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Effects of highway fencing and wildlife crossings on moose *Alces alces* movements and space use in southwestern Sweden

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Use of exclusion fencing is an effective method to reduce moose-vehicle collisions, and exclusion fences are commonly erected along Swedish highways. However, exclusion fences may pose a threat to the viability of wildlife populations because they serve as barriers to individual movements and may limit accessibility to resources. Various types of wildlife crossings intended to reduce road-kills and increase habitat connectivity across fenced highways have been constructed throughout the world. However, few studies have evaluated the effectiveness of these crossing structures with respect to movements before, during and after construction of highways and exclusion fencing. We studied movements of 24 GPS-collared moose *Alces alces* before, during and after an existing two-lane road was reconstructed to a fenced four-lane highway with three wildlife crossings designed for moose. We recorded 135 movements across the highway during 8,830 moose-monitoring days. Of these, 47 occurred before the construction began, 76 occurred during the construction, and 12 occurred after the highway was fenced. All movements registered after the fencing occurred across two of the three wildlife crossings. The average number of highway crossings per moose-day decreased by 67-89% after fencing. The number of moose-vehicle collisions decreased after the exclusion fencing, but the fenced highway served as a barrier to moose movements even though three wildlife crossings were created. Thus, exclusion fencing may reduce moose mortality and provide safer conditions for automobile travellers, but the fencing may have a negative impact on moose accessibility to resources, gene flow and recolonisation rates.

Key words: Alces alces, barrier effect, exclusion fence, highway, moose, wildlife crossings

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Transportation infrastructure has drastically changed the Swedish landscape over the past century, and the Swedish road network occupies approximately 1.2% of the country's land surface (Eriksson & Skoog 1996). Because of their large home range and preference for disjunctive foraging areas, moose *Alces alces* may be particularly impacted by roads. Moose numbers began to increase drastically in Sweden during the 1960s as a result of improved habitats (Lavsund et al. 2003), age and sex-specific hunting strategies, and lack of predators (Cederlund & Markegren 1987). Due to high moose densities and increased traffic volumes, moose-vehicle accidents have increased substantially over several decades (Seiler 2003). During the 1990s, Swedish police recorded > 4,000 moose collisions annually, but the total number of accidents is likely twice as high (Seiler 2003).

Various measures to limit moose-vehicle collisions have been tested (Almqvist et al. 1980). However, only exclusion fencing (2.1 m high) and roadside clearing have been cost-effective (Niklasson & Johansson 1987). More than 5,000 km, i.e. approximately 34%, of the highways and national roads have been fenced in Sweden (Seiler 2003). Although exclusion fencing reduces the risk of moose-vehicle accidents, the potential negative effects that these structures may have on moose and other wildlife are unclear. Reduced gene flow, reduced accessibility to resources, habitat degradation and small population size can lead to a greater vulnerability to environmental and demographic stochastic events (Jaeger & Fahrig 2004, Riley et al. 2006).

Construction of wildlife crossings along fenced roads can provide both safe road conditions for humans and mitigate barrier effects on wildlife (Andrews 1990, Bekker & Canters 1995, Foster & Humphrey 1995, Rodrigez et al. 1996, 1997, Clevenger & Waltho 2000). In Sweden, underpass structures for smaller vertebrates are common, but few passages designed specifically for large mammals exist (A. Sjölund & M. Lindqvist, Swedish National Road Administration (SNRA), pers. comm.). The objective of our study was to evaluate moose response to exclusion fencing and wildlife crossings in southwestern Sweden. Specifically, we monitored moose movements and space use before, during and after construction of a highway with three wildlife crossings.

Study area

Our study was conducted in southwestern Sweden along European highway 6 (E6) north of Uddevalla. In our study area, E6 was converted from a two-lane, non-fenced road to a fenced four-lane highway. A 15-km segment of E6 divides the study area into two equal-sized fragments (Fig. 1). The southernmost 6 km of this segment was finished in June 2000 and the 6 km in the middle in June 2004. The northernmost 3 km will be converted to a fenced highway in the summer of 2008, and thus was not fenced during our study. After fencing had been erected, moose could only cross the highway through three wildlife crossings, three conventional bridges, two conventional tunnels, and an unfenced section in the north. Ungulates inhabiting a 220 km^2 peninsula on the west side of E6 were likely to be most negatively impacted by the isolating effects of the fence. The segment of E6 that bisected our study area had an average traffic volume of about 12,000 vehicles/day throughout the study period (SNRA traffic volume database).

Forests dominated the landscape east of the highway (70% land area) with a small amount of farmlands (7%), whereas west of the highway, the landscape was comprised of a mosaic of forests (40%) and farmlands (30%). The percentage of clear-cut forest was the same (i.e. 10%) on both sides of the highway. Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* dominated the forest, but it also included deciduous species such as common alder *Alnus glutinosa*, oak *Quercus* sp., birch *Betula* sp., and mountain ash *Sorbus aucuparia*. In February 2004, a helicopter survey estimated the moose density within the study area to be 8.3 moose/10 km^2 (Svensk Naturförvaltning AB 2004).

We investigated three stages of road development which potentially could have altered the space use and movements of moose (see Fig. 1): 1) the period before construction (with a speed limit of 90 km/hour), lasting from February 2002 to September 2002 (the road in the southernmost 6 km of the study area was a fenced highway with two wildlife crossings, one overpass, and one underpass); 2) the period during highway construction (with a speed limit of 70 km/hour), lasting from October 2002 to May 2004 (during which the 6 km in the middle of the highway through the study area was under road construction); and 3) the period

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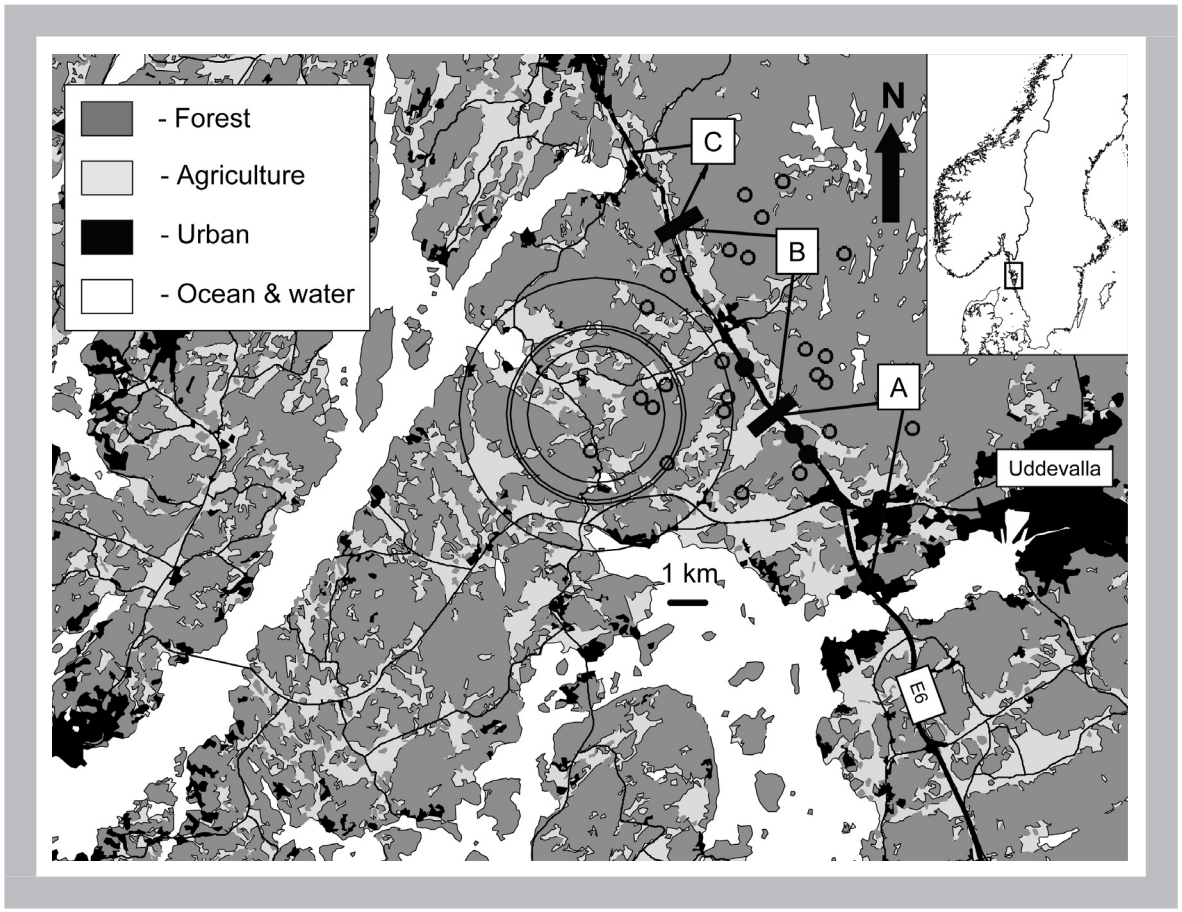


Figure 1. Location of the study area and highway E6 with the three wildlife passages (•) of which the southernmost wildlife overpass was completed in June 2000, the wildlife underpass in the middle in June 2000, and the most northerly wildlife overpass in June 2004. The highway reconstruction segments A-C were finished in June 2000 (A), in June 2004 (B) and in summer 2008 (C). Capture locations of the 24 collared moose are shown (○) and the large circles indicate mean annual home ranges of males and female moose calculated using minimum convex polygon method (MCP) and 95% fixed-kernel method. From the largest to the smallest circle, the mean annual home ranges are shown for MCP-male (48.6 km^2), MCP-female (20.8 km^2), 95% fixed-kernel-male (19.1 km^2) and 95% fixed-kernel-female (12.1 km^2), respectively.

after highway construction (with a speed limit of 110 km/hour), lasting from June 2004 to December 2005. The highway in our study area was fenced in June 2004 and moose could only cross the highway through three wildlife crossings, five conventional underpasses and overpasses, and through an unfenced section north of our study area. Two mountaintops were removed along the 15-km section of the highway, and the highway was lowered to level out the topography. The surrounding land was untouched, and two overpasses were built at the former topographic ground level, each being hourglass shaped, 60 m long and 17 m and 13 m wide at the centre, respectively. The sides of the overpasses were covered with 2-m high 'shields' to minimise highway disturbances. Both overpasses were covered with sand and combined with gravel roads with low traffic use (0.4 and 1.6 vehicles/hour, respectively). The underpass (being 35 m long, 4.7 m high and 13 m wide) was combined with a paved road (15 vehicles/hour) and was located between the two overpasses.

Methods

We collared a total of 24 moose, 10 males and 14 females during the winters of 2002, 2003 and 2004, and we monitored the moose until December 2005. Each captured moose was equipped with a GPS-collar (Televilt Inc., Lindesberg, Sweden) for up to 22 months before pre-programmed drop-off mechanisms were activated. All moose were captured

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within a 55 km^2 area transected by the highway. The average linear distance to highway E6 from the point of capture was 2 km (minimum = 470 m, maximum = 4,097 m and SD = 986 m). Because all three wildlife crossings were built within a 4-km stretch of highway E6, all collared moose, theoretically, had access to any of the three crossing points. Moose positions were collected at 2-hour intervals, and the number of moose positions totalled 76,170 during the 46 months of our study. We divided data on individual animals into four seasons based on climate conditions and moose biology in the following way: spring (16 March-15 May), summer (16 May-30 August), fall (1 September-30 November) and winter (1 December-15 March).

We used Arc View 3.3 (Environmental System Research Institute, Redlands, California, USA) and digital geographic land cover data (data acquisition, 2001) obtained from the National Land Survey (Gävle, Sweden) to determine highway crossings by collared moose. We defined a movement across the highway using two subsequent locations documented on each side of the highway and considered GPS errors and their influence on location accuracy. Moose movements were analysed using three data sets: 1) Before-after construction, 2) Before-during construction, and 3) During-after construction. The first data set included the total number of highway crossings per moose-day made by all GPS-collared moose (N = 21) before (February 2002-September 2002) and after (June 2004-December 2005) construction of the highway (Table 1). The second data set only included data on moose (N = 7) that were monitored both before and during the construction phase (February 2002-June 2004). No exclusion fence was present at the middle section during this stage of construction. The third data set only included data on moose (N = 12) that were monitored both during construction and after fencing of the middle section of E6 (February 2003-December 2005). For all analyses, we standardised the number of road crossings based on the total number of moose-days within each period. We determined wildlife crossing use from GPS-data, infrared camera surveillance (southern overpass) and by track counts in sand traps and excluded all highway crossings (N = 20) that occurred outside the study area from analysis. Because data were not normally distributed, we used χ^2 tests to determine whether differences existed in movement frequencies across the highway. We used Yeates correction to correct for estimation errors within 2×2 tables, and Kruskal-Wallis tests on ranks to examine seasonal effects among frequencies of highway crossings (Statistica 7.1).

We used the Animal Movement extension (Hooge & Eichenlaub 2000) to generate seasonal home ranges using the 100% minimum convex polygon (MCP) method (Mohr 1947). We used MCP as the outer home-range border and its location in relation to the highway was of interest, rather than how home-range core areas related to the highway. We analysed the location of seasonal home ranges (west of, east of, or intersected by the highway) before and after fencing using χ^2 tests. We used home-range frequencies in relation to the road during construction as the expected frequencies. We only used home-range data for moose that were collared over the period during construction and after fencing of the highway (N = 12; i.e. data set 3).

Results

We recorded 135 highway crossings during a total of 8,830 moose-days. Of these, 47 occurred before the construction was initiated, 76 during construction, and 12 occurred after the highway had been fenced. All highway crossings after fencing occurred at the two overpasses designed for moose. No crossings were observed at the wildlife underpass or the five conventional overpasses and underpasses during the entire study. Males crossed the highway more frequently than females, accounting for 95% of the total number of crossings during the entire study. Males also crossed the wildlife overpasses more often than females, accounting for 60% of the total

Table 1. Data on the reconstruction of the 6 km section in the middle of highway E6 near Uddevalla, Sweden, and on moose monitoring during each of the three periods, during February 2002-December 2005.

	Before fencing		After fencing
Construction	Before construction	During construction	After construction
Time period	02.2002-09.2002	10.2002-05.2004	06.2004-12.2005
Months	7	20	19
Moose monitoring days	1302	4384	3144

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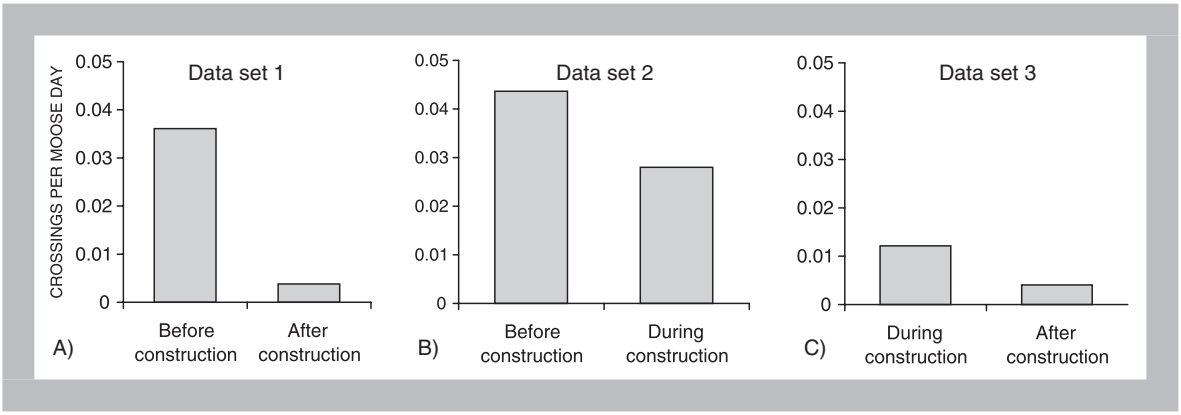


Figure 2. Mean number of highway E6 crossings per moose-day near Uddevalla, Sweden during 2002-2005. The three data sets used were: A) Before-after construction, B) Before-during construction and C) During-after construction.

number of crossings ($\chi^2 = 3.87$, df = 1, $P < 0.049$). We observed no seasonal effects among the crossing frequencies ($H_{3,128} = 2{,}15$; $P = 0.54$), but there was an indication that wintertime movements across the highway were less frequent than crossings during spring, summer and fall. The average number of crossings over the highway per moose-day decreased by 89%, from an average of 0.036 crossing/day before fencing to 0.0038 after fencing ($\chi^2 = 65.4$, df = 1; $P < 0.005$; Fig. 2; data set 1).

In data set 2, we monitored seven moose (five females and two males) before and during the construction phase. Two males routinely crossed the unfenced road during this period. A total of 97 crossings (47 before construction and 50 during construction) were recorded during a total of 2,862 moose-days. The average number of highway crossings per moose-day decreased by 36% ($\chi^2 = 4.76$, df = 1, $P < 0.029$) from an average of 0.044 before construction to 0.028 during construction (see Fig. 2; data set 2). In data set 3, we monitored 12 moose (seven females and five males) during and after construction. Of these moose, six routinely crossed the highway during the construction phase and two after the highway had been fenced. We recorded a total of 38 highway crossings during a total of 5,093 moose-days. Of these, 26 occurred before and 12 after the highway had been fenced. No crossings were documented at the wildlife underpass or at the conventional overpasses and underpasses. The average number of highway crossings per moose-day decreased by 67% ($\chi^2 = 24.8$, df = 1, $P < 0{,}005$) from an average of 0.012 during construction to 0.0041 after construction (see Fig. 2; data set 3).

Home-range location changed significantly from before to after the highway fencing had been erected ($\chi^2 = 9{,}44$, df = 2, $P = 0{,}009$). The percentage of seasonal home ranges that were intersected by the highway decreased from 26% (10 of 38) before fencing to 13% (five of 38) after fencing. Most of the moose that had home ranges that were bisected by the highway prior to the fencing changed their movement behaviour and moved their home ranges to the west of the highway after fencing.

Discussion

In our study, we documented reduced moose crossing rates during the two stages of road reconstruction. The overall effect (data set 1) revealed an 89% reduction in crossing frequency; however, different animals were collared during these two periods. In data set 3, crossing rates decreased by 67%. However, these moose may also have been affected (as moose in data set 2) during construction, and hence an initial lowered crossing rate might have occurred. Male crossings were decreased more by exclusion fencing than were those of females. However, females had a very low crossing frequency during the whole study period, which may relate to their smaller home ranges and that they consequently encounter roads less often than males. The importance and use of wildlife crossings are not only affected by passage dimensions and landscape features (Yanes et al. 1995, Rodrigez et al. 1996, Ng et al. 2004, Clevenger & Waltho 2005), but also by presence of other more preferred crossing opportunities (Clevenger et al. 2002). As in previous studies (Clevenger

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et al. 2002), moose in our area were selective towards overpasses even though an underpass was located < 700 m away.

Few studies have quantified barrier effects from road networks on large ungulates, but a study with GPS-collared caribou *Rangifer tarandus* in Alberta identified unfenced roads as potential barriers, which were crossed up to six times less frequently than simulated road networks (Dyer et al. 2002). Other linear structures such as pipelines can also inhibit movement patterns of large ungulates. In Alaska, caribou crossed roads parallel to pipelines less frequently than expected (Curatolo & Murphy 1986, Murphy & Curatolo 1986). Although restricted movements caused by fencing may impact wildlife populations negatively (Jaeger & Fahrig 2004, Jaeger et al. 2005), decreased mortality due to collisions with vehicles might be beneficial to population viability (Bekker & Canters 1995, Foster & Humphrey 1995). However, today, moose-vehicle collisions are not a threat to the viability of the Swedish moose population, but local impacts may be significant (Seiler 2003). The number of reported moose-vehicle accidents within our E6 study area decreased after fencing and the creation of the wildlife crossings. On average, 2.7 moose-vehicle accidents per year (N = 35) were reported along the unfenced road segment during 1990-2001 (with a speed limit of 90 km/hour during 153 months), whereas only 1.8 accidents per year (N = 3) were reported during the construction phase (with a speed limit of 70 km/hour during 20 months) of the middle section. Furthermore, no moose-vehicle accidents have been reported since the highway was completed in June 2004 (with a speed limit of 110 km/hour during 31 months).

Barriers caused by infrastructure may reduce gene flow (Riley et al. 2006) and recolonisation rates, and small isolated populations may be more vulnerable to external effects such as hunting (Sæther et al. 2003). Whereas too few individual moose used the overpass to compensate for annual mortalities associated with hunting, enough did so to maintain gene flow between otherwise isolated subpopulations (Mills & Allendorf 1996). It is most likely that the wildlife crossings will be used more frequently in the future, as individuals adapt to structural attributes and redirect their movements according to their location (Clevenger et al. 2002). Subjects related to barriers and their effect on the demographics of small populations, recolonisation rates, and the effects of hunting, must be evaluated further. It is important to identify and optimise effective wildlife crossings both with respect to construction cost and efficiency for ungulates and other wildlife, and thereby reduce wildlife-vehicle collisions at associated highways.

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