, during and after development, the landscape variables aspect (in degrees), and elevation (m.a.s.l.). Prior to analysis, we checked for correlation between covariates (i.e. vegetation, elevation and aspect) using Spearman's rank correlation, excluding the assumed least relevant from the models when $r > 0.5$. Thus, we did not include vegetation from the analysis since it correlated with elevation ($r=0.56$). We included animal ids and year as random effects to account for individual and yearly variations (Zuur et al. 2009; Bates et al. 2014). All statistical analyses were conducted in R version 3.3.3 (R Core Team 2015).

Results of our case study from the separate analysis of each WF area in relation to distance and period showed more use before compared to after for WF1 (within 10 km), but no differences between before and during

(Table 3). Furthermore, we found a negative effect from WF1 in the before period, i.e. there was more use further away. More importantly, the results showed that the reindeer was closer to WF1 during compared to before, but further away after (Table 3). For WF2, we found no differences in the overall use between the three periods. We found a positive effect of WF2 in the before period, i.e. more use closer. Compared to before, the animals were further away during, but were closer after (Table 3). For WF3, in general, we found more use after compared to before, but no differences between before and during. Furthermore, we found a positive effect of WF3 in the before period, i.e. more use closer. Compared to before, both during and after had more use further away from WF3 (Table 3).

The model with yearly periods (Fig. 2) showed differences in use within 10 km from the WFs amongst years. Generally, we found more use with increasing distance from WF1 in the years 2009, 2011, 2013, 2014 and 2015, but no such effect in 2010, 2012 and 2016. For WF2, there was less use with increasing distance every year, except for 2013, which showed a weak increase for the first 3–4 km. For WF3, we found a decrease in use with distance in the years 2009 and 2011, more use at closer distances within 2–4 km from the WF in 2010 and 2013 (a general increase after 2–4 km), more use at increasing distance in 2012, and no clear effects in 2014, 2015 and 2016 (no effects within 3–5 km). We found that non-existent (fictive and planned

Table 3 Parameter estimates of a mixed logistic regression model predicting reindeer resource selection during spring (April–June) as a function of aspect ($^{\circ}$), elevation (m), distance (m) from three fictive

wind farms (WFs), and before (2009–2011), during (2012–2013) and after (2014–2016) construction in Fosen, Norway (Fig. 1)

Effect	WF1				WF2				WF3			
	Estimate	SE	Z value	P value	Estimate	SE	Z value	P value	Estimate	SE	Z value	P value
Intercept	-0.387	0.287	-1.346	0.178	0.596	0.179	3.330	0.001	-1.133	0.191	-5.930	<0.001
Aspect	0.027	0.012	2.297	0.022	0.044	0.006	7.150	<0.001	0.152	0.008	19.630	<0.001
I(Aspect ²)	0.015	0.012	1.175	0.240	0.019	0.007	2.710	0.007	0.032	0.009	3.580	<0.001
Elevation	0.174	0.014	12.147	<0.001	0.002	0.006	0.290	0.771	0.423	0.008	51.160	<0.001
I(Elevation ²)	-0.302	0.012	-26.102	<0.001	-0.148	0.005	-31.090	<0.001	-0.160	0.007	-22.260	<0.001
Distance	0.574	0.029	20.592	<0.001	-0.551	0.011	-49.170	<0.001	-0.172	0.016	-10.590	<0.001
I(Distance ²)	-0.091	0.027	-3.375	0.001	-0.168	0.011	-15.360	<0.001	0.081	0.016	5.060	<0.001
During	-0.525	0.352	-1.492	0.136	-0.033	0.170	-0.200	0.844	0.089	0.223	0.400	0.689
After	-1.144	0.318	-3.599	<0.001	-0.282	0.154	-1.840	0.066	0.816	0.202	4.040	<0.001
Distance \times during	-0.147	0.037	-3.932	<0.001	0.201	0.015	12.980	<0.001	0.613	0.021	28.710	<0.001
I(Distance ²) \times during	0.547	0.034	15.999	<0.001	-0.065	0.015	-4.350	<0.001	0.053	0.022	2.460	0.014
Distance \times after	0.222	0.038	5.861	<0.001	-0.071	0.016	-4.400	<0.001	0.259	0.021	12.650	<0.001
I(Distance ²) \times after	0.171	0.037	4.687	<0.001	-0.013	0.016	-0.800	0.423	-0.057	0.020	-2.790	0.005

Year and animal id were used as random factors to account for individual and yearly variations. We used annual population home range to determine availability using seasonal annual 100% MCP in a landscape (i.e. second-order home range)

Random-effects standard deviations: WF1 (animal id=1.53 and year=0.38), WF2 (animal id=1.22 and year=0.18), and WF3 (animal id=1.09 and year=0.24)

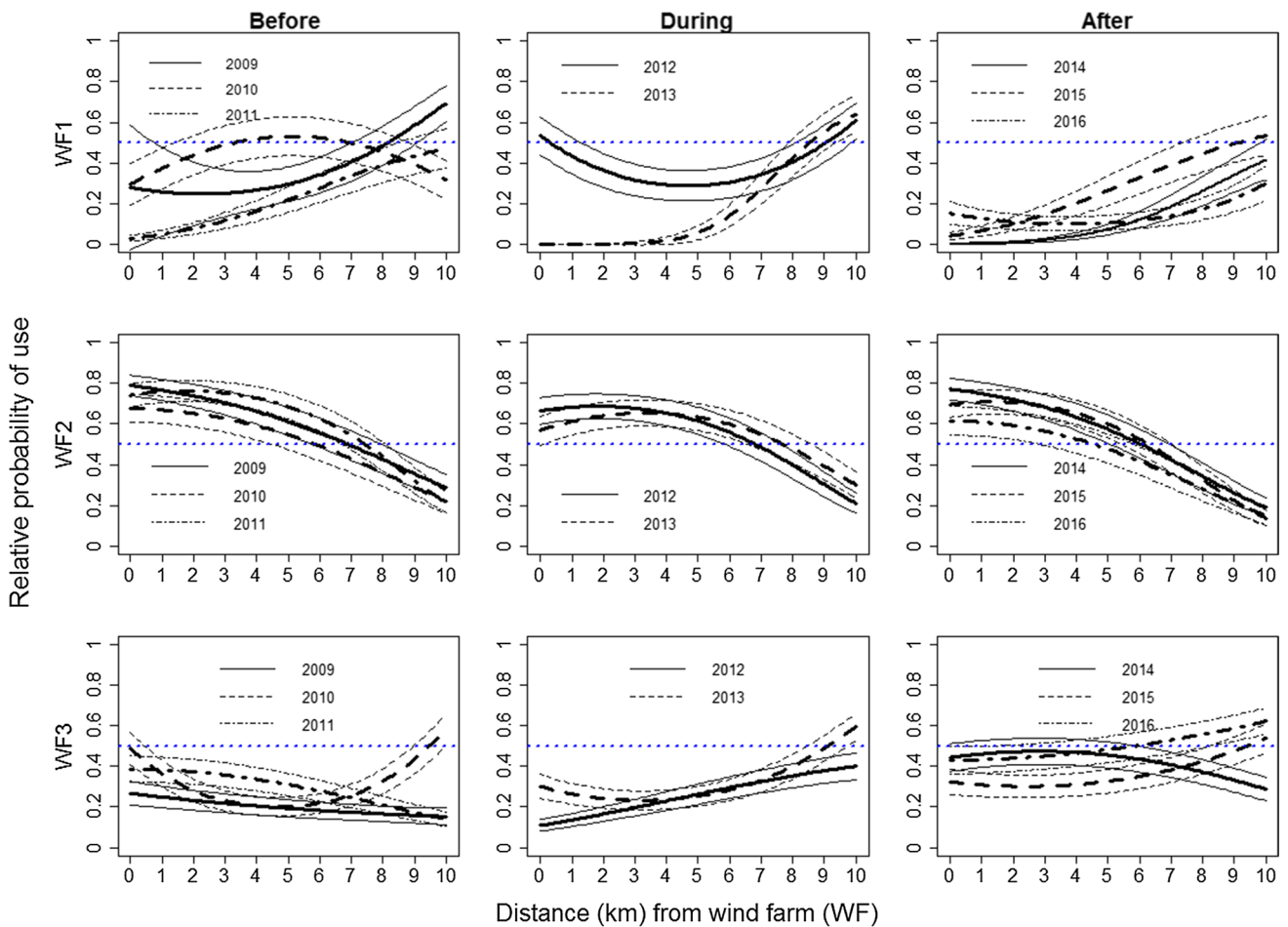


Fig. 2 Predicted probability of use ($\pm 95\%$ CI) by reindeer during spring (April–June) showing yearly variability in relation to distance from the planned and fictive wind farms (WFs), before (2009–2011), during (2012–2013) and after (2014–2016) construction in Fosen, Norway. Estimates overlapping 0.5 (horizontal dotted line) represent use proportional to availability, estimates larger than 0.5 represent

selection, and estimates smaller than 0.5 represent less use. Prediction was based on a model for each WF that included distance and year interaction, aspect and elevation kept at their mean. Animal ids were used as random factors to account for individual variation. We used seasonal annual population home range to determine availability using 100% MCP in a landscape (i.e. second-order home range)

but not yet built) WFs show both yearly and periodic negative effects on area use of reindeer.

From the interaction model (Fig. 3; Online resource 2), predicted use showed that the difference between before and during indicated totally opposite effects from WF1 for these two periods, at least in the distance interval 0–5 km. WF2 had a positive effect in all periods, even if there were differences between the three periods. For WF3, we found some differences between before and during/after, but a clear trend was more use further away from WF3 during, and no such trend after.

The yearly variation in spatial area use at the three WF sites leads to differences in area use between defined periods before, during and after development, and even a significant three-way interaction effect for the BACI design analysis. This illustrates a possible pit-fall in similarly designed studies and serves as a background scenario

for an evaluation of the papers that met our selected parameters.

Limitation of study design

When studying anthropogenic effects on area use, the factors themselves are not randomly distributed and may cover landscape scales at home range level, potentially affecting both second- and third-order habitat selection (for details see Johnson 1980; Johnson et al. 2006). Differences in area use among years for WF1 and WF3 in our case study clearly illustrate how the area of home range changes over time, as it is defined by the habitat selection of a population, complicating evaluations of infrastructure effects. In contrast, third-order selection functions for fine-grained habitat components distributed within

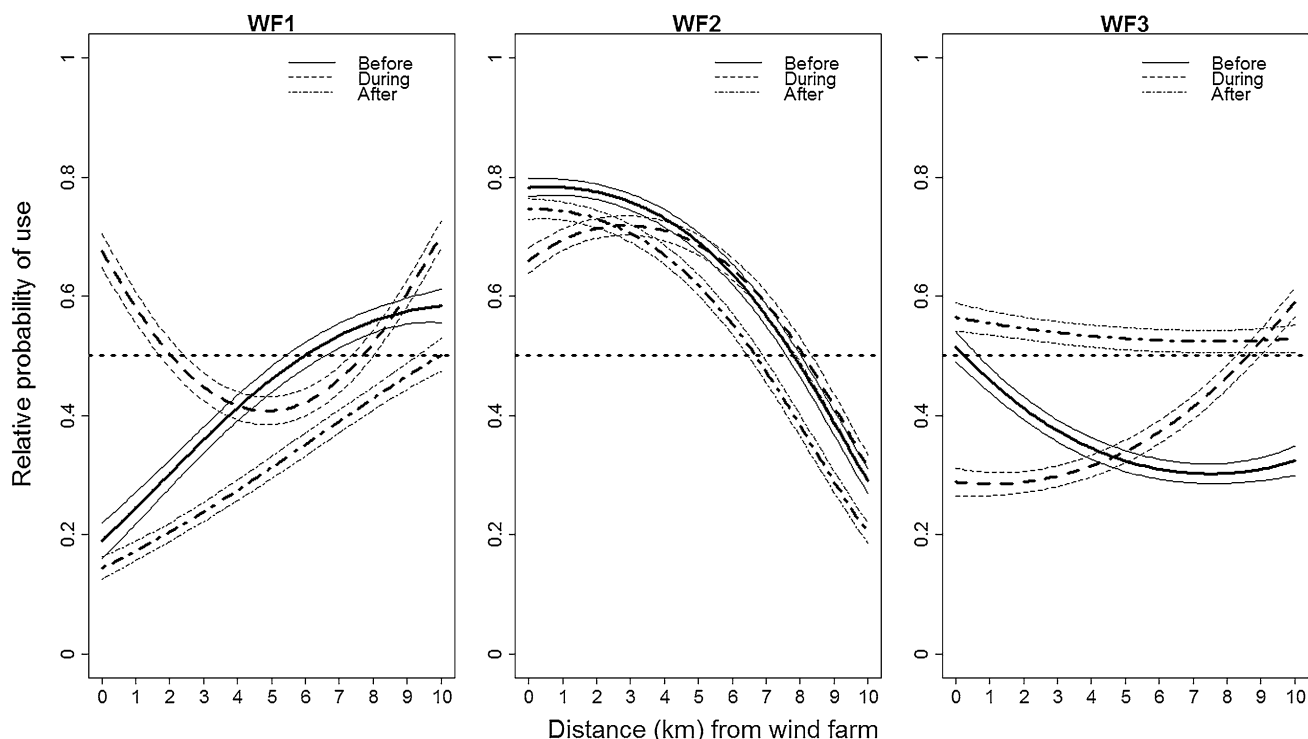


Fig. 3 Predicted probability of use ($\pm 95\%$ CI) by reindeer during spring (April–June) showing interaction effects of WFs sites, distance from WFs and period (before, during and after development) imitating a BACI design in Fosen, Norway. Estimates overlapping 0.5 (horizontal dotted line) represent use proportional to availability, estimates larger than 0.5 represent selection, and estimates smaller

than 0.5 represent less use. Aspect and elevation kept at their mean. Animal ids and year were included as random factors to account for individual and yearly variation. We used seasonal annual population home range to determine availability using 100% MCP in a landscape (i.e. second-order home range)

the home range (e.g. vegetation types) can be more precisely modelled based on the data for *Rangifer* space use and geographical data for habitat components within the entire home range (e.g. Polfus et al. 2011; Leblond et al. 2013; Panzacchi et al. 2013; Lesmerises et al. 2018). Since anthropogenic effect studies at landscape level may conclude wrongly about the possible effects if not also interpreting how fluctuations in area use around infrastructure may occur independent of the disturbance itself, the choice of appropriate study design seems crucial (Bartzke et al. 2014). Ideally, we should compare habitat selection in the affected areas and control areas, both before and after infrastructure development (BACI designs), and for long enough time periods to include spatial fluctuations in home range (Smokorowski and Randall 2017). However, similarity in habitat characteristics between control and treatment sites is hard to find when studying large-scaled effects on area use in heterogeneous landscapes, and planning and budget limitations may impede long-term data gathering in test and control areas over multiple years before and after the onset of new infrastructure. Thus, true BACI designs may seldom have been implemented in studies on *Rangifer* large-scale spatial use and are probably more realistic for

experimental, local, and direct disturbance effect studies (e.g. Conner et al. 2016).

From our reviewed papers, the majority of analyses spanned 6 years or less (i.e. 34 out of 58), and only 8 out of 58 covered a study period of > 10 years (for details see Online Resource 1). Furthermore, 40 of the analyses were based solely on data from the period after construction of new infrastructure. Interestingly, three of these after analyses considered habituation by dividing and testing the “after period” in two periods (Haskell and Ballard 2008; Helle et al. 2012; Johnson and Russell 2014). Three analyses from two studies were based on data during and after construction of new infrastructure (Boulanger et al. 2012; Colman et al. 2013), and one out of two analyses in Tsegaye et al. (2017) had only before and during data. The remaining 14 analyses from 13 studies had a before–after design (Dau and Cameron 1986; Cameron et al. 1992; Mahoney and Schaefer 2002; Nellemann et al. 2003, 2010; Noel et al. 2004; Weir et al. 2007; Colman et al. 2013, 2015; Leblond et al. 2013; Eftestøl et al. 2016; Skarin and Alam 2017; Tsegaye et al. 2017). Out of these 14 analyses, three (Colman et al. 2013, 2015; Eftestøl et al. 2016) reported negative effect only during the construction period when human activity is high,

with no effects in the operation period of the new infrastructure. Two of the 14 before–after analyses (Noel et al. 2004; Tsegaye et al. 2017) reported no consistent influence of infrastructure, both in construction and operation periods. The remaining nine before–after analyses reported negative effects both during construction and operation periods. However, from the 14 before–after analyses, we found only one (Colman et al. 2013) with a control area and, thus, a true BACI design (Kuvlesky et al. 2007; Bartzke et al. 2014).

Our present knowledge about anthropogenic effects on *Rangifer* spatial use is based on a large number of studies (71% of studies reviewed here), with no before data on area use of the animals in focus, and 13 out of 14 before–after studies reviewed here did not include a control area for the analysis. A majority of the reviewed studies have sampled *Rangifer* area use for a substantially shorter time period than our case study of 8 years (< 7 years in 34 out of 58 studies, see Online Resource 1) and some investigate infrastructure in the outskirts of the range, where higher yearly fluctuation in area use is expected (Vistnes et al. 2004; Johnson and Russell 2014). Thus, we are concerned that some studies may have concluded wrongly about the effects of human activities and infrastructure. For reliable data to test the effects of human activity and infrastructure on *Rangifer* area use, mainly two study design approaches are available: (1) if direct behavioural effects are expected on local scale, a BACI design possibly replicating several independent treatment and control areas could be useful, (2) if indirect avoidance effects are expected at larger landscape scales, a BA design with multiple years before, during and after infrastructure development, and including multiple spatial scales (preferably both population and individual home range levels) is probably the best option. However, since BA-designed studies on large-scaled spatial effects are not robust when it comes to bias from spatiotemporal fluctuations in *Rangifer* area use if temporal data-series are short, we recommend comparing area use in control areas (if available) in such cases (e.g. Colman et al. 2013).

Confounding habitat factors

In heterogeneous landscapes, spatial use analyses of infrastructure effects require an inclusion of potentially confounding habitat factors, even more so if data sets do not allow BACI designs or long-term BA designs, but exclusively test data from after infrastructure are already constructed. Depending on the characteristics of the study area, factors known to affect spatial use may be elevation, vegetation type and quality, landscape ruggedness, natural barriers and edges in the landscape (Nellemann and Fry 1995; Iversen et al. 2014; Colman et al. 2015; Panzacchi et al. 2015). In addition, temporal variables affecting spatial use, like

population size/density (Bergerud et al. 1984; Reimers and Colman 2006), presence of predators (Nybakk et al. 1999, 2002; Rivrud et al. 2018), other sympatric species (Colman et al. 2012), and snow cover and onset of spring green up (Bischof et al. 2012; Rivrud et al. 2016, 2018) should be investigated if possible. A frequently overlooked fact among wild and domestic reindeer is that previous domestication has preserved a hard wired behavioural trait in some reindeer herds exhibiting less fright responses towards humans that extensive hunting has only altered slightly (Reimers et al. 2012). Hence, when recording reindeer area use in relation to human infrastructure, past genetic history should also be addressed. Moreover, recent improvements in GIS- and RSF analyses have facilitated an understanding of spatial habitat use of animals in detail (Johnson et al. 2006, 2015; Johnson and Russell 2014; Pape and Löffler 2015a, b, 2016), although issues like sampling techniques and available data for analyses that relate to appropriate sampling scale resolution (Bissonette 2017) are still challenging.

A majority of our reviewed studies (40 out of 58 analyses) included static habitat variables, where vegetation type and elevation were most often controlled for in the analyses (Table 4). The improved availability since the 1990s of GIS data for habitat factors makes such analyses possible, increasing our understanding of habitat selection in *Rangifer* (Panzacchi et al. 2015), separating avoidance of environments from avoidance towards infrastructure (e.g. Lesmerises et al. 2018; Plante et al. 2018). Actually, 23 out of 26 studies based on GPS-data have included either static habitat variables (18) or both static and dynamic variables (5) in the analyses of *Rangifer* spp. area use (Table 4). However, as shown for our case study, incorrect interpretations about infrastructure effects may still appear, either if some relevant factors or variables are missing in the analysis (e.g. Noel et al. 2004; Joly et al. 2006), or if area use is affected by random animal movement patterns (e.g. Fauchald and Tveraa 2003). Clearly, data for certain dynamic habitat variables like predation risk or snow cover (thickness and hardness) may be unavailable, but of crucial importance when explaining fluctuations in *Rangifer* area use (Rivrud et al. 2018). Also, some factors may be difficult to categorize and incorporate for analyses, e.g. topographic barriers or edge effects (With et al. 1997), but should affect how we interpret results on *Rangifer* area use when not having data from before infrastructure development. Moreover, since infrastructure is not randomly distributed (e.g. often is located at the outskirts and/or at lower altitude than natural *Rangifer* habitats, for example in valleys), low spatial use may be misinterpreted as avoidance (Reimers and Colman 2006). As technology advances, multiple variables need to be included in the future analyses to produce unbiased effect estimates. Although some authors likely ran various models with factors not included in their final models, only 10% of the

Table 4 Summary of analyses by confounding factors and spatiotemporal variation (total=58, since 6 studies used two of the four category of data types, i.e. GPS, aerial, visual animal observation, and field sign surveys)

Confounding factors included	Spatiotemporal variation included			
	Year	Random	Year+random	None
GPS/VHF				
Dynamic variables				
Static variables	1	6	1	10
Dynamic + static variables		4		1
None				3
Aerial survey				
Dynamic variables				
Static variables				6
Dynamic + static variables				1
None				5
Visual animal observation				
Dynamic variables	1			
Static variables			1	6
Dynamic + static variables				
None		1		3
Field sign surveys (pellets/lichens measurements)				
Dynamic variables				
Static variables	1	4	1	2
Dynamic + static variables				
None				
Total	3	15	3	37

Dynamic variables refer to spatial variables that vary during the study period (e.g. snow cover, NDVI); static variables refer to spatial habitat variables that are constant throughout the study period (e.g. vegetation type). Some studies include year as a fixed effect term in their analysis to account for time series effects. Many recent studies include random factors in the analysis to account for pseudo-replication or to estimate variability attributable to the factor

analyses reviewed here presented both static and dynamic variables when testing the effects of human activity or infrastructure on *Rangifer* area use.

Accounting for spatiotemporal fluctuation

When studying avoidance responses in *Rangifer*, we try to understand what affects area use of individuals that are mainly gathered in flocks drifting over large grazing areas and between seasonal pastures through time. For instance, the 23 wild reindeer areas in southern Norway are delineated as discrete management units that generally meet the biological requirement for the herds (e.g. Panzacchi et al. 2015). An individual, or even the entire herd, cannot use its entire available area over a shorter time-span (a few years); some parts will always be used less and other parts more. Reasons why parts of the available range of a population

have no or little use for a given period may be; (1) pastures are seasonally distributed and vary in accessibility depending on weather (e.g. insect harassment during summer, snow cover and icing during winter), and quality (e.g. green sprouting following snow melt) (Skogland 1989; Vistnes and Nellemann 2008b), (2) seasonal area use varies with previous temporal variation in degree of overgrazing or recovery from previous overgrazing (i.e. especially winter pastures of lichen) (Skogland 1986), (3) predator territory boundaries and general predator densities vary throughout time (Nybak et al. 2002; Tveraa et al. 2007), (4) social group behaviour with elements of learning is associated with gradual fluctuations in area use, predator avoidance and harvest policy (Mooring and Hart 1992; Lingle 2001), and (5) intra- and interspecific interactions and competition (Moe et al. 1999) that may also vary through changes in population size (Bednekoff and Lima 2004). For semi-domestic reindeer, the human aspect of herders controlling movements and migration patterns and choosing their herds' grazing areas is also important. Moreover, it is not clear to what extent random movement patterns affect space use at different spatial scales within a population, suggesting that the use of areas may change without a particular reason.

Spatiotemporal analyses should provide improved understanding of how *Rangifer* make small- and large-scaled habitat selections while moving within vast ranges and in landscapes affected by infrastructure and human disturbance. Apart from including static and dynamic habitat variables, we found that some studies also included yearly and/or random spatiotemporal variation in analyses on *Rangifer* area use (Table 4). However, none of the 58 analyses included a combination of dynamic and static habitat variables and yearly and random spatiotemporal variation together in the same model. Obviously, data sets may be too limited to enable such complex analyses, but we see improvement of methods in the more recent studies (Table 4; Online Resource 1), e.g. 12 out of 26 GPS-studies and 6 out of 8 field sign surveys (pellet/lichens measurement) have included both confounding variables (static and/or dynamic) and spatiotemporal variation (i.e. yearly and/or random), while only three out of 12 visual animal observation studies and no aerial studies have included any of the spatiotemporal variation. Probably, most studies prior to the introduction of GPS technology and GIS analyses have too limited data for making complicated analyses on area use, both estimating effects of infrastructure, habitat factors, and spatiotemporal fluctuations (Table 4). Thus, we base much of our scientific knowledge about infrastructure effects on *Rangifer* spp. on estimates that are likely inadequate and even biased.

Research projects sampling data for large-scale area use in relation to anthropogenic disturbance over a period of just a few years may misinterpret natural variation as avoidance effects (Hinkes et al. 2005). For caribou and

semi-domesticated reindeer, it has been shown how preferences for habitat types (Leblond et al. 2011; Pape and Lofler 2015a, b), predator avoidance (Sivertsen et al. 2016) and plant phenology selection (Iversen et al. 2014) result in temporal changes in spatial use. Some anthropogenic effect studies (Mahoney and Schaefer 2002; Polfus et al. 2011; Boulanger et al. 2012; Johnson and Russell 2014; Colman et al. 2015) have incorporated spatiotemporal covariates like changes in snow cover and/or plant phenology (e.g. NDVI data) in the analyses, thus being able to explain more of the spatiotemporal changes in *Rangifer* area use.

Interestingly, 13 out of 18 GPS analyses in Canada considered different spatial availability varying with time in their testing/models (i.e. temporal variation considered in defining the available area), while only one out of eight GPS analyses from Scandinavia considered this. Six long time GPS studies (> 3 years) from Quebec (Leblond et al. 2011, 2013; Dussault et al. 2012; Leclerc et al. 2012; Pinard et al. 2012) and one study from Norway (Panzacchi et al. 2013) on anthropogenic effects on spatial use of *Rangifer* have based analyses on yearly/seasonal home ranges, thus being more able to separate natural/uncontrolled spatial fluctuations among years from the effects of infrastructure. However, spatial fluctuations also appear in shorter time intervals, and in order to make anthropogenic effect estimates more precise, methodological improvements have appeared. These are based on the resource selection functions where the available area for individuals is narrowed down to a circular area defined by current position and movement distance estimates (Johnson et al. 2005), and avoiding effect estimates for infrastructure outside this area. As such, the studies by Johnson et al. (2005, 2015) and Boulanger et al. (2012) may avoid distorted effect estimates due to spatiotemporal fluctuation. However, the circular areas for estimating infrastructure effects increase with increasing time intervals for consecutive GPS positions and seem related to some unrealistic avoidance distances (e.g. up to 140 km distance in Johnson et al. (2005)). Also, since the method is based on circular areas, it may include areas being isolated by barriers (e.g. mountains or rivers) or without *Rangifer* habitat.

The approach used in Dussault et al. (2012), Pinard et al. (2012), Leclerc et al. (2012), and Leclerc et al. (2014) is another way to reduce the effect of spatiotemporal fluctuation. They defined available areas based on GPS positions on different scales, both at annual population home range, annual individual home range and/or at local scales (e.g. forest stand scale). Furthermore, the effects were tested from calculated densities of both infrastructure and habitats within buffer zones around animal locations and random points (e.g. 1 km). These studies mainly relate calf survival with female habitat selection and infrastructure, showing a clearer connection between cause and effect compared to just differences in area use.

Analysing resource selection in the available area as defined by the animals' current position implies third-order habitat selection (Johnson 1980), thus, from the approach in Johnson et al. (2005), the possible infrastructure effects at home range level (i.e. second-order selection) can hardly be evaluated. Probably, time series of spatial use covering several decades are necessary in order to reveal infrastructure effects at the home range level in many cases (Hinkes et al. 2005; Plante et al. 2018); however, population management have markedly changed the size of several *Rangifer* populations over recent decades (e.g. Uboni et al. 2016), thereby influencing grazing pressure and population ranges, hampering analyses on long time effects of infrastructure. As examples, the calving ranges of the Hardangervidda wild reindeer population in Norway have gradually changed significantly over the last 20–30 years seemingly independent of human disturbance (Strand et al. 2006; Falldorf 2013), and both the Hardangervidda and Snøhetta wild reindeer population have increased their home range, crossing human infrastructure in periods of high abundance and grazing pressure (e.g. Bergerud et al. 1984). Thus, long time studies on area use demands careful consideration of what factors have changed through the same time period and how that may relate to changes in population ranges and home ranges (Bergerud et al. 2008).

Long-term variation in area use is expected for most *Rangifer* populations, and our current knowledge base on the effects of human activity and infrastructure on *Rangifer* is inadequate. No analyses reviewed here included both dynamic and static habitat variables and yearly and random spatiotemporal variation together in the same model. With methodological and technological improvements, natural spatiotemporal variation in *Rangifer* area use can be better incorporated into future studies. However, it is crucial to also consider the possible effects of population dynamics on area use for long-term studies.

Constraints from sampling procedures

Earlier studies based on non-randomized visual observations of *Rangifer* (e.g. aerial surveys) may have provided biased data on area use, as compared to GPS monitoring of animals. Data sets from aerial surveys are often part of population management programs covering long time series, where herd size, sex and age structure may be the main purpose of the sampling procedure, while the data itself may be of varying quality for spatial analyses (Reimers 2006; Bjerketvedt et al. 2014). In a Norwegian context, wild reindeer populations have been monitored since the 1960s by population counts based on photographs from light aircrafts, and/or snowmobile surveys and counts from ground made by local game managers. In fact, a few studies on anthropogenic effects

of infrastructure on wild reindeer in Norway are based on the data that cover a time span of 10–30 years with yearly sampling of the entire population (Nellemann et al. 2001; Vistnes et al. 2001; Reimers et al. 2007), but with non-randomized sampling (counts often being made once a year, in periods of good visibility late in winter, when reindeer are easier to find and counting is simplified due to larger groups leaving visible tracks). On the other hand, several recent studies based on GPS cover short time series and are based on a small sample of collared animals (e.g. Polfus et al. 2011). Thus, new projects based on multiple sampling per year over many years, and along systematic transects on ground (e.g. Nellemann et al. 2010; Colman et al. 2013; Tsegaye et al. 2017), or from continuous long-term monitoring by GPS (Johnson et al. 2015; Plante et al. 2018), provide more representative data of *Rangifer* spatial use throughout the season/year and how it differs between seasons/years. If study periods are also long enough to uncover the dynamic nature of *Rangifer* spatial use (e.g. Panzacchi et al. 2013; Johnson et al. 2015), and combined with the inclusion of multiple variables and preferably control areas, we will be more certain about possible shifts in area use related to human infrastructure.

Publication bias in anthropogenic effect studies?

Within this field of research, we are consistently testing the hypothesis that *Rangifer* avoid areas affected by infrastructure and human disturbance (Skarin and Åhman 2014). An alternative hypothesis would be that *Rangifer* are attracted to certain types of infrastructure. For instance, Serrouya et al. (2017) indicated strong selection for forestry roads when trailing *Rangifer* in snow and argued that it might be due to movement along roads being less energy consuming. Some recent studies have found that human activity displaces predators, inducing spatial refuge from predation along roads and trails (Muhly et al. 2011). Only few studies take into consideration positive or neutral results (i.e. attraction or no effect) in cases of infrastructure and *Rangifer* in their discussion before concluding the presence of avoidance or lack thereof (e.g. Cronin et al. 1998; Noel et al. 2004). We found that for 64% of the 58 published analyses (Online Resource 1) authors presented a main conclusion of negative effects from infrastructure, and for 14% mixed effects were focused but with main emphasis on negative ones. However, from the same number of analyses, we found that only 53% of the 404 specific outcomes in the analyses actually show negative effects (Table 2). Thus, even if positive effects exist and are presented in the results, there is a bias towards focusing discussions and conclusions towards negative results. In most cases, we found that the positive effects are either

ignored (e.g. Johnson and Russell 2014; Johnson et al. 2015) or addressed critically to a larger extent (Boulanger et al. 2012; Skarin and Alam 2017).

When reviewing different studies on the same type of disturbances, it is apparent how some report strong negative effects (e.g. Nellemann et al. 2001; Vistnes et al. 2001), while others have found weak (e.g. Noel et al. 2004; Anttonen et al. 2011; Eftestøl et al. 2016) or no effect (Yost and Wright 2001; Serrouya et al. 2017). Different findings may simply reflect the complexity of nature, where environmental factors and interactions not being included in the analyses affect the area use of the studied individuals and bias the isolated effect of a disturbance (e.g. Reimers and Colman 2006; Panzacchi et al. 2013; Skarin and Åhman 2014). As such, the approach used in Panzacchi et al. (2013) is a way forward, using path models to identify direct and indirect effects of infrastructure on habitat use. However, different findings could also be related to shortcomings in study design and sampling procedure. Our case study illustrates some pitfalls of reporting effects of infrastructure on *Rangifer* area use, when obviously there must be other reasons (i.e. correlation does not mean causation). Testing of hypotheses in controlled experimental studies may provide clear enough evidence to reject or accept a null hypothesis, while field studies in ecology often deal with complex data sets and many covariates (i.e. well-controlled research environments rarely exist), thus using multi-model inference. The best-fitted model may show several trends that provide an important new insight apart from the traditional hypothesis testing paradigm (e.g. Johnson 2002; Saltz 2011; Aho et al. 2014). However, complex models with several effect outcomes make interpretations challenging and it could be that most GPS studies relating to conservation biological issues (Online resource 1) emphasize more on trends in support of a main hypothesis of large-scaled human disturbance effects, while ignoring effect sizes (i.e. biological significance) or alternative explanations. On the other hand, it remains possible that some studies showing no effects are due to low sample sizes or inappropriate study sites (e.g. Vistnes and Nellemann 2008a). Another aspect of this is whether researchers collectively are conducting a systematic sorting of existing data sets, choosing to neglect some data, while working further on data sets showing promising tendencies in relation to a relevant hypothesis (Csada et al. 1996; Benítez-López et al. 2010). Such a “file-drawer problem” is also related to the possible bias of no-effect studies being more difficult to get published (Møller and Jennions 2001).

Based on the available data presented in the 52 reviewed papers, we found limited support in a majority of the cases (53% negative outcomes) for the general hypothesis that human infrastructure interferes negatively with *Rangifer* area use and population ecology. However, in large study areas with relatively large distances between infrastructures

(e.g. Johnson et al. 2005), there is a need to control for natural variation. If this is not possible, authors need to better consider positive results before concluding.

Previous literature reviews on anthropogenic effects on *Rangifer* spatial use have lacked some of the methodological issues discussed above, especially the interdependency between spatial and temporal scale. Vistnes and Nellemann (2008a) and Skarin and Åhman (2014) conclude from the literature reviews that avoidance from human disturbance for *Rangifer* more often is found in the studies performed at large landscape/spatial scale than for intermediate or local scale studies and emphasized the importance of large-scaled study designs to investigate avoidance responses since they appear at long distance from disturbances. However, they do not consider that a higher proportion of large scale than intermediate or local scale studies could make incorrect interpretations simply because the complexity of analysing explanatory factors increases with increasing spatial scale. Importantly, the larger the spatial scale in a study, the more important becomes the necessity of longer temporal scale. Actually, our review has shown that a majority of publications have not evaluated or analysed effects of spatial fluctuations at longer time intervals, and that a number of studies have not estimated the effects of confounding elements within the habitat, especially in terms of temporal variables. Future studies could also include various experimental approaches, for instance by manipulating the presence/absence of human disturbances or infrastructure while keeping as many remaining environmental factors as constant as possible (e.g. Flydal et al. 2004; Nellemann et al. 2010).

Conclusions

To improve our current knowledge base and provide new information relevant for decision making and optimal management, research needs the incorporation of long-term studies that take into account natural temporal variation on a large spatial scale, possibly control areas, and environmental data crucial for *Rangifer* habitats to fully understand spatial use of areas affected by infrastructure and human disturbance. While we focus on *Rangifer* as an example, our review and case study apply to many large, gregarious herbivores with similar behaviour ecologies and inhabiting areas with increasing amounts of anthropogenic disturbances.

Since spatiotemporal fluctuations complicate estimation of effects from human activity and infrastructure on *Rangifer* area use, we suggest two alternative study design approaches for future studies: (1) a BACI design possibly replicating several independent treatment and control areas if direct behavioural effects are expected on local scale, and (2) a BA design with multiple years before, during and after

infrastructure development, and including multiple spatial scales (preferably both population and individual home range levels), if indirect avoidance effects are expected at larger landscape scales.

Long-term variation in area use is expected for most *Rangifer* populations, and our current knowledge base on the effects of human activity and infrastructure on *Rangifer* is inadequate. Only 10% of the analyses reviewed here included both static and dynamic habitat variables when testing the effects of human activity or infrastructure on *Rangifer* area use. No analyses reviewed here included both dynamic and static habitat variables and yearly and random spatiotemporal variation together in the same model. With methodological and technological improvements, natural spatiotemporal variation in *Rangifer* area use can be better incorporated into future studies.

Random and preferably multiple sampling of *Rangifer* positions over long time periods is necessary to gather representative data on their area use, both spatially and temporally. It needs to be acknowledged that some studies do not have representative data for the areas in question. While previous reviews have emphasized how long distance avoidance from human disturbance in *Rangifer* require large-scaled study designs, we also highlight the need for longer time series to account for increased spatiotemporal variation with increasing spatial scale.

Less or more use of an area does not automatically relate to avoidance or attraction, as *Rangifer* naturally use some areas more or less than other. Methodological shortcomings for most studies investigating the effects of human activity and infrastructure on *Rangifer* area use have led to unsubstantiated conclusions, but also a bias towards reporting and highlighting negative effects. Although our review shows a 53% majority of negative effect outcomes, confirming the vulnerability of *Rangifer* to human disturbance, the remaining 47%, i.e. no and positive effect outcomes, may also suggest that disturbance effects are context specific and some human developments may have minor or no effect.

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Compliance with ethical standards

Conflict of interest We have no conflict of interest to declare.

References

- Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95:631–636. <https://doi.org/10.1890/13-1452.1>

- Allen AM, Mansson J, Jarnemo A, Bunnefeld N (2014) The impacts of landscape structure on the winter movements and habitat selection of female red deer. *Eur J Wildl Res* 60:411–421. <https://doi.org/10.1007/s10344-014-0797-0>
- Anttonen M, Kumpula J, Colpaert A (2011) Range selection by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in relation to infrastructure and human activity in the boreal forest environment, Northern Finland. *Arctic* 64:1–14
- Bartumeus F, Da Luz MGE, Viswanathan GM, Catalan J (2005) Animal search strategies: a quantitative random-walk analysis. *Ecolgy* 86:3078–3087. <https://doi.org/10.1890/04-1806>
- Bartzke GS, May R, Bevanger K, Stokke S, Røskoft E (2014) The effects of power lines on ungulates and implications for power line routing and rights-of-way management. *Int J Biodivers Conserv* 6:647–662. <https://doi.org/10.5897/IJBC2014.0716>
- Bates D, Mächler M, Bolker BM, Walker SC (2014) Fitting linear mixed-effects models using lme4. <http://arxiv.org/pdf/1406.5823.pdf>. Accessed 7 Sept 2018
- Bednekoff PA, Lima SL (2004) Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. *Proc Roy Soc B Biol Sci* 271:1491–1496
- Benítez-López A, Alkemade R, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol Conserv* 143:1307–1316
- Bergerud AT, Jakimchuk RD, Carruthers DR (1984) The Buffalo of the North-Caribou (*Rangifer tarandus*) and human developments. *Arctic* 37:7–22
- Bergerud AT, Lutich SN, Camps L (2008) The return of caribou to ungava. McGill-Queens University Press, Montreal
- Bischof R, Loe LE, Meisingset EL, Zimmermann B, Van Moorter B, Mysterud A (2012) A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am Nat* 180:407–424. <https://doi.org/10.1086/667590>
- Bissonette JA (2017) Avoiding the scale sampling problem: a consilient solution. *J Wildl Manag* 81:192–205. <https://doi.org/10.1002/jwmg.21187>
- Bjerketvedt DK, Reimers E, Parker H, Borgstrom R (2014) The Hardangervidda wild reindeer herd: a problematic management history. *Rangifer* 34:57–72
- Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650. <https://doi.org/10.1111/j.1461-0248.2008.01182.x>
- Boulanger J, Poole KG, Gunn A, Wierzchowski J (2012) Estimating the zone of influence of industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. *Wildl Biol* 18:164–179. <https://doi.org/10.2981/11-045>
- Boyce MS (2006) Scale for resource selection functions. *Divers Distrib* 12:269–276. <https://doi.org/10.1111/j.1366-9516.2006.00243.x>
- Cameron RD, Reed DJ, Dau JR, Smith WT (1992) Redistribution of calving caribou in response to oil-field development on the arctic slope of Alaska. *Arctic* 45:338–342
- Colman JE et al (2012) Behavioral interference between sympatric reindeer and domesticated sheep in Norway. *Rangel Ecol Manag* 65:299–308. <https://doi.org/10.2111/Rem-D-11-00094.1>
- Colman JE, Eftestøl S, Tsegaye D, Flydal K, Mysterud A (2013) Summer distribution of semi-domesticated reindeer relative to a new wind-power plant. *Eur J Wildl Res* 59:359–370. <https://doi.org/10.1007/s10344-012-0682-7>
- Colman JE, Tsegaye D, Flydal K, Rivrud IM, Reimers E, Eftestøl S (2015) High-voltage power lines near wild reindeer calving areas. *Eur J Wildl Res* 61:881–893. <https://doi.org/10.1007/s10344-015-0965-x>
- Colman JE, Bergmo T, Tsegaye D, Flydal K, Eftestøl S, Lilleeng MS, Moe SR (2017) Wildlife response to infrastructure: the problem with confounding factors. *Polar Biol* 40:477–482. <https://doi.org/10.1007/s00300-016-1960-8>
- Conner MM, Saunders WC, Bouwes N, Jordan C (2016) Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration. *Environ Monit Assess* 188:555
- Courtois R, Ouellet JP, Gingras A, Dussault C, Breton L, Maltais J (2003) Historical changes and current distribution of Caribou, *Rangifer tarandus*, in Quebec. *Can Field Nat* 117:399–414
- Cronin MA, Amstrup SC, Durner GM, Noel LE, McDonald TL, Ballard WB (1998) Caribou distribution during the post-calving period in relation to infrastructure in the Prudhoe Bay oil field, Alaska. *Arctic* 51:85–93
- Csada RD, James PC, Espie RHM (1996) The “file drawer problem” of non-significant results: does it apply to biological research? *Oikos* 76:591–593. <https://doi.org/10.2307/3546355>
- Dau JR, Cameron RD (1986) Effects of a road system on caribou distribution during calving. *Rangifer Spec Issue* 1:95–101
- DeCesare NJ et al (2012) Transcending scale dependence in identifying habitat with resource selection functions. *Ecol Appl* 22:1068–1083
- Dussault C, Pinard V, Ouellet JP, Courtois R, Fortin D (2012) Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proc Roy Soc B Biol Sci* 279:4481–4488. <https://doi.org/10.1098/rspb.2012.1700>
- Eftestøl S, Tsegaye D, Flydal K, Colman JE (2016) From high voltage (300 kV) to higher voltage (420 kV) power lines: reindeer avoid construction activities. *Polar Biol* 39:689–699. <https://doi.org/10.1007/s00300-015-1825-6>
- Falldorf T (2013) Habitat use of wild reindeer (*Rangifer t. tarandus*) in Hardangervidda, Norway. NINA report 982
- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288. [https://doi.org/10.1890/0012-9658\(2003\)084\[0282:Ufpti\]2.0.Co;2](https://doi.org/10.1890/0012-9658(2003)084[0282:Ufpti]2.0.Co;2)
- Flydal K, Eftestøl S, Reimers E, Colman JE (2004) Effects of wind turbines on area use and behaviour of semi-domestic reindeer in enclosures. *Rangifer* 24:55–66
- Gunn A, Russell D, White RG, Kofinas G (2009) Facing a future of change: wild migratory caribou and reindeer. *Arctic* 62:3–6
- Haskell SP, Ballard WB (2008) Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. *Can J Zool* 86:627–637. <https://doi.org/10.1139/z08-039>
- Helle T, Hallikainen V, Särkelä M, Haapalehto M, Niva A, Puoskari J (2012) Effects of a holiday resort on the distribution of semi-domesticated reindeer. *Ann Zool Fenn* 49:23–35
- Hinkes MT, Collins GH, Van Daele LJ, Kovach SD, Aderman AR, Woolington JD, Seavoy RJ (2005) Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *J Wildl Manag* 69:1147–1162. [https://doi.org/10.2193/0022-541x\(2005\)069\[1147:Iopgoc\]2.0.Co;2](https://doi.org/10.2193/0022-541x(2005)069[1147:Iopgoc]2.0.Co;2)
- Hobbs NT (2003) Challenges and opportunities in integrating ecological knowledge across scales. *For Ecol Manag* 181:223–238. [https://doi.org/10.1016/S0378-1127\(03\)00135-X](https://doi.org/10.1016/S0378-1127(03)00135-X)
- Iversen M, Fauchald P, Langeland K, Ims RA, Yoccoz NG, Bråthen KA (2014) Phenology and cover of plant growth forms predict herbivore habitat selection in a high latitude ecosystem. *PLoS One* 9:e100780
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71. <https://doi.org/10.2307/1937156>
- Johnson DH (2002) The role of hypothesis testing in wildlife science. *J Wildl Manag* 66:272–276. <https://doi.org/10.2307/3803159>

- Johnson CJ, Russell DE (2014) Long-term distribution responses of a migratory caribou herd to human disturbance. *Biol Conserv* 177:52–63. <https://doi.org/10.1016/j.biocon.2014.06.007>
- 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
- Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *J Wildl Manag* 70:347–357. [https://doi.org/10.2193/0022-541x\(2006\)70\[347:Rsfbou\]2.0.Co;2](https://doi.org/10.2193/0022-541x(2006)70[347:Rsfbou]2.0.Co;2)
- Johnson CJ, Ehlers LPW, Seip DR (2015) Witnessing extinction—cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biol Conserv* 186:176–186. <https://doi.org/10.1016/j.biocon.2015.03.012>
- Joly K, Nellemann C, Vistnes I (2006) A reevaluation of caribou distribution near an oilfield road on Alaska's North Slope. *Wildl Soc Bull* 34:866–869. [https://doi.org/10.2193/0091-7648\(2006\)34\[866:Arocdn\]2.0.Co;2](https://doi.org/10.2193/0091-7648(2006)34[866:Arocdn]2.0.Co;2)
- Jørgensen NH, Steinheim G, Holand Ø (2018) Does scale matter? Variation in area use across spatiotemporal scales of two sheep breeds in two contrasting alpine environments. *Rangel Ecol Manag* 71:189–195. <https://doi.org/10.1016/j.rama.2017.11.001>
- Klein DR (1994) Structures for caribou management and their status in the circumpolar north. *Rangifer Spec Issue* 9:245–252
- Kuvlesky WP, Brennan LA, Morrison ML, Boydston KK, Ballard BM, Bryant FC (2007) Wind energy development and wildlife conservation: challenges and opportunities. *J Wildl Manag* 71:2487–2498. <https://doi.org/10.2193/2007-248>
- Leblond M, Frair J, Fortin D, Dussault C, Ouellet JP, Courtois R (2011) Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. *Landsc Ecol* 26:1433–1446. <https://doi.org/10.1007/s10980-011-9647-6>
- Leblond M, Dussault C, Ouellet JP (2013) Avoidance of roads by large herbivores and its relation to disturbance intensity. *J Zool* 289:32–40. <https://doi.org/10.1111/j.1469-7998.2012.00959.x>
- Leclerc M, Dussault C, St-Laurent MH (2012) Multiscale assessment of the impacts of roads and cutovers on calving site selection in woodland caribou. *For Ecol Manag* 286:59–65. <https://doi.org/10.1016/j.foreco.2012.09.010>
- Leclerc M, Dussault C, St-Laurent M-H (2014) Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia* 176:297–306. <https://doi.org/10.1007/s00442-014-3012-9>
- Lesmerises F, Dery F, Johnson CJ, St-Laurent MH (2018) Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. *Biol Conserv* 217:149–156. <https://doi.org/10.1016/j.biocon.2017.10.030>
- Lingle S (2001) Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107:295–314
- Loe LE et al (2016) Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere* 7:e01374
- Lone K, Loe LE, Gobakken T, Linnell JDC, Odden J, Remmen J, Mysterud A (2014) Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123:641–651. <https://doi.org/10.1111/j.1600-0706.2013.00938.x>
- Long JA, Webb SL, Nelson TA, Gee KL (2015) Mapping areas of spatial-temporal overlap from wildlife tracking data. *Mov Ecol* 3:38
- Mahoney SP, Schaefer JA (2002) Long-term changes in demography and migration of Newfoundland caribou. *J Mammal* 83:957–963
- Moe SR, Holand Ø, Colman JE, Reimers E (1999) Reindeer (*Rangifer tarandus*) response to feces and urine from sheep (*Ovis aries*) and reindeer. *Rangifer* 19:55–60
- Møller AP, Jennions MD (2001) Testing and adjusting for publication bias. *Trends Ecol Evol* 16:580–586
- Mooring MS, Hart BL (1992) Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123:173–193
- Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M (2011) Human activity helps prey win the predator-prey space race. *PLoS One* 6:e17050. <https://doi.org/10.1371/journal.pone.0017050>
- Nellemann C, Fry G (1995) Quantitative analysis of terrain ruggedness in reindeer winter grounds. *Arctic* 48:172–176
- Nellemann C, Vistnes I, Jordhøy P, Strand O (2001) Winter distribution of wild reindeer in relation to power lines, roads and resorts. *Biol Conserv* 101:351–360. [https://doi.org/10.1016/S0006-3207\(01\)00082-9](https://doi.org/10.1016/S0006-3207(01)00082-9)
- Nellemann C, Vistnes I, Jordhøy P, Strand O, Newton A (2003) Progressive impact of piecemeal infrastructure development on wild reindeer. *Biol Conserv* 113:307–317. [https://doi.org/10.1016/S0006-3207\(03\)00048-X](https://doi.org/10.1016/S0006-3207(03)00048-X)
- Nellemann C, Vistnes I, Jordhøy P, Støen OG, Kaltenborn BP, Hanssen F, Helgesen R (2010) effects of recreational cabins, trails and their removal for restoration of reindeer winter ranges. *Restor Ecol* 18:873–881. <https://doi.org/10.1111/j.1526-100X.2009.00517.x>
- Noel LE, Parker KR, Cronin AA (2004) Caribou distribution near an oilfield road on Alaska's North Slope, 1978–2001. *Wildl Soc Bull* 32:757–771. [https://doi.org/10.2193/0091-7648\(2004\)032\[0757:Cdnaor\]2.0.Co;2](https://doi.org/10.2193/0091-7648(2004)032[0757:Cdnaor]2.0.Co;2)
- Northrup JM, Anderson CR, Hooten MB, Wittemyer G (2016) Movement reveals scale dependence in habitat selection of a large ungulate. *Ecol Appl* 26:2744–2755. <https://doi.org/10.1002/eap.1403>
- Nybakk K, Kjelvik O, Kvam T (1999) Golden eagle predation on semi-domestic reindeer. *Wildl Soc Bull* 27:1038–1042
- Nybakk K, Kjelvik A, Kvam T, Overskaug K, Sunde P (2002) Mortality of semi-domestic reindeer *Rangifer tarandus* in central Norway. *Wildl Biol* 8:63–68
- Panzacchi M, Van Moorter B, Jordhøy P, Strand O (2013) Learning from the past to predict the future: using archaeological findings and GPS data to quantify reindeer sensitivity to anthropogenic disturbance in Norway. *Landsc Ecol* 28:847–859. <https://doi.org/10.1007/s10980-012-9793-5>
- Panzacchi M, Van Moorter B, Strand O, Loe LE, Reimers E (2015) Searching for the fundamental niche using individual-based habitat selection modelling across populations. *Ecography* 38:659–669. <https://doi.org/10.1111/ecog.01075>
- Pape R, Loffler J (2015a) Ecological dynamics in habitat selection of reindeer: an interplay of spatial scale, time, and individual animal's choice. *Polar Biol* 38:1891–1903. <https://doi.org/10.1007/s00300-015-1750-8>
- Pape R, Loffler J (2015b) Seasonality of habitat selection shown to buffer alpine reindeer pastoralism against climate variability. *Ecosphere* 6:260. <https://doi.org/10.1890/Es15-00169.1>
- Pape R, Loffler J (2016) Spatial patterns of alpine phytomass, primary productivity, and related calorific resources. *Ecosphere* 7:e01347. <https://doi.org/10.1002/ecs2.1347>
- Pinard V, Dussault C, Ouellet JP, Fortin D, Courtois R (2012) Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *J Wildl Manag* 76:189–199. <https://doi.org/10.1002/jwmg.217>
- Plante S, Dussault C, Richard JH, Cote SD (2018) Human disturbance effects and cumulative habitat loss in endangered migratory caribou. *Biol Conserv* 224:129–143. <https://doi.org/10.1016/j.biocon.2018.05.022>
- 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. <https://doi.org/10.1016/j.biocon.2011.07.023>
- Post E et al (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358. <https://doi.org/10.1126/science.1173113>
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reimers E (2006) Wild reindeer calf recruitment variations; biology or methodology. *Rangifer* 26:7–14
- Reimers E, Colman JE (2006) Reindeer and caribou (*Rangifer tarandus*) response to human activity. *Rangifer* 26:55–71
- Reimers E, Dahle B, Eftestøl S, Colman JE, Gaare E (2007) Effects of a power line on migration and range use of wild reindeer. *Biol Conserv* 134:484–494. <https://doi.org/10.1016/j.biocon.2006.08.034>
- Reimers E, Røed KH, Colman JE (2012) Persistence of vigilance and flight response behaviour in wild reindeer with varying domestic ancestry. *J Evol Biol* 25:1543–1554
- Rivrud IM, Heurich M, Krupczynski P, Muller J, Mysterud A (2016) Green wave tracking by large herbivores: an experimental approach. *Ecology* 97:3547–3553. <https://doi.org/10.1002/ecy.1596>
- Rivrud IM, Sivertsen TR, Mysterud A, Ahman B, Stoen OG, Skarin A (2018) Reindeer green-wave surfing constrained by predators. *Ecosphere* 9:e02210. <https://doi.org/10.1002/ecs2.2210>
- Saltz D (2011) Statistical inference and decision making in conservation biology. *Isr J Ecol Evol* 57:309–317. <https://doi.org/10.1560/IJEE.57.4.309>
- Serrouya R, Kellner A, Pavan G, Lewis DW, DeMars CA, McLellan BN (2017) Time vs. distance: alternate metrics of animal resource selection provide opposing inference. *Ecosphere* 8:e01730. <https://doi.org/10.1002/ecs2>
- Sivertsen TR et al (2016) Reindeer habitat selection under the risk of brown bear predation during calving season. *Ecosphere* 7:e01583. <https://doi.org/10.1002/ecs2.1583>
- Skarin A, Åhman B (2014) Do human activity and infrastructure disturb domesticated reindeer? The need for the reindeer's perspective. *Polar Biol* 37:1041–1054. <https://doi.org/10.1007/s00300-014-1499-5>
- Skarin A, Alam M (2017) Reindeer habitat use in relation to two small wind farms, during preconstruction, construction, and operation. *Ecol Evol* 7:3870–3882. <https://doi.org/10.1002/ece3.2941>
- Skogland T (1986) Movements of tagged and radio-instrumented wild reindeer in relation to habitat alteration in the snøhetta region norway. *Rangifer* 6:267–272
- Skogland T (1989) Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Adv Ethol* 29:3–74
- Smokorowski KE, Randall RG (2017) Cautions on using the before–after-control-impact design in environmental effects monitoring programs. *Facets* 2:212–232. <https://doi.org/10.1139/facets-2016-0058>
- Strand O, Bevanger K, Falldorf T (2006) Reinens bruk av Hardangervidda. Sluttrapport fra Rv7-prosjektet (in Norwegian with English summary: use of Hardangervidda by reindeer. Final report from the state road 7-project) vol 131. NINA Rapport. Norsk institutt for naturforvaltning, Trondheim
- Taillon J, Festa-Bianchet M, Cote SD (2012) Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biol Conserv* 147:163–173. <https://doi.org/10.1016/j.biocon.2011.12.027>
- Theobald DM, Miller JR, Hobbs NT (1997) Estimating the cumulative effects of development on wildlife habitat. *Landsc Urban Plan* 39:25–36. [https://doi.org/10.1016/S0169-2046\(97\)00041-8](https://doi.org/10.1016/S0169-2046(97)00041-8)
- Tsegaye D, Colman JE, Eftestøl S, Flydal K, Rothe G, Rapp K (2017) Reindeer spatial use before, during and after construction of a wind farm. *Appl Anim Behav Sci* 195:103–111. <https://doi.org/10.1016/j.applanim.2017.05.023>
- Tucker MA et al (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359:466–469. <https://doi.org/10.1126/science.aam9712>
- Tveraa T, Fauchald P, Yoccoz NG, Ims RA, Aanes R, Hogda KA (2007) What regulate and limit reindeer populations in Norway? *Oikos* 116:706–715. <https://doi.org/10.1111/j.2007.0030-1299.15257.x>
- Uboni A et al (2016) Long-term trends and role of climate in the population dynamics of Eurasian reindeer. *PLoS One* 11:e0158359. <https://doi.org/10.1371/journal.pone.0158359>
- van Moorter B, Bunnefeld N, Panzacchi M, Rolandsen CM, Solberg EJ, Saether BE (2013) Understanding scales of movement: animals ride waves and ripples of environmental change. *J Anim Ecol* 82:770–780. <https://doi.org/10.1111/1365-2656.12045>
- Vistnes I, Nellemann C (2008a) The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biol* 31:399–407. <https://doi.org/10.1007/s00300-007-0377-9>
- Vistnes I, Nellemann C (2008b) Reindeer winter grazing in alpine tundra: impacts on ridge community composition in Norway. *Arct Antarct Alp Res* 40:215–224. [https://doi.org/10.1657/1523-0430\(07-001\)\[vistnes\]2.0.co;2](https://doi.org/10.1657/1523-0430(07-001)[vistnes]2.0.co;2)
- Vistnes I, Nellemann C, Jordhøy P, Strand O (2001) Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biol* 24:531–537
- 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
- Vowles T, Lovehø C, Molau U, Bjork RG (2017) Contrasting impacts of reindeer grazing in two tundra grasslands. *Environ Res Lett* 12:034018. <https://doi.org/10.1088/1748-9326/aa62af>
- Weir JN, Mahoney SP, McLaren B, Ferguson SH (2007) Effects of mine development on woodland caribou *Rangifer tarandus* distribution. *Wildl Biol* 13:66–74. [https://doi.org/10.2981/0909-6396\(2007\)13\[66:Eomdow\]2.0.Co;2](https://doi.org/10.2981/0909-6396(2007)13[66:Eomdow]2.0.Co;2)
- With KA, Gardner RH, Turner MG (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151–169. <https://doi.org/10.2307/3545811>
- Wolfe SA, Griffith B, Wolfe CAG (2000) Response of reindeer and caribou to human activities. *Polar Res* 19:63–73
- Yost AC, Wright RG (2001) Moose, caribou, and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. *Arctic* 54:41–48
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York