Management and Conservation Article

Behavior of Moose Relative to a Road Network

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ABSTRACT Roads often negatively affect terrestrial wildlife, via habitat loss or fragmentation, noise, and direct mortality. We studied moose (*Alces alces*) behavior relative to a road network, in an area with a history of moose–vehicle accidents, to determine when moose were crossing roadways or using areas near roads and to investigate if environmental factors were involved in this behavior. We tracked 47 adult moose with Global Positioning System collars in a study area crossed by highways and forest roads. We hypothesized that moose would avoid crossing roads but would make occasional visits to roadsides to feed on sodium-rich vegetation and avoid biting insects. Further, we expected moose avoidance to be greater for highways than forest roads. We recorded 196,710 movement segments but only observed 328 highway and 1,172 forest-road crossings (16 and 10 times lower than expected by chance). Moose usually avoided road proximity up to $\geq$500 m on each side but 20% of collared moose made visits to areas within 50 m of highways, which might have resulted from moose searching for sodium in vegetation and roadside salt pools. In fact, vegetation along highways had higher sodium concentrations and was browsed in similar proportions to vegetation in adjacent forest, despite moose avoidance of these zones. Moose, however, did not use areas near roads more during periods of biting insect abundance. Our results supported the hypothesis of scale-dependent selection by moose; avoidance of highways at a coarse scale may confer long-term benefits, whereas selection of highway corridors at finer scales may be part of a strategy to overcome short-term limiting factors such as sodium deficiency. We found a positive relationship between home-range size and the proportion of road axes they contained, suggesting that moose either compensated for habitat loss or made specific movements along highways to gather sodium. The presence of sodium along highways likely increases moose–vehicle accident risks. Removal of salt pools or use of a de-icing salt other than sodium chloride should render highway surroundings less attractive to moose. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1550–1557; 2008)

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Roads affect terrestrial and aquatic ecosystems in various ways and cause mortality for many species (Forman and Alexander 1998, Rondinini and Doncaster 2002). Many direct effects of roads are obvious during construction, but more insidious effects are permanent and can extend substantially beyond the actual road (road-effect zone; Forman 2000).

In terrestrial ecosystems, road construction modifies habitat (e.g., fragmentation and loss, creation of new habitats, pollution, introduction of invasive species) and may increase human–wildlife interactions (e.g., hunting pressure, road accidents). For terrestrial wildlife, the most important road effects include habitat fragmentation (barrier to movement) and noise disturbance (Forman and Alexander 1998, Spellerberg 1998). Roads have been shown to hamper movement of mammals such as caribou (*Rangifer tarandus*; James and Stuart-Smith 2000, Dyer et al. 2002) and wolf (*Canis lupus*, Whittington et al. 2004). The barrier effect of roads and the noise disturbance created might also result in avoidance of adjacent areas (Seiler and Eriksson 1997, Forman and Alexander 1998, Dyer et al. 2002). Although they can successfully adapt to urban environments (Garrett and Conway 1999), the reaction of moose and other ungulates to road disturbance may differ in rural or wild areas where individuals are not as habituated to anthropogenic activities. Moose were found to be more agitated and to adopt vigilance behavior more frequently when feeding along highways (Singer 1978, Yost and Wright 2001).

Roads and their surroundings may offer some benefits to wildlife because roads can create highly desirable resources or microhabitats that are otherwise rare. Roads may create additional ecotone habitat and favor the growth of deciduous shrubs preferred by ungulates (Child 1998) or funnel winds and deter biting-insect harassment of ungulates (Kelsall and Simpson 1987). In Nordic regions, the use of road de-icers on highways may result in elevated sodium concentrations in vegetation bordering the roadway and, thus, attract ungulates (Grenier 1974, 1980; Leblond et al. 2007; Laurian et al. 2008). Understanding animal behavior in relation to road networks is necessary to better assess the impact of road development on wildlife and to implement appropriate mitigation measures.

We studied moose behavior relative to a road network in

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an area with a history of moose–vehicle accident problems (60 to 70 accidents/yr during the past decade; Dussault et al. 2006). Specifically, we wanted to determine when moose were crossing roadways or visiting their environs and investigate if environmental factors were involved in this behavior. To better understand the effect of disturbance on moose behavior, we considered both highways (paved surface, high vehicle speed and traffic level) and forest roads (unpaved, medium or low vehicle speed, low traffic level). We hypothesized that moose would avoid crossing roads but that they would make occasional visits along highways during spring and summer to feed on sodium-rich vegetation and to avoid biting insects. We predicted 1) moose would avoid crossing roads and using areas near roadways, 2) avoidance would be more pronounced for highways than forest roads, and greater during day than night, due to increased disturbance, and 3) avoidance would be lower during periods of biting insect abundance. Despite the general avoidance of roads, we expected moose to eat a higher proportion of available vegetation along highways compared to forest roads in spring and summer because of the higher sodium content of roadside vegetation. Finally, because we consider roads and their surroundings to be generally avoided by moose, leading to habitat loss (Seiler and Eriksson 1997), we also expected moose home-range size to increase proportionally with increasing roadway area.

STUDY AREA

We conducted our study in the northern part of the Laurentides Wildlife Reserve, about 100 km north of Québec City, Québec, Canada. Two highways (175 and 169) and a well-developed forest-road network occurred in the study area (1,800 km^2; Fig. 1), totaling road densities of 0.06 km/km^2 for highways and 0.16 km/km^2 for forest roads. Highways were paved, with generally only one lane in each direction. In 2002, mean daily traffic was estimated to be 1,460 vehicles on highway 169 and 2,800 vehicles on highway 175. The highway speed limit was 90 km/hour.

The study area was situated within the Canadian Shield where soils were mostly composed of glacial deposits, undifferentiated tills that were thinner on mountaintops and thicker in valley bottoms. Forests in the study area were typical of the boreal region: coniferous stands with balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) dominated high plateaus, whereas low-lying areas and valleys were dominated by mixed and deciduous stands. Common deciduous trees included white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), yellow birch (*B. alleghaniensis*), and maples (*Acer rubrum* and *A. saccharum*). Topography was gently rolling with some 100–350-m-deep river valleys. Winters were usually harsh in the Laurentides Wildlife Reserve with among the highest snow precipitation in the world (total annual snowfall >550 cm in some areas), rendering winter driving hazardous (Jolicoeur and Crête 1994). Each winter >100 metric tons of de-icing salts/km of highway were typically used (Jolicoeur and Crête 1994). Mean maximal and minimal daily temperatures were, respectively, −9.0° C and −21.7° C in January and 9.5° C and 21.7° C in July (Environment Canada 2005).

Moose were the most abundant ungulate in the study area. Moose density was estimated at 0.22 moose/km^2 in the Laurentides Wildlife Reserve during the last aerial survey in winter 1994 (St-Onge et al. 1995) but was found to be higher in the northern part of the reserve where we conducted this study (average of approx. 0.5 moose/km^2 and up to 0.8 moose/km^2), because of favorable habitat. Moose density has likely increased substantially since 1994 because of the implementation of more conservative hunting regulations (Lamontagne and Jean 1999). White-tailed deer (*Odocoileus virginianus*) were also present in the study area but density was low (no survey available).

METHODS

To locate moose, we conducted an aerial survey over a 2-km strip on each side of the highway prior to capture. Because we were studying behavior of moose in relation to highways, we arbitrarily wanted 65% of captured moose to be within the 2-km strip to obtain a sufficient sample of individuals likely to come into contact with highways. We captured some moose >2 km from highways to provide a sample of moose potentially less impacted by highways. We conducted captures following methods approved by the Animal Welfare Committee of Faune Québec (certificate no. 03-00-01). We captured an initial sample of 30 adult moose (>2.5 yr; 22 F and 8 M) in January–February 2003. In January–March 2004, we recaptured 17 of these moose to download data and replace collar batteries. We also installed Global Positioning System (GPS) collars on 12 new adults (6 M and 6 F) to replace mortalities or defective collars. Similarly, during January–March 2005, we recaptured 18 moose (4 M and 14 F) and captured 13 new adults (6 M and 7 F). We recaptured all individuals during January–April 2006 to recover collars. The recording capacity of the GPS collars we used enabled us to schedule one location every 2 hours. We estimated location error to be <35 m 95% of the time (Dussault et al. 2001). We conducted ≥3 telemetry flights each year to identify dead moose and defective collars.

We analyzed moose behavior relative to road axes by overlaying moose GPS locations on 1:20,000 digital maps of the study area, including road network, using ArcGIS 9.0. We only considered roads suitable for motor vehicles in the analyses because trails, restricted to access by foot, quad, or snowmobile, were less likely to disturb moose. We defined the study area as the minimum convex polygon (MCP; Mohr 1947) encompassing the locations of all moose monitored during the study. We used the MCP method to delineate moose annual home ranges. We selected the MCP method because a preliminary examination of the data indicated that visits near roads delimited the boundary of moose home ranges and that, in most cases, other home-range estimation methods excluded those locations. We calculated a different home range each year for individuals we followed >1 year. We conducted preliminary analyses

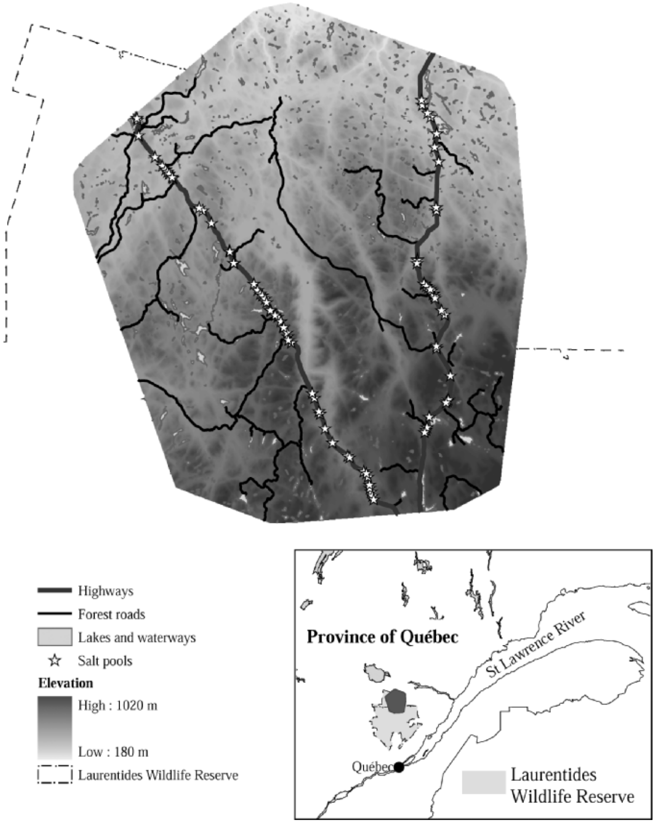

Figure 1. Map of the study area where we studied the behaviour of moose relative to a road network from 2003 to 2006. The study area was located in the north of the Laurentides Wildlife Reserve, Québec, Canada. The map shows the distribution of highways, forest roads, lakes and waterways, and salt pools.

that indicated behavior of males and females relative to road axes did not differ. On that basis, we pooled all individuals for subsequent analyses.

To determine whether roads were a barrier to moose movement, we successively simulated 100 road networks within the home range of each moose and determined the crossing frequency of real and simulated roads (Dyer et al. 2002). To do so, we identified moose road crossings by linearly connecting successive locations. We assumed that a crossing occurred each time one of these interlocation lines intersected a road. We generated simulated road networks by moving the highways and forest roads existing within each moose home range into a new random position within the home range, while keeping the same geographical orientation for random roads to take into account topographical constraints that might have influenced both road layout and animal movement. We recognized that actual roads were likely not distributed randomly with regard to topography and expected simulated roads to be less likely to follow the bottom of valleys compared to actual roads. Moose, however, were already found to travel preferentially in the bottom of valleys (Gundersen and Andreassen 1998; Dussault et al. 2006, 2007). This potential bias would overestimate moose utilization of actual compared to random roads. We therefore considered our method to be a conservative approach to detect road avoidance by moose. Using locations spaced 2 hours apart may have underestimated the true number of road crossings by moose but because the same bias also existed for our estimates of simulated road crossings, we could directly compare the crossing rate between real and simulated road networks.

We created an index of road-crossing rate by dividing the number of crossings by highway (or forest road) length (i.e., no. crossings/km) within home ranges. We first used an analysis of variance (ANOVA) to determine if crossing rate differed between highways and forest roads. Second, we conducted 2 separate ANOVAs, one for highways and one for forest roads, to determine if road-crossing frequency differed between the existing and random road networks. We used year and moose identity as random factors in the preceding analyses. We used only individuals having both forest roads and highways within their home range in this analysis ($n = 45$). We determined if frequency of highway crossings by moose differed by time of day (i.e., night, including dawn and dusk vs. day), as well as by month, using separate chi-square tests. We defined dawn and dusk as 2-hour periods centered on sunrise and sunset, respectively. We obtained times of sunrise and sunset on a daily basis at a weather station located near the study area, which allowed us to precisely categorize each movement segment relative to the time of day, given that sunrise and sunset varied according to time of year.

We assessed moose preference towards roadways and their surroundings by creating a series of buffer strips centered on highways and forest roads: $\leq$50 m, $>$50–250 m, $>$250–500 m, $>$500–1,000 m, $>$1,000–1,500 m, $>$1,500–2,000 m, and $>$2,000 m. We considered the roadway of highways and forest roads to have a width of 20 m and 6 m, respectively, which meant that the 0–50-m buffer strip began 10 m on either side of the highway centerline and 3 m from the middle of forest roads.

For each moose, we calculated a selection ratio for each buffer strip along highways and forest roads as the proportion of locations in a strip relative to proportion of that strip in the moose's home range. We inferred avoidance of a given strip when the selection ratio was significantly $<$1.0. We determined whether selection ratio varied with respect to distance from the roadway and month using ANOVAs, with year and individual as random factors. We conducted separate analyses for highways and forest roads.

We conducted biting insect (i.e., gadflies [Tabanidae spp.], mosquitoes [Culicidae spp.], and black flies [Simuliidae spp.]) surveys to create an index of insect abundance between late May and mid-August in 2004 and 2005. We conducted these surveys every 2–4 days using 18 permanent stations consisting of 9 pairs of stations, half of which were localized $<$5 m from a highway and the others being in the nearby forest $>$100 m from the highway. For all stations, an observer (always the same) noted the subjective level of insect harassment for each group of biting insects as follows: 0 = no insect, 1 = insects are present but no harassment, 2 = low harassment, 3 = medium harassment, 4 = high harassment. We grouped insect data by 2-week periods a posteriori: 1–15 June, 16–30 June, 1–15 July, 16–31 July, and 1–15 August. We used ANOVAs with year as a random factor to determine if insect abundance differed among 2-week periods and with distance from highways. For moose with a highway in their home range, we calculated selection ratios for each 2-week period to assess preference of moose towards highways and their immediate surroundings (i.e., the roadway plus a 50-m buffer strip) as well as for forested sites located >50 m from highways. We calculated the selection ratios for each moose as proportion of radio-locations on the highway and in the 0–50-m strip (or proportion of locations >50 m from a highway) divided by proportion of highway plus the 0–50-m strip (or proportion of forested habitat >50 m from a highway) in home range. We used an ANOVA, with year and individual as random factors, to determine if selection towards roadways and their immediate surroundings was higher during periods when biting insects were most abundant.

Leaves of deciduous shrubs and trees were generally available from early June to mid-October in the Laurentides Wildlife Reserve. We collected vegetation samples along highways to measure their sodium content on 3 occasions in summer 2005: 29 June, 1 August, and 7 September. We collected leaves and annual shoots from 0.5 m to 3 m above ground for 3 moose-preferred shrubs (white birch, trembling aspen, and willows [*Salix* spp.]) at 90 sites, half of which were along highways (<10 m from roadway) where de-icing salts were used and the other half of which were along forest roads >200 m from a highway. We dried, crushed, ashed, and dissolved samples in a 20% chloride acid solution. We then prepared control Inductively Coupled Plasma solutions with 100 ppm of sodium. We analyzed 5 replicates for each site × period combination. We used separate ANOVAs to determine the influence of sampling period and sampling location (i.e., close to highway or in forest) on sodium concentrations by species.

We estimated browsing rate of moose in various habitats by visually assessing the proportion of browsed twigs in a 10-m radius (i.e., 0–5%, 6–20%, 21–40%, . . . , 95–100%). We sampled 196 plots distributed in sites located ≤ 50 m from a highway, ≤ 50 m from a forest road, and in forested areas >50 m from a road axis. Because browsed proportions were low, we had to collapse the 6–100% classes to avoid 0.0 values, leaving 2 classes remaining. We used log-linear analyses to determine if browsing rate differed according to distance from roadways for deciduous and coniferous (balsam fir only) species independently. In the same survey plots, we assessed food availability in 10-m^2 subplots by counting the number of stems with ≥ 1 browsable twig (>5 cm length and between 0.5 m and 3 m high). We used a Kruskal–Wallis test to determine if food availability differed among sampling plots close to highways, close to forest roads, and in the forest.

We assessed the influence of road network on home-range size with a linear regression between home-range area and proportion of roadways (area of highways plus a 10-m buffer zone and forest roads plus a 3-m buffer zone) within home range. Moose movement in the study area was highest during summer, and previous studies indicated summer home-range area included >90% of annual home-range area (Dussault et al. 2005). As such, we did not include in this analysis 4 moose that we did not monitor for a full summer. We conducted one analysis, grouping both highways and forest roads, because preliminary analyses indicated that moose reactions towards these 2 road types were similar.

We performed all statistical analyses using SAS version 8.2 (SAS Institute, Cary, NC) with an a priori significance level of 0.05. We log-transformed dependent variables when necessary to normalize residuals of the regression.

RESULTS

We captured moose on average (±SE) 3.32 ± 0.27 km (range = 0.3–11 km) from a highway. Because moose home ranges averaged 53.9 ± 4.3 km^2, we believed that all moose were likely to come into contact with highways and forest roads because both of these were widely distributed over the study area.

We monitored individual moose for 2–36 months. We monitored 47 moose; we followed 29, 11, and 7 moose during 1, 2, and 3 years, respectively (72 moose-yr). Telemetry data acquisition terminated prematurely because of death for 22 moose and because of collar failure for 9 moose. We obtained 199,118 GPS telemetry locations ($\bar{x} \pm \text{SE} = 4{,}187 \pm 349$ locations/moose).

Among the 47 moose monitored, 19 never crossed a highway and 11 never crossed a forest road, even though 45 home ranges included such features. Among the 196,710 movement segments recorded, we observed 328 highway crossings (1.85 ± 0.39 crossing/km of highway in the home range or 4.57 ± 1.20 crossings/moose/yr) and 1,172 forest-road crossings (1.85 ± 0.23 crossing/km of forest road or 16.28 ± 2.29 crossings/moose/yr). Some moose crossed road axes more often than others (75th percentile: highways = 8.0; forest roads = 25.5). Highways and forest roads were crossed at a similar rate ($F_{1,156} = 0.29$, $P = 0.592$) and the interaction between road type and road status (real vs. simulated) was not significant ($F_{1,156} = 1.76$, $P = 0.186$). Highway and forest-road crossing frequencies were, respectively, 16 times and 10 times lower than expected, based on simulated road networks (30.53 ± 21.25 crossings/km for simulated highways and 18.33 ± 14.19 crossings/km for simulated forest roads, $F_{1,156} = 70.16$, $P < 0.001$). The road-crossing frequency by moose differed by month ($\chi^2 = 655.9$, df = 11, $P < 0.001$, $n = 328$ for highways and $\chi^2 = 1{,}893.9$, df = 11, $P < 0.001$, $n = 1{,}172$ for forest roads). Most highway and forest-road crossings occurred during May–July (54% of highway and 59% of forest-road crossings; Fig. 2). A second moderate peak appeared in October for highways and in September for forest roads, and crossings were less abundant during January–March. Finally, crossings were more frequent at night for highways ($\chi^2 = 245.1$, df = 1, $P < 0.001$) and forest roads ($\chi^2 = 3.28$, df = 1, $P = 0.070$; Fig. 2).

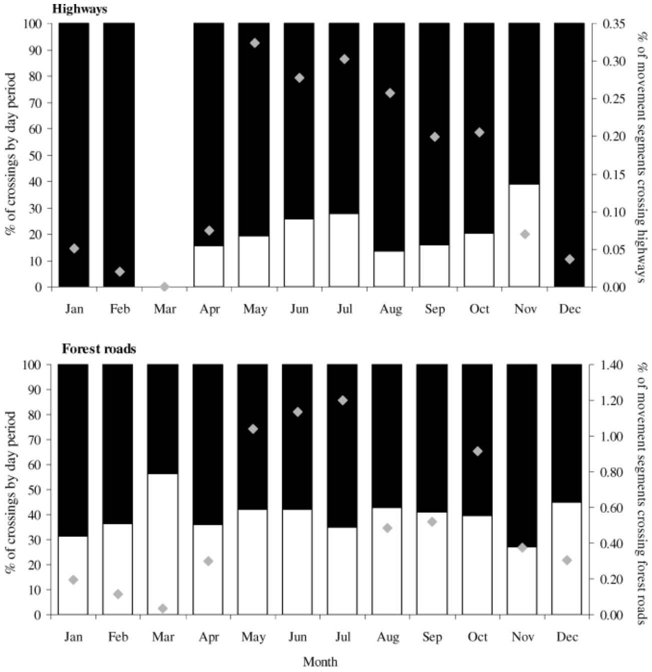

Figure 2. Monthly proportion of crossings by day period (day vs. night crossings ◧) and monthly proportion of movement segments crossing a road axis (i.e., no. of crossings/total no. of locations ◆) by moose for highways and forest roads between 2003–2006, Laurentides Wildlife Reserve, Québec, Canada.

Moose did not use strips around highways ($F_{7,4248}$ = 171.17, $P < 0.001$) and forest roads ($F_{7,4855} = 196.45$, $P < 0.001$) randomly. Year-round moose avoidance was most pronounced near the roadway itself and less pronounced for the >2,000-m surrounding strip for both highways and forest roads (Fig. 3), and use was less than expected in strips up to 500 m from highways and up to 1,000 m near forest roads. Moose avoided strips >1,000–2,000 m from highways ($P < 0.010$). The month × strip category interaction was significant for highways ($F_{77,4248} = 1.68$, $P < 0.001$) but not for forest roads ($F_{77,4855} = 0.93$, $P = 0.654$). Strips <500 m from highways were mostly visited by moose in May and June but rarely during December–April, and the use of other strips was similar year-round (Fig. 4). Not all individuals had the same reaction to roads. Although the 0–50-m strip was on average avoided by moose ($t_{345} = -6.84$, $P < 0.001$), 4 individuals highly preferred it (selection ratio = 7.8 to 393.2), and it was moderately preferred by 4 others (selection ratio = 1.1 to 1.8; Fig. 3).

Abundance of biting insects varied among sampling periods for each species ($F_{5,415} > 3.11$, $P < 0.009$), but usually did not differ between highway and forest sampling sites ($F_{1,32} > 1.64$, $P > 0.079$), except for gadflies, which were less abundant along highways ($F_{1,32} = 5.13$, $P = 0.030$). Gadflies and black flies were more abundant from mid-June to late July. Mosquitoes peaked in early July but were also abundant from mid-June to late July. Overall, biting insects were most abundant in July. However, the relative preference of moose for highways and their immediate surroundings did not increase during these periods of high biting-insect abundance (Table 1).

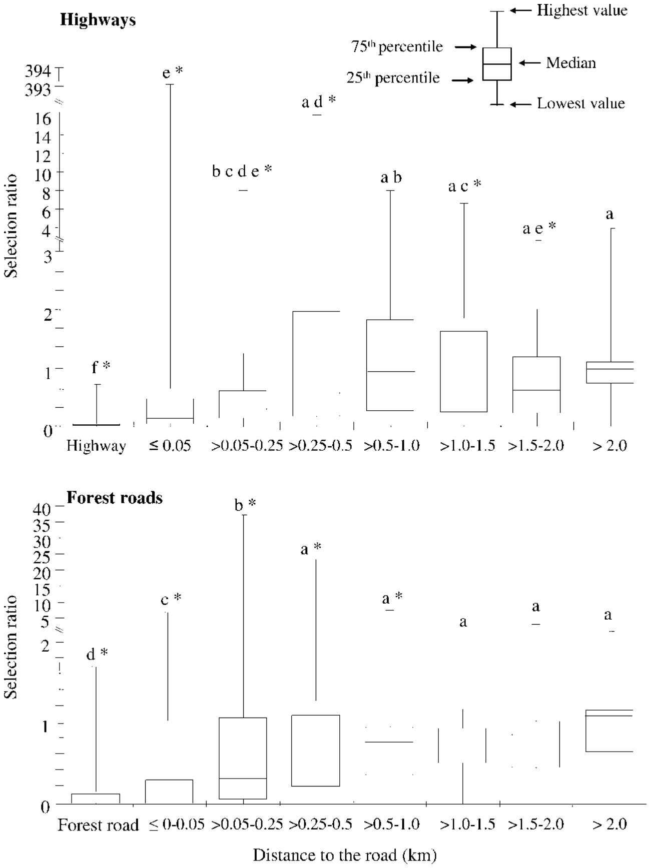

Figure 3. Box-plot diagram of selection ratios of moose toward roads and their surroundings at the home-range scale between 2003–2006, Laurentides Wildlife Reserve, Québec, Canada. * indicates a significant difference between use and availability; bars with the same letter do not differ significantly.

Sodium concentration in vegetation did not differ among the 3 sampling periods for both highways and forest roads (white birch: $F_{2,84} = 0.27$, $P = 0.760$; trembling aspen: $F_{2,84} = 1.47$, $P = 0.236$; willows: $F_{2,84} = 1.13$, $P = 0.329$), but it was higher along highways than along forest roads for all species (Table 2; white birch: $F_{1,84} = 19.72$, $P < 0.001$; trembling aspen: $F_{1,84} = 16.78$, $P < 0.001$; willows: $F_{1,84} = 23.07$, $P < 0.001$). Differences between highways and forest roads were greater at the end of June than in early August and September for trembling aspen ($F_{2,84} = 6.37$, $P = 0.003$) and willows ($F_{2,84} = 3.43$, $P = 0.037$).

The proportion of browsed twigs in sample plots was usually <5% for both deciduous and coniferous stems and did not differ among highway sides, forest-roads' sides, and forest, for both deciduous ($\chi^2 = 1.08$, $P = 0.578$, df = 2, $n = 180$) and coniferous ($\chi^2 = 1.88$, $P = 0.392$, df = 2, $n = 184$) species. Availability of deciduous stems did not differ among highway, forest road, and forest sites ($H = 0.53$, $P = 0.768$, $n = 98$ sites), but coniferous species were less abundant along highways than elsewhere ($H = 6.17$, $P = 0.057$, $n = 98$).

Highways and forest roads occupied ≤0.54% of moose home ranges ($\bar{x}$ = 0.22 ± 0.02%), but home-range area increased with increasing roadway area ($F_{1,66} = 6.80$, $P = 0.011$; ln[home-range area] = 0.119 × ln[proportion of road

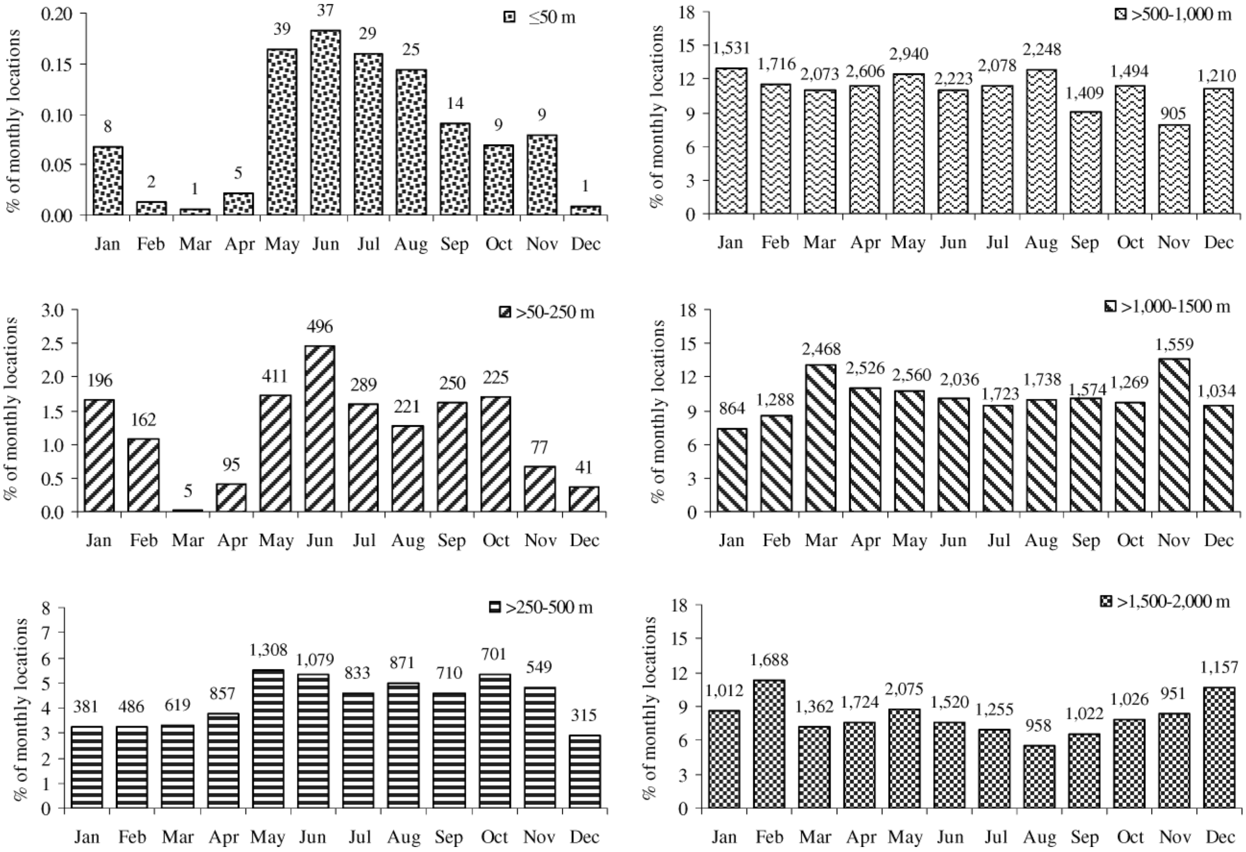

Figure 4. Monthly distribution of moose locations in a series of strips centered on highways between 2003–2006, Laurentides Wildlife Reserve, Québec, Canada. Numbers on top of bars are number of locations.

axes in the home range + 0.01] + 4.046). Highway and forest-road area explained only 9% of the variation in home-range size. Moose home ranges containing a high proportion of roaded area were about 11% larger than those containing little roaded area.

DISCUSSION

As expected, moose avoided crossing roads and frequenting their surroundings. Moose may avoid proximity of road axes for several reasons, including dislike of the roadway and associated forest opening, vehicle traffic (i.e., density or noise), or predation (Forman and Alexander 1998, Dyer et al. 2002). Similar to white-tailed deer, moose may adapt behaviorally to roads by avoiding nearby habitats where traffic noise inhibits predator detection and may prefer to cross roads at specific sites and time periods, as we observed (Forman and Deblinger 2000, Dussault et al. 2007). Interestingly, moose highway crossings were 4 times more likely to occur at night, when traffic level was 33% of that observed during the day (J. David, Ministère des Transports du Québec, unpublished data). These results were similar to findings of Dyer et al. (2001, 2002), who found road avoidance by caribou to increase with traffic level and to Joyal et al. (1984) who found avoidance of moose toward power lines to increase with right-of-way width.

In agreement with Burson et al. (2000) and Yost and Wright (2001), our data suggest road avoidance by moose in contrast with previous generalizations that environmental factors may attract moose to road corridors (Thompson and Stewart 1998). We found little evidence that moose used highways and forest roads as a refuge from biting insects as suggested by Kelsall and Simpson (1987). We did find moose more often in the 0–50-m strip along highways during June and July, the 2 months with the highest biting-insect abundance, but moose did not increase use of highways and their surroundings with increased insect abundance within these 2 months. Moreover, our data did not lend support to the hypothesis that biting-insect abundance is lower in roadway corridors than in surrounding areas of vegetation. The low proportion of moose locations on or near highways overall also suggests that use of roads for insect avoidance is unlikely.

Higher sodium concentration in vegetation has been previously suggested as a mechanism attracting moose close to highways (Thompson and Stewart 1998). We found sodium concentration to be higher in vegetation collected along roads where de-icing salt was used in winter. However, the proportion of browsed twigs did not differ among sites along highways, forest roads, or in the forest. The fact that moose browsed a similar proportion of available food along highways is noteworthy, considering avoidance of these areas. These results support the hypothesis of scale-dependent selection by moose (Rettie and Messier 2000, Dussault et al. 2005). General avoidance

Table 1. Results of analyses of variance we used to test if moose-selection ratio for the roadway of highways and their immediate surroundings (0–50-m strip) varied among periods with differing biting insect abundance between 2003–2006, Laurentides Wildlife Reserve, Québec, Canada.

Yr	Source	df	*F*	*P*
2004	Period[a]	4	1.01	0.406
	Distance from roadway[b]	1	87.67	<0.001
	Period × distance from roadway	4	1.16	0.336
2005	Period	4	0.36	0.838
	Distance from roadway	1	52.83	<0.001
	Period × distance from roadway	4	0.49	0.743

[a] Period relates to biting-fly abundance periods: 1–15 Jun, 16–30 Jun, 1–15 Jul, 16–31 Jul, 1–15 Aug.

[b] Highway and 0–50-m strip vs. >50-m strips.

Table 2. Mean sodium concentration (ppm ± SE) in vegetation sampled along highways and forest roads in summer 2005, Laurentides Wildlife Reserve, Québec, Canada.

	Along highways		Along forest roads	
Vegetation type	$\bar{x}$	SE	$\bar{x}$	SE
White birch	147.9	12.8	89.7	9.1
Trembling aspen	170.3	25.3	98.6	7.8
Willows	281.3	64.3	114.6	8.4

of highways at coarse scales may confer long-term benefits to moose (e.g., better predator detection, avoidance of vehicle-collision mortality), whereas selection of highway corridors at finer scales during some periods may be beneficial to overcome short-term limiting factors (e.g., sodium deficiency). We cannot reject the hypothesis that moose used areas along highways, at least partially, to feed on sodium-rich vegetation. We also found increased highway crossing and use of the 0–50-m strip in spring and early summer; vegetation is known to green-up faster in these open habitats (Rea 2003). We did not find deciduous-stems density to be higher along roadways, as previously reported (Child 1998, Finder et al. 1999).

We found some moose to make frequent visits to the 0–50-m strip located on either side of highways. Nearly 20% of collared moose showed this behavior, which could be interpreted as a quest for sodium. Sodium was readily available in vegetation close to highways and also in roadside salt pools. Salt pools are formed in poorly drained sites following accumulation of de-icing salts (mainly composed of sodium chloride) and were found to have mean sodium concentrations of 500–600 ppm (Grenier 1980, Fraser 1979, Fraser and Thomas 1982, Dussault et al. 2006, Leblond et al. 2007). Such sodium concentrations are even higher than those found in aquatic vegetation (MacCracken et al. 1993). Laurian et al. (2008) demonstrated that moose were making directional movements to reach salt pools, which were often located at home-range boundaries, thereby increasing their home-range area.

We hypothesize that moose visited highway surroundings primarily to obtain sodium from salt pools and vegetation. Sodium is essential to moose because it plays a major role in many vital functions (Church et al. 1971, Robbins 1993); however, sodium is rare in northern ecosystems such as the Laurentides Wildlife Reserve, as outlined by Jordan et al. (1973). It has been suggested that, at the onset of spring, moose need more sodium than they can obtain from terrestrial vegetation alone (Weeks and Kirkpatrick 1976, Belovsky and Jordan 1981, Fraser et al. 1982, Jordan 1987, Ohlson and Staaland 2001). In our study, use of sodium-rich environments by moose was highest in spring and early summer, a time when aquatic vegetation was less available. Some moose appear to have fulfilled their needs efficiently, by feeding on sodium-rich vegetation or drinking brackish water in roadside salt pools.

MANAGEMENT IMPLICATIONS

Our results demonstrate that moose globally perceive road networks, including up to $\geq$500 m beyond the roadway, as low-quality habitat. Moose crossing highways were more likely to do it at night, which is problematic because of the reduction in motorists' visual acuity in the dark (Joyce and Mahoney 2001), making roadway lighting a potentially important mitigation measure (Reed 1981). Because our results suggest that moose frequented the vicinity of highways to consume sodium from salt pools and vegetation, especially in spring and summer, presence of sodium along highways may be a key risk factor for moose–vehicle accidents (Dussault et al. 2006). Removal (e.g., drainage and filling with rock boulders [Leblond et al. 2007]) of salt pools should render highway surroundings less attractive to moose. Use of a de-icing salt other than sodium chloride, such as calcium chloride or calcium–magnesium acetate, is also likely to keep moose away from highways. Our results should guide managers in assessing the impact of further road-development projects on moose and on moose–human interactions.

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