A road in the middle of one of the last wild reindeer migration routes in Norway: crossing behaviour and threats to conservation

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Abstract: The development of roads and associated infrastructure has interrupted several traditional migrations of wild reindeer *(Rangifer tarandus tarandus)* in Norway. The population in the Setesdal Austhei wild reindeer area still migrates from winter to calving grounds by semi-annually crossing a cabin-lined road through a narrow corridor, in which further anthropogenic development is planned. To understand if and how infrastructure affected reindeer migration patterns we studied the movements of 10 female reindeer equipped with GPS collars between 2002 and 2010. First, we identified the start and end of the migration period, and then we compared trajectory parameters (net displacement, step length and turning angles) recorded during migration with those recorded in proximity of the road. The analysis of the net displacement indicated that during spring migration reindeer moved at a constant pace towards the calving ground covering a net linear distance of 25 km in 40 days. In the middle of migration, reindeer changed travel direction and roamed parallel to the road for ca. 5 days without approaching further, possibly searching for an undisturbed place and time to cross. Reindeer finally crossed the road before daylight with highly directed movements, increasing their travel speed up to the highest values recorded during migration (4 km/3 hrs vs. 0.5 km/3 hrs). After crossing, reindeer moved quickly toward their calving ground covering the remaining 25 km net distance in less than a week. Migration patterns were markedly affected by disturbance during spring, as the road crossings occurred in the period characterized by the high traffic volume and intense human activities related to Easter holidays; during autumn, on the contrary, the hampering effect of the road was minimal. The results suggest that the current disturbance associated to the road hampers spring migration and might delay the arrival to the calving ground. The planned construction of a large number of recreational cabins in the migration corridor has the potential to threaten the migration and obstruct the access to the calving ground.

Key words: Calving ground; human disturbance; migration; *Rangifer;* roads; trajectory.

Introduction

Movement is one of the most striking features of the ecology of reindeer *(Rangifer tarandus tarandus).* The species inhabits the highly seasonal circumpolar environment, and typically follows greening vegetation by migrating from lichen-rich winter habitat with relatively little snow cover to highly productive and insect-free calving and summer pastures. The importance of the search for the optimal seasonal habitat to fitness is such that some *Rangifer* populations perform the longest overland movements in the world (Bergman *et al.,* 2000). However, the ongoing expansion of human-dominated areas

and the rapid development of transportation infrastructure interfere with the persistence of large-scale animal movements; many of the most spectacular migrations worldwide have either disappeared, or are in steep decline (Wilcove & Wikelski, 2008; Harris *et al.*, 2009).

Before industrial development Norwegian wild reindeer were grouped into two to three large population units that performed seasonal migrations between adjacent mountain systems, with summer ranges typically located in the west and winter ranges in the east. Nowadays, Norwegian wild reindeer are divided into 23 more or less isolated populations. Due to the development of roads, infrastructures and human disturbance, mainly along valley bottoms, several of the most important migration corridors were lost in the past centuries, and two of the most important remaining key corridors were abandoned in the 1980s (Skogland, 1986; Vistnes *et al.*, 2004). Recently, global position-

ing system (GPS) radio-collar data of reindeer from several parts of Norway show that most of the remaining movement corridors connecting different sub-populations are being used progressively less often or are being abandoned (*e.g.,* Vistnes *et al.*, 2004; Bevanger *et al.*, 2005; Strand *et al.*, 2006; Dahle *et al.,* 2008). The population of Setesdal Austhei is one of the few that still perform distinct seasonal migrations between non-overlapping summer and winter ranges. However, a road surrounded by cabins lies in the middle of the migration route, and reindeer have to cross it through a narrow corridor in which further anthropogenic development is planned. We studied the effect of this road on migration behavioral and movement patterns of GPS radio-collared females from the Setesdal Austhei population to understand if and how the proposed land development plan might affect the persistence of this migration.
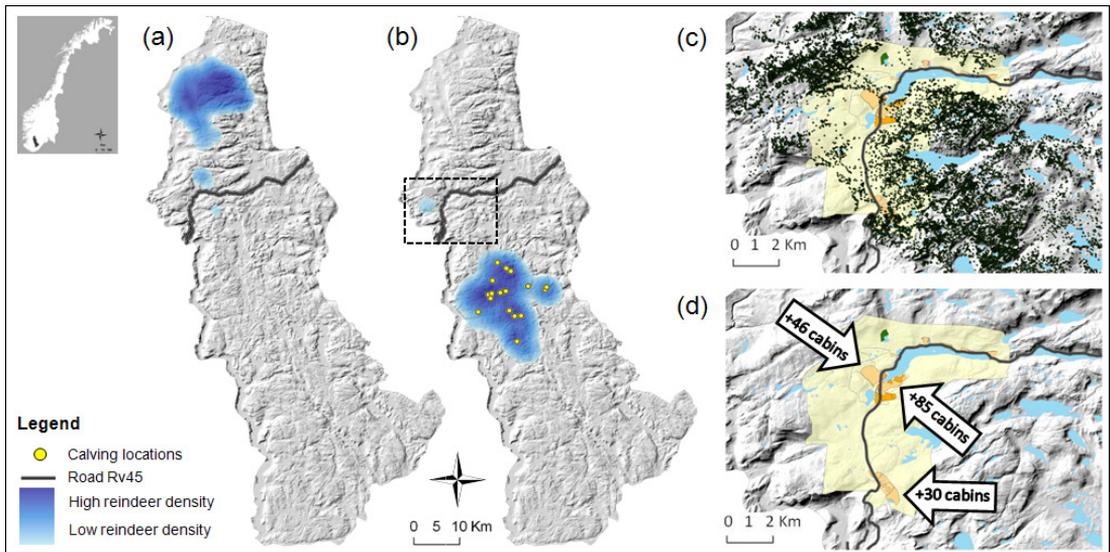
Fig. 1. The Setesdal Austhei study area. The location of a) winter (February) and b) calving range May15th – June 30th are represented by a 95% kernel density of the GPS radio-collar locations of 10 female reindeer monitored from 2002 to 2010. In (b) the yellow dots represent the locations of the calving events (*n* = 20) estimated for each individual each year. The dashed rectangle in b depicts the location of the area illustrated in (c), reindeer GPS radio-collar locations indicating the location of the two migration corridors, and (d), details of the land development plan for Bjørnevatn, indicating the planned location of the construction of several cabins for recreational use.

Methods

Study area

The Setesdal Austhei wild reindeer area (7° 78' E, 59° 23' N) is one of the two southernmost remaining populations of wild reindeer in Europe. The area was defined as a wild reindeer area in 1980 and opened for hunting in 1981; earlier, the reindeer inhabiting Setesdal Austhei were semi-domesticated. The area is confined by roads, which impede virtually any movement from or to other neighboring reindeer areas, and is bisected into a northern and southern part by a 45 km segment of the public road Rv 45, running parallel to a long dammed lake, Store Bjørnevatn, and cabins (Fig. 1). The average weekly daily traffic (AWDT) on Rv 45 is rather low but varies with time, being higher (AWDT ≈ 500 vehicles/day; Statens vegvesen, 2011) in spring during Easter holidays, which occur most often in the 8th week of the year, thus coinciding with the spring reindeer road crossing, and lower during the road crossing in autumn (AWDT ≈ 300). The northern area (ca. 770 km²) is dominated by mountains up to 1537 m asl, while the southern area (ca. 1600 km²) is characterized by low altitude hills and is mostly covered by forests. Further information regarding the study area can be found in Strand *et al.* (2011).

Reindeer migrate from their winter pastures in the northern area to the calving and summer areas in south. The reindeer GPS radio-collar data (see below) indicates that there are two migration corridors (Fig. 1c, d). One is approximately 1 km wide, and it is located adjacent to the western edge of the dammed lake, between Store Bjørnevatn and Lisle Bjørnevatn; the other is ca. 4 km wide, and is located south west of Lisle Bjørnevatn. However, we suggest that to characterize the location of the migration corridor more precisely further studies and data from a larger sample of animals, collected at finer temporal scales, are needed. The land development plan for Bjørnevatn includes the construction of a total of 161 cabins for recreational use (Kommuneplan for Bjørnevatn, 2008) in the migration corridors (Fig. 1c, d).

GPS radio-collar data

We captured 10 reindeer females in Setesdal Austhei and studied their movement pattern from 2002 to 2010. The animals were darted from helicopter, anesthetized using a mix of Salopine and Ketalar, equipped with GPS collars (Vectronics) with drop-off systems, and reversed using the antidote Narketan. The collars were programmed to record 1 GPS location every 3 hours. Outliers were identified and removed using the script provided in Bjørneraas *et al.* (2010).

Trajectory analyses

To understand whether and how Rv 45 affects reindeer migration patterns we first identified the migration period for each individual, calculated trajectory parameters during migration, and compared them with trajectory parameters calculated in proximity of the road. For each individual we selected 1 location every 3 hours and calculated the following trajectory parameters: step length (SL), turning angles (TA), net squared displacement (NSD), and net displacement (ND; Kareiva & Shigesada, 1983; Calenge *et al.,* 2009) using the package *adehabitat* (Calenge, 2006) in R 11.1 (R Development Core Team, 2011). ND is the mean distance between the first relocation of the trajectory and the last relocation of the current step (NSD is the same measurement, squared; Kareiva & Shigesada, 1983); hence, it describes the position of a step relative to other steps of the trajectory, and can be viewed as illustrating the movement towards or away from a starting point. Even though the analysis of ND throughout the year well describes an animal's movement patterns, the annual NDs of different individuals can be compared only if a common starting point is used for its calcula-

tion. As a starting point for the calculation of reindeer displacement we used calving sites, all situated in the southern part of the range. To investigate differences in ND before and after the road crossing, for each individual we performed linear regressions between ND and the number of locations before and after crossing. We compared the slope of the regression before and after crossings with a Wilcoxon paired signed-rank test. SL and TA during migration in different seasons, 5 days before/after crossing, and during crossing were compared using t-tests. Finally, we calculated summary statistics of the time of crossing using circular statistics (Jammalamadaka & SenGupta, 2001), which is commonly used when analyzing directional data such as time of day. In particular, we calculated the mean crossing time, and *rho,* which is a measure of the spread of the data; *rho* ranges from 0 (all values are concentrated in one point; *i.e.*, zero variance) to 1 (uniform distribution, with values uniformly scattered throughout the circular range; *i.e.*, in our case the clock).

Identifying calving sites
We did not know the exact calving dates of the GPS-collared females in the area. Hence, we estimated their calving dates by analyzing variations in trajectory parameters during the calving season (Van Moorter *et al.*, unpublished data.). As calving occurs after reindeer reach the calving area south from Rv 45, for each individual we analyzed movement patterns during the period starting after the road crossing and terminating on July 15th. In particular, for each female we calculated the residence time (RT) which quantifies the time (*i.e.*, number of locations) spent within a patch of a given radius, in our case the estimated calving site, before moving further (Barraquand & Benhamou, 2008). RT was calculated within 8 buffers of different radii (10, 25, 50, 75, 100, 150, 200, 500 m), chosen based on information on the specie's calving behavior. We assumed that calving oc-

curs on the day with the highest peak in RT. As the mean observed calving dates of wild reindeer in mainland Norway range between May 7 and May 28, and calving typically occurs very synchronously within each wild reindeer area (Reimers *et al.* 1983; Skogland, 1984; Reimers, 2002), we assumed that the best calving model was the one providing the most synchronous calving season (*i.e.*, the one providing the lowest variance in calving dates). The location of each individual during the average calving date was taken as a starting point for the calculation of its annual NSD, to investigate migration patterns.

Identifying the migration period
We calculated the average start and end date of the migration period by investigating the NSD of those individuals for which a full year of data, from one calving season to the next, was available (*n* = 21 reindeer-years). When animals move from a summer area to a winter area and back, the plot of their annual NSD appears like a double sigmoid: NSD increases during the autumn migration, reaches an asymptote when the animals reach the winter ground, and decreases again during the spring migration approaching zero if the animal comes back to the starting point (*i.e.*, the calving site). Hence, following Bunnefeld *et al.* (2011), we fitted a double sigmoid to the annual NSD of each individual:

$$NSD = \frac{\delta}{1+\exp(\frac{\theta_s - t}{\varphi_s})} + \frac{-\delta}{1+\exp(\frac{\theta_a - t}{\varphi_a})} \; ;$$

(Equation 1) where δ is the asymptotic height, θ_s and θ_a are the timing at which the migration reaches half its asymptotic height in spring and autumn, respectively, φ_s and φ_a models the timing elapsed between reaching half and

$\frac{1}{1+e^{-1}} \cong \frac{3}{4}$ of migration in spring and autumn, respectively, and t as time. Hence, the first sigmoid represents the autumn migration and the

second the return to the calving ground. The inflection point of each sigmoid indicates the time at which an individual has reached the middle distance between summer and winter areas, while the distance between the upper and lower asymptotes reflects the distance between the start and the end point of migration. Equation 1 was fitted by non-linear least squares using the nls function in R. For each individual, we defined the start and the end of the seasonal migration as the number of days required to move from 5% to 95% of each sigmoid (Fig. 2). All trajectory parameters (SL, TA, and NSD) were calculated within the migration period.

Results

We monitored 10 reindeer for a total of 21 reindeer-years; for each reindeer-year we obtained a minimum of 1085 locations, and a maximum of 2921 locations, for a total of 48 256 GPS positions, which can be viewed at http://www.dyreposisjoner.no.

Road crossing

All radio-monitored reindeer crossed Rv 45 twice a year during the seasonal migration. All crossings occurred during one single time
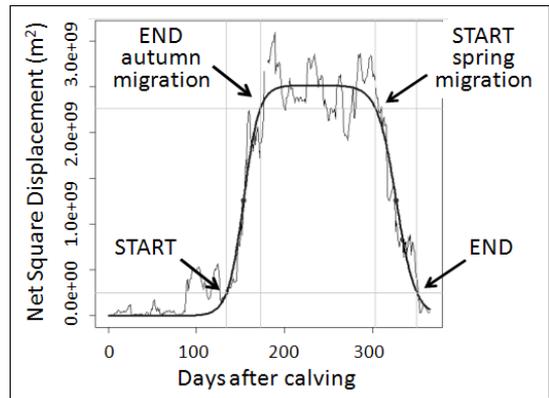
Fig. 2. Example of the migration parameters estimated for one focal individual based on its annual Net Square Displacement (NSD). The smooth line represents the model fitted to the focal individual to describe its migratory movement from the calving range to the winter range and back (Bunnefeld *et al.,* 2011). Grey lines identify the start and end of migration, defined as 5% and 95% of the sigmoid.

bout, except for one case in autumn. All spring crossings occurred between April 11th and May 8th (average ± SD: April 23rd ± 6 days, *n* =18) and during autumn/winter between Sept. 9th and Jan. 2nd (Oct. 9th ± 23 days, *n* = 22; note: in only two cases reindeer crossed after Oct. 13th). Circular statistics (Jammalamadaka &
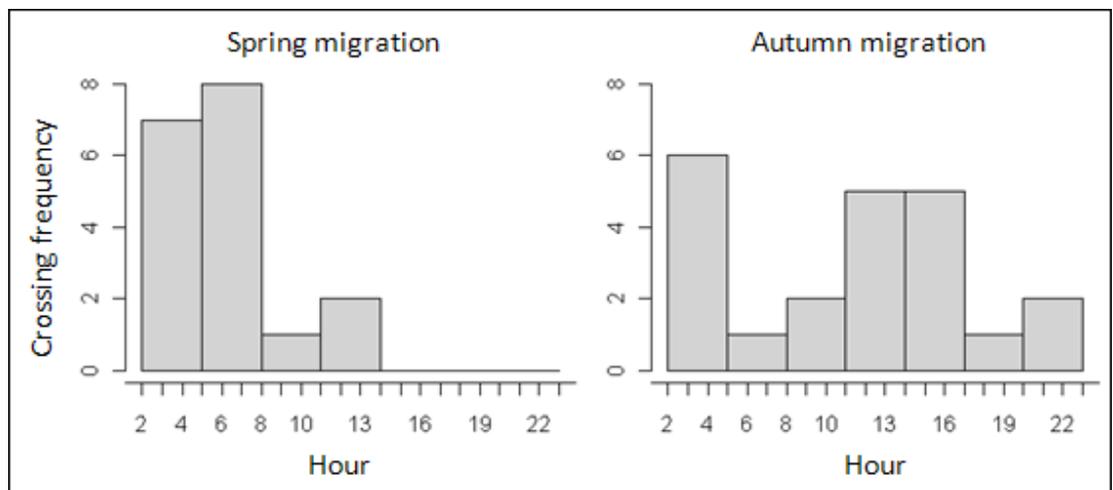
Fig. 3. Reindeer crossing frequency of road Rv 45 in Setesdal Austhei with respect to time of day during spring and autumn migration.

Table 1. Summary of the estimated start and end dates of migration, estimated calving dates, and observed dates and times of road crossing (± SD).

Period	Variable	Average	Range
Spring migration	Start date	Mar 15 ± 21 dd	Feb 22 - Apr 5
	Road crossing date	23 Apr ± 6 dd	Apr 11 - May 8
	Road crossing time	07:37 am (rho: 2.9) *	
	End date	3 May ± 9 dd	Apr 24 - May 12
	Calving	May 13 ± 5 dd	May 6 - May 23
Autumn migration	Start date	Sep 20 ± 15 dd	5 Sep - Oct 5
	Road crossing date	Oct 9 ± 23 dd	Sep 9 - Jan 2
	Road crossing time	18:18 pm (rho:0.7) *	
	End date	Nov 28 ± 23 dd	Nov 5 - Dec 20**

* Mean crossing time calculated with circular statistic (Jammalamadaka & SenGupta, 2001).
** Note: one individual that crossed on Jan 2nd was not included in the analyses of the migration period as we did not have enough data; however, for that individual the end of the autumn migration falls after Jan 2.

SenGupta, 2001), required for directional data, such as time of day, showed that most crossings occurred around 8:00 am (rho = 0.98). Seasonal differences in crossing time were detected (Fig. 3), with a higher frequency of crossings in the first hours of the day in spring (mean: 7:37 am) with very little variability (rho = 2.9), and no differences in autumn (mean: 6:18 pm, large variability: rho = 0.7); the difference between spring and autumn in the observed number of crossings in each of the eight 3-hour time bins was significant (X^2 = 27.943, df = 7, P < 0.001).

Calving dates
The method which performed best was the RT calculated within a radius of 150 m. Based on this method we estimated 20 calving dates (*i.e.*, for 10 adult females followed in 1 to 3 years). Calving occurred from May 6th to May 23rd (average: May 13th ± 4.6 days, SD). Calving occurred on average 21.6 ± 7.1 days (*n* = 17; range: 9 – 32 days) after the spring road crossing. In two cases the precision of our estimate was low, and did not allow us to estimate

calving dates. This means that either the animals did not calve, or that the mother did not change movement patterns markedly during calving days.

Migration time
The double sigmoid model described well the reindeer migratory movements, as it explained on average 94.2 % (± 1.7, *n* = 10) of the variance in individual annual NSD. However, the method did not always perform well in identifying with high precision the start and end day of migration. The reason is that NSD is strongly dependent on the location of the starting point, and as common starting point we chose the calving sites, which are not too spatially concentrated within the summer range. Hence, calving sites located closer to the road led to a slightly delayed estimated start of migration, while calving sites located at the extreme south of the distribution range led to a slightly early start of migration. However, our results indicate that autumn and spring migration started on average on Sept. 20th (± 15 days) and March 15th (± 21 days), lasted 49 and 69 days, respec-
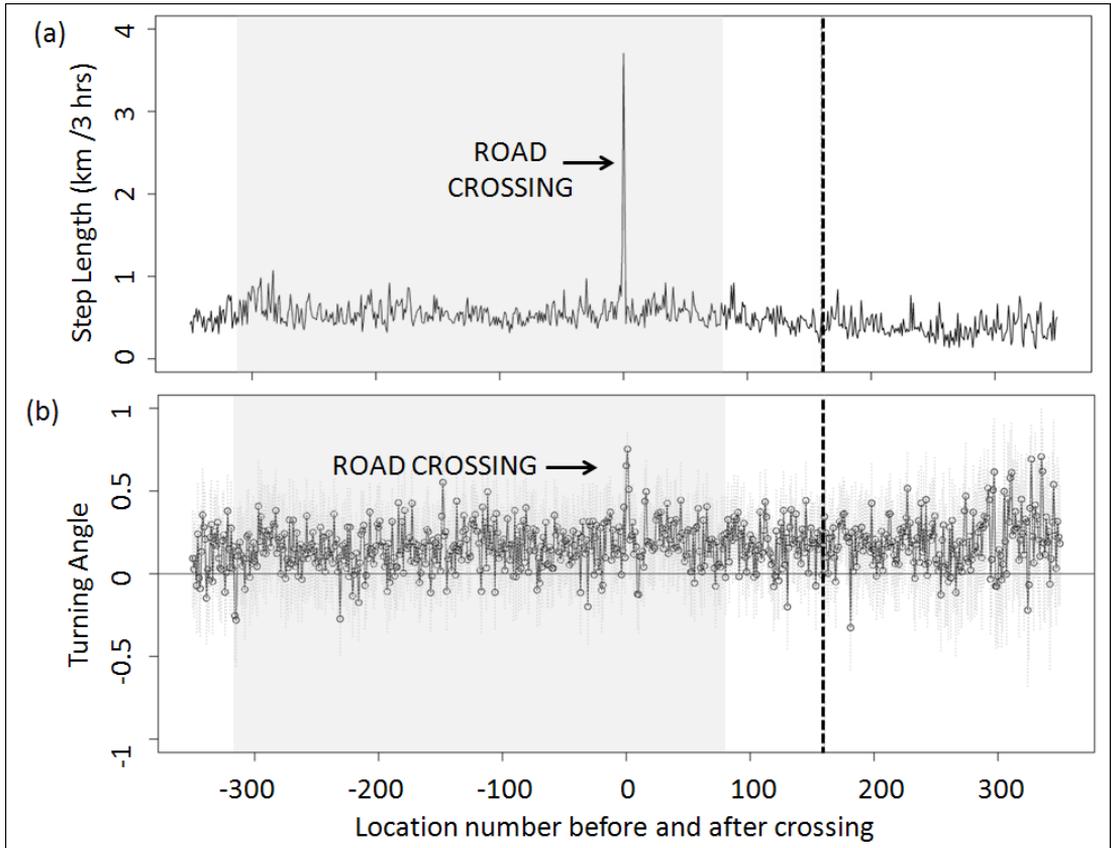
Fig. 4. Step length (upper graph) and turning angles (lower) of reindeer during 45 days (350 radio-locations) before and after the crossing of road Rv 45. The crossing occurs at the location coded 0, in the centre of the figure. The shaded area indicates the estimated migration period; the dashed line indicates the average estimated calving date.

tively, and covered 56.4 ± 5.4 km. A summary of the estimated migration periods, calving periods, and of the observed crossing dates is presented in Table 1.

Step length and turning angles

The average year-round SL was 0.493 km/3hrs ($\pm$ 0.632, n = 47 866). When the animals crossed the road the average travel speed increased up to 3.706 km/3hrs ($\pm$ 1.578, n = 37), with no difference between spring and autumn, and was much higher than the speed recorded during the 5 days (*i.e.*, 40 locations) before or after the crossing (0.613 km/3hrs $\pm$ 0.722, n

= 2917; $t_{36.191}$ = 11.905, $P < 0.001$) or during the whole migration ($t_{110.296}$ = -10.398, $P < 0.001$; Fig. 4). Similarly, during the crossing in spring and autumn the average cosine of the turning angles was much higher than the one recorded during the 5 days before and after the crossing (0.515 $\pm$ 0.565, n = 93 vs. 0.162 $\pm$ 0.719, $t_{104.254}$ = -5.844, $P < 0.001$), or during migration (0.132 $\pm$ 0.717, n = 48256; $t_{113.048}$ = -6.286, $P < 0.001$), indicating very directional movements.

Net displacement

If the presence of the road had no effect on the

spatial behavior during migration, we would expect the ND calculated from the crossing point to decrease linearly while the reindeer were approaching the road, and increase linearly after the road crossing (Fig. 5a). This is what we observed in autumn (Fig. 5b), as the slopes of the regression lines calculated for each individual between ND and the number of locations did not differ before and after crossing ($V = 87$, $n = 18$, $P = 0.644$). On the contrary, during spring the slopes of the regression lines were much higher after crossing compared to when approaching the road ($V = 165$, $n = 18$, $P < 0.001$). Indeed, during spring ND decreased slowly as the reindeer approached the road, it suddenly dropped before the road cross, and increased sharply after the crossing, with very little individual variability (Fig. 5c), due to the fact that after crossing the road movements became much more directional, with reindeer heading straight and quickly to their calving ground. While during spring reindeer migrated slowly towards the road covering a net linear distance of ca. 25 km in ca. 40 days, after the crossing they quickly drifted away from the road covering the same net distance in a week, and after 20 days they were displaced 35 km south of the road (Fig. 5b).

Discussion

Several wild reindeer populations in Norway have abandoned their historical migration routes due to the expansion of human activities, namely transportation infrastructure and recreational facilities. We present the case of the population in Setesdal Austhei, which still performs distinct seasonal migrations between winter and calving grounds by crossing a road located in the middle of the migration corridor. Our results, however, show that all trajectory parameters are markedly altered in proximity of the road during both spring and autumn, as while crossing the road reindeer increase their travel speed to reach the highest values record-
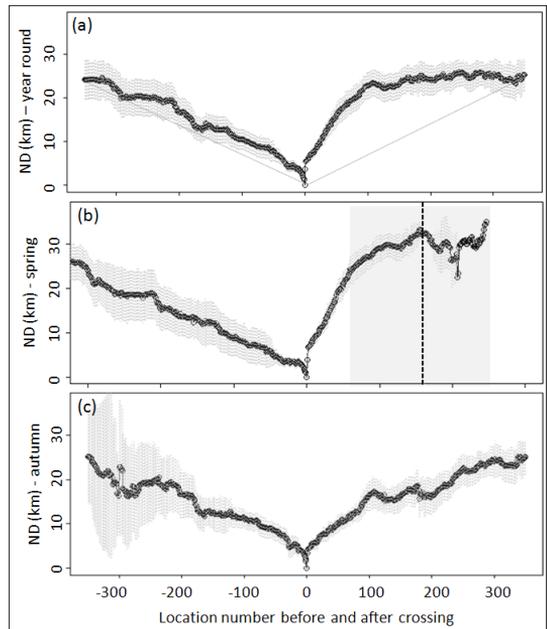
Fig. 5. Average Net Displacement (ND, km), which illustrates the speed of the movements towards and away from the road, calculated from the crossing point (coded 0) during 350 locations (ca. 45 days) before and after the crossing of road Rv 45 during both spring and autumn migration (a), and separately during spring (b) and autumn (c); dashed bars indicate standard errors. The dotted line in (a) indicates a theoretical ND if reindeer moved between the summer and winter areas at a constant speed (i.e., if the presence of the road had no effect on the spatial behavior during migration). The shaded area and the dashed line in (b) indicate, respectively, the estimated calving range and average estimated calving date.

ed during migration, perform highly directional movements, and cross during hours when the traffic is minimal. Most importantly, as the spring road crossings occur in the period characterized by the high traffic volume and intense use of private cabins related to Easter holidays, the overall spring migration patterns change as reindeer approach the road, and remain altered up to the arrival to the calving ground. During spring reindeer migrate at a constant pace towards the calving ground covering a net linear distance of 25 km in 40 days. As rein-

deer approach the road, they change travel direction and roam parallel to the road for ca. 5 days without approaching further, possibly searching for an undisturbed place and time to cross. As the pregnant reindeer cross the road, they speed up and quickly head toward calving ground covering the remaining 25 km net distance in less than a week. This suggests that the current disturbance associated with the road hampers spring migration and may delay the arrival to the calving ground. Interestingly, during autumn we could only identify short-term effects of the road (*i.e.*, travel speed increased and movements were highly directional during crossing), but no longer-term alteration of the migration patterns could be detected. This is probably due both to the lower traffic volume during autumn and to the lower physiological urgency of reaching the winter range.

The impact of infrastructure on *Rangifer* distribution and habitat use has been extensively documented worldwide during the last decades (Mahoney & Schaefer, 2002; Vistnes *et al.*, 2004; Johnson *et al.,* 2005; Nellemann *et al.,* 2010). Several studies reported range shifts in response to the construction of infrastructure (*e.g.*, Nellemann *et al.*, 2001; Dyer *et al.,* 2002), or documented the avoidance of potentially suitable habitat for several kilometers around disturbed areas, with little or no sign of habituation in the following decades (Vistnes & Nellemann, 2008; Nelleman *et al.,* 2010) or centuries (Schaefer, 2003). Not all studies, however, reached similar conclusions, and it has become clear that the responses to disturbance can vary greatly spatially and temporally depending on the type and size of the infrastructure, its location with respect to the core area of reindeer distribution range, variations in the intensity of disturbance, winter harshness, food availability and population density, and the degree of wildness of the population (Skogland, 1986; Carruthers & Jakimchuk, 1987; Duchesne *et al.,* 2000; Mahoney & Schaefer, 2002; Reimers *et al.*, 2007).

The list of confounding factors complicating the assessment of reindeer responses to human disturbance likely increases if the infrastructure is located in the middle of a migration corridor, as during migration reindeer may be forced to tolerate, up to a certain degree, higher levels of disturbance to avoid potentially serious population consequences. Dahle *et al.* (2008), for example, documented a clear avoidance of a buffer area surrounding a road, but no aversion could be detected along the same road in proximity of a traditional migration corridor. Hence, the drive for migration is such that it is often difficult to recognize the tipping point turning a permeable barrier into an effective barrier to migration in time useful for implementing mitigation measures. The construction of a railway and a parallel road in Norway, for example, obstructed a key migration corridor for decades. As the population, trapped in one of the seasonal ranges, reached high densities and faced overgrazing and starvation, reindeer started crossing the infrastructure occasionally during harsh winters. However, coincident with the increase in traffic and a reduction in deer numbers, all crossings finally stopped during the 1980s (Skogland, 1986). Hence, if the drive for migration is high, a given infrastructure can represent a barrier under some circumstances but not others, and the long-term population response may become evident only when the implementation of mitigation measures would be more complex and costly.

Previous analyses (Panzacchi *et al.,* 2011) showed that the motivation pushing the Setesdal Austhei population to continue migrating is high, as the optimal calving and winter grounds are located on the opposite sides of the road, and none of seasonal ranges seem to contain preferred resources year-round. Our study shows that even though reindeer still migrate through a narrow bottleneck on the west side of the road, migratory patterns are markedly

altered by the disturbance associated with the road, especially during the spring migration to the calving ground. Considering the high drive for migration, our results suggest that the Setesdal Austhei population is already forced to tolerate relatively high levels of disturbance during spring migration to reach the preferred calving ground. The long-term consequences of the present intensity of disturbance associated with the road, cabins and dam are difficult to predict. However, based on previous experiences (*e.g.*, Skogland, 1986), it is plausible that the planned construction of additional 161 private cabins in the migration bottleneck (Strand *et al.,* 2011; Fig. 1c, d) will have critical consequences for the persistence of migration and for population viability. The data for the 10 GPS radio-collared females indicate that the migration corridors are very small: one is located in a very small geographic bottleneck of ca 1 km between two lakes, and the other covers an area of ca. 4 km (Fig. 1c, d). This implies that the implementation of mitigation measures at this stage might still be relatively cost-efficient. We are currently collecting GPS data for more animals on a finer temporal scale (*i.e.*, 15 min) to be able to assess more precisely the location of the migration corridor and analyze the relative effect of factors affecting the time and location of crossing, in order to assist the development of efficient mitigation measures. We recommend developing urgent, targeted and sound conservation plans to secure a future for the migration of the Setesdal Aushtei population.

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