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Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape

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Summary

1. Roads cause functional habitat loss, alter movement patterns and can become ecological traps for wildlife. Many of the negative effects of roads are likely to be a function of the human use of roads, not the road itself. However, few studies have examined the effect of temporally and spatially varying traffic patterns on large mammals, which could lead to misinterpretations about the impact of roads on wildlife.

2. We developed models of traffic volume for an entire road network in south-western Alberta, Canada, and documented for the first time the response of grizzly bears *Ursus arctos* L to a wide range of traffic levels.

3. Traffic patterns caused a clear behavioural shift in grizzly bears, with increased use of areas near roads and movement across roads during the night when traffic was low. Bears selected areas near roads travelled by fewer than 20 vehicles per day and were more likely to cross these roads. Bears avoided roads receiving moderate traffic (20–100 vehicles per day) and strongly avoided high-use roads (> 100 vehicles per day) at all times.

4. *Synthesis and applications*. Grizzly bear responses to traffic caused a departure from typical behavioural patterns, with bears in our study being largely nocturnal. In addition, bears selected private agricultural land, which had lower traffic levels, but higher road density, over multi-use public land. These results improve our understanding of bear responses to roads and can be used to refine management practices. Future management plans should employ a multi-pronged approach aimed at limiting both road density and traffic in core habitats. Access management will be critical in such plans and is an important tool for conserving threatened wildlife populations.

Key-words: access management, Alberta, grizzly bear, habitat selection, movement, resource selection function, roads, step-selection function, traffic model, *Ursus arctos*

Introduction

The ecological effects of roads are among the most pressing issues facing wildlife managers. Roads fragment habitats (Oxley, Fenton & Carmody 1974; Vos & Chardon 1998) and can influence animal behaviour, survival, abundance and community structure (Adams & Geis 1983; Forman & Alexander 1998; Trombulak & Frissell 2000; Spellerberg 2002; Fahrig & Rytwinski 2009). However, the relationship between roads and wildlife is highly complex, with effects often being area, species or sex specific (McLellan & Shackelton 1988; Spellerberg 2002), and varying by time of day and season (Mattson, Knight & Blanchard 1987). Furthermore, these effects can be confounded by human use along roads and habitat characteristics (Roever, Boyce & Stenhouse 2008). Such confounding factors can obscure the relationship between wildlife and roads and reduce the effectiveness of management strategies aimed at reducing negative impacts.

One factor influencing wildlife response to roads is vehicle traffic. Traffic has been shown to influence wildlife distribution and abundance (Fahrig *et al.* 1995; Carr &

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Fahrig 2001; Mazzerolle 2004) and can cause greater displacement from areas around roads and other developments for several mammalian species including mule deer *Odocoileus hemionus* Raf. (Sawyer, Kauffman & Nielson 2009), caribou *Rangifer tarandus* L (Dyer *et al.* 2001), elk *Cervus elaphus* L (Rowland *et al.* 2000), wolves *Canis lupus* L (Whittington, St. Clair & Mercer 2004) and grizzly bears *Ursus arctos* L (Mace *et al.* 1996; Wielgus, Vernier & Schivatcheva 2002; Apps *et al.* 2004). However, traffic patterns can be complex (Stathopoulos & Karlaftis 2001; Wilson 2008) and usually vary temporally among roads of similar type. As a result, traffic can be difficult to quantify and is often simplified in analyses of road effects by examining a subset of roads with known traffic, or using relative indices (e.g. Dyer *et al.* 2001; Wielgus, Vernier & Schivatcheva 2002; Chruszcz *et al.* 2003; Apps *et al.* 2004; Waller & Servheen 2005), which can obscure inherent variation in human use of roads. Much of our current understanding of the influence of roads on wildlife is in the absence of accurate traffic information.

The influence of traffic is of particular importance for grizzly bears, which have a complex relationship with roads. In some areas, bears are attracted to roads because of roadside foods or for use of roads as movement conduits (Roever, Boyce & Stenhouse 2008, 2010). In other areas, bears avoid roadsides and may not establish home ranges in areas with high road densities (Archibald, Ellis & Hamilton 1987; Mattson, Knight & Blanchard 1987; McLellan & Shackelton 1988; Mace *et al.* 1996). Furthermore, grizzly bears respond to roads differently by season (Mattson, Knight & Blanchard 1987; Mace *et al.* 1996), sex and age classes (McLellan & Shackelton 1988; Hood & Parker 2001; Gibeau *et al.* 2002; Chruszcz *et al.* 2003), and traffic probably influences these responses (Mace *et al.* 1996; Wielgus, Vernier & Schivatcheva 2002; Chruszcz *et al.* 2003; Waller & Servheen 2005). Understanding this complex relationship is critically important because most grizzly bear mortalities occur near roads (McLellan 1989; Benn & Herrero 2002; Johnson *et al.* 2004; Nielsen *et al.* 2004; Nielsen, Stenhouse & Boyce 2006). Access management, the limiting of road access, is often suggested as a means to reduce mortalities but requires detailed knowledge of the response of bears to road traffic. Gaining such knowledge is an important step towards more effective management.

We examined the influence of road traffic on grizzly bear response to roads. We created a spatially and temporally accurate representation of vehicle traffic patterns for the entire road network in our study area. Second, we examined the influence of these traffic patterns on grizzly bear habitat selection and movement. We hypothesized that traffic would significantly influence grizzly bear habitat selection and movement near roads, and that bears would avoid roads with higher traffic volumes.

Materials and methods

STUDY AREA

The 3000-km^2 study area was located near Pincher Creek in south-western Alberta, and was composed of private agricultural land (*c.* 1200 km^2), multi-use public land (*c.* 1300 km^2), Waterton Lakes National Park (WLNP; *c.* 500 km^2), and provincial parks and recreation areas (<12 km^2). The study area was bounded by Highway 3 to the north, the British Columbia–Alberta border to the west, the United States–Canada border to the south and the extent of grizzly bear range to the east. The landscape is characterized by a dramatic rise from prairies to mountaintops over a relatively short distance. Private land in the eastern half of the study area was dominated by cattle ranches where recreational access was controlled by landowners. Activities in the western part of the study area were dominated by recreational use including off highway vehicle (OHV) use, hunting, fishing and hiking, as well as industrial traffic related to natural gas extraction.

The study area encompassed 2273 km of roads with a density of 0·73 km km^{-2} overall (0·21 km km^{-2} truck trails, 0·44 km km^{-2} gravel and unimproved roads, and 0·08 km km^{-2} paved roads), 0·18 km km^{-2} in WLNP (0·008 km km^{-2} truck trails, 0·06 km km^{-2} gravel and unimproved roads, and 0·12 km km^{-2} paved roads), 1·3 km km^{-2} on private land (0·24 km km^{-2} truck trails, 0·91 km km^{-2} gravel and unimproved roads, and 0·15 km km^{-2} paved roads), and 0·55 km km^{-2} on multi-use public land (0·31 km km^{-2} truck trails, 0·23 km km^{-2} gravel and unimproved roads, and 0·009 km km^{-2} paved roads).

TRAFFIC

We obtained road and trail layers current to 2007 from the Foothills Research Institute Grizzly Bear Project (http://foothillsresearchinstitute.ca). We combined these layers in ARCMAP 9.2 and overlaid them with aerial photographs to ensure that all roads were accurately portrayed in the GIS layer. Although there were changes to the road network during our study, these changes were minor and represented <1% of all roads.

From May 2008 to November 2009, we deployed a total of 46 traffic counters (Diamond Traffic Products, Oakridge, OR, USA) on roads and trails. Counters were deployed for variable time periods (3 months to >1 year) because of equipment availability or failure. We deployed traffic counters with the intent to cover as large a geographic area as possible and to sample a variety of road types (e.g. paved roads, gravel roads, truck trails). We also obtained traffic data from three Alberta Transportation traffic counters (http://www2.infratrans.gov.ab.ca/mapping/), and three counters deployed in WLNP by park staff.

From April to November 2008, we deployed 21 remotely activated trail cameras (RECONYX, Creekside, WI, USA) at randomly selected locations on roads and trails. Motorized use triggered the trail cameras' infrared sensor to produce time-stamped photographs. Pictures of motorized vehicles were counted manually to provide hourly traffic values along these roads.

Data from cameras were added to the data from the traffic counters, above, and used to estimate models of traffic volume during the night, weekday day-time (WD) and weekend day-time (WE; see Appendix S1, Supporting Information). We used these models to predict WD, WE and night-time traffic counts for all roads in the study area. Covariate data for all road segments (an uninterrupted stretch of road, between intersections; $n = 21\ 104$) were extracted using ARCMAP 9.2 (see Appendix S1, Supporting information), and traffic counts were predicted using coefficients estimated from the final models for each time period.

MODELLING GRIZZLY BEAR RESPONSE TO TRAFFIC

Grizzly bear data

Between 2003 and 2008, we captured and immobilized 14 grizzly bears in the study area (six adult males, two subadult males, three females with cubs, two adult females and one subadult female) using helicopter, culvert traps and foot snares, following Cattet, Caulkett & Stenhouse (2003; all captures approved by the University of Alberta and University of Saskatchewan Animal Care Committees). Bears were collared with Televilt Tellus II and Simplex (Televilt Ltd., Lindesberg, Sweden) and ATS (Advanced Telemetry Systems, Isanti, MN, USA) global positioning system (GPS) radiocollars. GPS fix-attempt schedules ranged from once every hour to once every 5 h. Data from two additional bears (one adult female and one subadult female), radiocollared in Montana, USA and British Columbia, Canada that moved into our study area during the study were included in our analyses. We classified locations into weekend vs. weekday and day vs. night, with night defined as the time between the average sunrise and sunset for Lethbridge, AB (*c.* 100 km east of the study area) during each month that a location was taken (http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html).

Using the above-mentioned data, we took a multi-stage approach to examining grizzly bear responses to roads and traffic. First, we examined the response of bears to roads in the absence of other habitat variables to determine broad-scale patterns. Second, we used the results of this habitat-independent response to categorize roads into traffic volume classes and to examine potential distance thresholds and the effect of traffic on movement patterns. Last, we modelled grizzly bear habitat selection and movement as a function of broader landscape characteristics and traffic to determine the influence of traffic on grizzly bear habitat selection relative to other landscape characteristics.

Traffic volume classification and broad-scale response to roads

To examine the habitat-independent responses of bears to roads, we categorized roads into traffic volume classes based on selection ratios (proportion of used locations relative to proportion of random locations; Manly *et al.* 2002) to identify distance buffers around roads. We defined our sampling unit to be the individual bear, and all calculations were conducted following design II in Manly *et al.* (2002). We generated random points at a density of 30 points per km^2 within the composite 100% Alberta minimum convex polygon for all bears (some bears travelled to British Columbia and Montana, and these data were excluded from the analysis). We randomly assigned these points to WE, WD or night with proportions equal to actual proportions throughout the active period for bears (29% of locations listed as weekend, 40% listed as night).

We presumed that the distance at which bears responded to roads would vary with traffic: the analysis of this response is a multidimensional problem involving both traffic and distance. Our intention was first to examine the data for a traffic volume threshold and then to use any such thresholds to categorize roads by traffic volume for an examination of distance responses. Previous studies have consistently shown 500 m to be the distance at which grizzly bears avoid roads (Mattson, Knight & Blanchard 1987; Mace *et al.* 1996; Ciarniello *et al.* 2009), and we used this distance as a cut-off point to examine potential traffic volume thresholds. We split the road layer into 11 traffic categories (upper limits of bins: 5, 10, 20, 30, 40, 60, 80, 100, 150, 1000 and >1000 vehicles per 24 h). We calculated selection ratios (Manly *et al.* 2002) for areas within 500 m of roads in each of the 11 traffic volume bins, plotted these selection ratios and visually examined the results to identify potential thresholds.

The results of the above-mentioned analysis showed substantial changes in bear selection as a function of traffic (Fig. 1). On the basis of these results, we split roads into three traffic volume classes (low, ≤ 20; medium, >20 and ≤ 100; and high, >100 vehicles per day) and divided the area within 500 m of roads into 50 m buffers and the area between 500 and 1000 m from roads into 100 m buffers. We then calculated selection ratios, as previously, for each distance bin, around each traffic volume class of road.

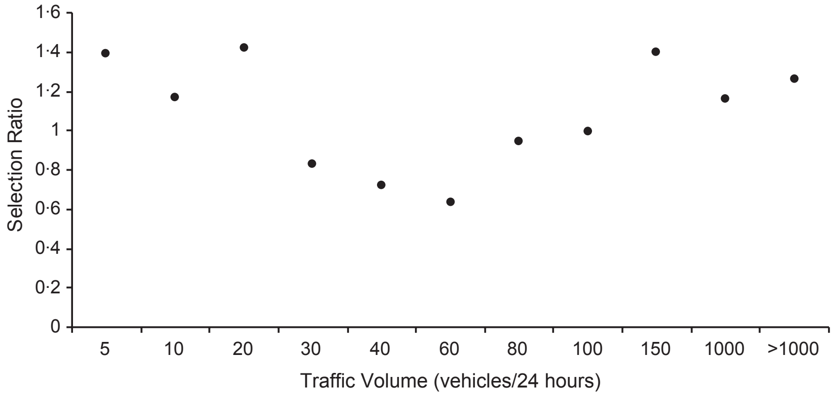

Fig. 1. Selection ratios for areas within 500 m of roads by traffic volume of road for 11 traffic volume classes, calculated using data from 16 global positioning system (GPS) collared grizzly bears in south-western Alberta, Canada.

Table 1. Variables used in resource selection function (RSF) and step-selection function (SSF) modelling, description of variable, source or citation, and which models the variables were used in: RSF, SSF or both models (Both)

Variable	Description (source or citation)	Models
cut	Distance to cutlines and trails calculated in ARCMAP 9.2 (cutlines and trails layer obtained from FRI*)	Both
stream	Natural log distance to streams and rivers calculated in ARCMAP 9.2 (streams layer obtained from FRI*)	Both
ndvi	Normalized difference vegetation index calculated at a pixel size of 1 × 1 km (Townshend & Justice 1986; FRI*)	Both
cti	Compound topographic index (Nielsen *et al.* 2004)	Both
edge_e	Distance to forest edge from points outside of treed land cover calculated in ARCMAP 9.2 (Franklin *et al.* 2001)	Both
edge_i	Distance to forest edge from points in treed land cover calculated in ARCMAP 9.2 (Franklin *et al.* 2001)	Both
age	Forest age (FRI*)	Both
shrub	Binary variable indicating shrub land cover (Franklin *et al.* 2001)	Both
herb	Binary variable indicating herbaceous land cover (Franklin *et al.* 2001)	Both
d_rds	Distance to roads	Both
d_low	Natural log distance to roads classified as low traffic (see Supporting information)	Both
d_med	Natural log distance to roads classified as medium traffic (see Supporting information)	Both
d_high	Natural log distance to roads classified as high traffic (see Supporting information)	Both
tri	Terrain ruggedness index (Nielsen *et al.* 2004)	RSF
barren	Binary variable indicating barren land cover (Franklin *et al.* 2001)	RSF
traffic	The traffic volume of the nearest road (see Supporting information)	RSF
tri_lwm	Length-weighted mean terrain ruggedness calculated using Hawth's Tools in ARCMAP 9.2	SSF
x_barren	Binary variable indicating if the step crossed through barren land cover (Franklin *et al.* 2001)	SSF
x_low	Binary variable indicating if the step crossed a low-volume road (see Supporting information)	SSF
x_med	Binary variable indicating if the step crossed a medium-volume road (see Supporting information)	SSF
x_high	Binary variable indicating if the step crossed a high-volume road (see Supporting information)	SSF
cross	Binary variable indicating if the step crossed any road (see Supporting information)	SSF
cross_traff	The traffic volume of the road if the step crossed a road (see Supporting information)	SSF

All variables were calculated at a pixel size of 30 × 30 m unless otherwise noted.*FRI indicates layers obtained from the Foothills Research Institute Grizzly Bear Project (http://foothillsresearchinstitute.ca), which develops, maintains and updates GIS layers for grizzly bear range in the province of Alberta, including annual updates of roads, trails, streams and rivers using remote sensing tools.

Table 2. Population-level model selection results for day- and night-time resource selection functions (RSFs) fit to 12 grizzly bears in south-west Alberta, Canada

Model rank	Model covariates	Mean AIC weight day	Mean AIC weight night
1	*cut + stream + ndvi + cti + edge_i + edge_e + tri + age + shrub + herb + barren + d_low + d_med + d_high*	0·65	0·65
2	*cut + stream + ndvi + cti + edge_i + edge_e + tri + age + shrub + herb + barren + d_rds + traffic*	0·19	0·18
3	*cut + stream + ndvi + cti + edge_i + edge_e + tri + age + shrub + herb + barren + d_rds*	0·16	0·17

AIC, Akaike's Information Criterion.

Effect of traffic patterns on road crossings by bears

To examine the influence of traffic volume on road crossings by grizzly bears, we calculated the percentage of steps (straight line between subsequent locations; Turchin 1998) that crossed roads and the mean traffic volume of roads crossed by grizzly bears during the day, night and across periods. We excluded all steps over missed fixes because such steps are taken over longer time periods, and thus, the distance is not comparable to those over a shorter time. To examine the influence of traffic on distances moved by bears, we compared mean step lengths of movements crossing roads of different traffic volumes as well as to those steps that did not cross roads using *t*-tests. We compared these movements for bears with radiocollars set to obtain fixes once per hour and once every 5 h separately.

Effect of traffic on grizzly bear habitat selection and movement

To examine the responses of bears to road traffic in a multivariable context, we fit resource selection functions (RSFs; Manly *et al.* 2002; Johnson *et al.* 2006) and step-selection functions (SSFs; Fortin *et al.* 2005) to GPS data from 12 of the bears (analysis restricted to 12 bears because of small sample sizes for four bears). We fit RSFs in a use-available design, assuming the selection function took the exponential form and estimated coefficient values using logistic regression (Johnson *et al.* 2006). We drew 5000 random locations for each bear from within their 100% Alberta MCP. Random points were assigned to weekend or weekday as for the selection ratio analysis, above. RSFs fit in this manner provide information on the selection of habitats

Table 3. Population-level model selection results for day- and night-time step-selection functions (SSFs) fit to seven grizzly bears in south-west Alberta, Canada

Model rank Day	Model rank Night	Model covariates	Mean AIC weight day	Mean AIC weight night
1	2	*cut + stream + ndvi + cti + edge_i + edge_e + tri_lwm + age + shrub + herb + x_barren + d_rds + cross*	0·33	0·49
2	1	*cut + stream + ndvi + cti + edge_i + edge_e + tri_lwm + age + shrub + herb + x_barren + d_low + d_med + d_high + x_low + x_med + x_high*	0·50	0·43
3	3	*cut + stream + ndvi + cti + edge_i + edge_e + tri_lwm + age + shrub + herb + x_barren + d_low + d_med + d_high + cross_traff*	0·17	0·08

AIC, Akaike's Information Criterion.

relative to their availability within the home range. Because fix success was below 90% for all collars, we weighted all used locations by the inverse of the probability of a successful fix using the models of Frair *et al.* (2004) and Hebblewhite, Percy & Merrill (2007).

Step-selection functions provide information on movement choices relative to movements that could have been taken by the animal (Fortin *et al.* 2005). Step lengths can be indicative of behavioural states (Morales *et al.* 2004). Because movements over longer time periods likely will measure different behavioural states, we examined only data from the seven bears equipped with GPS radiocollars set to obtain hourly fixes. We drew 20 random movements for each used step and used conditional logistic regression to obtain estimates of coefficients for landscape and traffic variables.

Modelling framework and fitting

For both RSFs and SSFs, we developed a set of three candidate models specifically formulated to evaluate the prediction that the addition of information on traffic would better explain habitat selection and movement than information on habitat and roads alone. The first of these models was comprised of covariates shown in previous studies to influence grizzly bear habitat selection or movement in Alberta (Tables 1–3; Nielsen *et al.* 2002, 2004; Roever, Boyce & Stenhouse 2008; Northrup, Stenhouse & Boyce 2012). These models included road variables but not traffic variables. The remaining models had an identical structure to those above but included traffic variables (Tables 2 and 3). We compared all models using Akaike's Information Criterion (AIC; Burnham & Anderson 2002) to determine which had the greater weight of evidence. This analysis allowed us to evaluate the relative importance of traffic to grizzly bear habitat selection and movement, above-and-beyond the influence of roads themselves, while also controlling for habitat. Northrup, Stenhouse & Boyce (2012) found grizzly bear habitat selection to differ between night and day in this study area, and road traffic varied substantially between these time periods, thus we fit separate models for night and day.

For RSFs and SSFs, we used the two-step modelling approach described by Fieberg *et al.* (2010). We fit each of the candidate models described earlier to each bear individually. We then calculated AIC values and AIC weights for each individual bear model following Burnham & Anderson (2002). We next averaged model weights for each of the three candidate models across all bears as suggested by Fieberg *et al.* (2010) and selected the best model as the one with the highest mean weight. To obtain population-level coefficient estimates, we then averaged coefficient values from the best model across all bears (Fieberg *et al.* 2010). Prior to fitting models, we examined correlations among variables and only included variables that were not highly correlated ($|r| < 0{\cdot}7$). All of the above-mentioned analyses were conducted using the R statistical software.

Results

BROAD-SCALE RESPONSE TO ROADS

Traffic volume was similar between WE and WD with 36% of all roads classified as low-volume, 52% classified as medium-volume, and 12% classified as high-volume during both times so we have reported results for day vs.

night only. Grizzly bear selection of areas near roads differed by traffic volume (Fig. 1). We identified three classes of traffic volume based on selection ratios (low, ≤ 20; medium, >20 and ≤ 100; and high, >100 vehicles per day). Grizzly bears exhibited different response to these classes by distance with greatest avoidance of areas close to high-traffic roads (Fig. 2). These patterns persisted between day and night, although with significantly stronger selection during the night than the day for bins closest to medium- and low-volume roads (Fig. 2).

Analysing consecutive successful fixes only, 13% of grizzly bear steps crossed roads ($n = 2146$ of 16 601 steps), and crossings were more common at night (19% of steps), relative to the day (6%). During the night, bears crossed roads with significantly less traffic than those crossed during the day ($\bar{x}$ traffic volume of roads crossed at night = 18·3, $\bar{x}$ during the day = 146, $P < 0{\cdot}0001$). The relationship between traffic volume and step length was weak for both groups of bears (1 h fixes $r = 0{\cdot}2$, >1 h fixes $r = 0{\cdot}3$).

RSFS AND SSFS

For RSFs, models containing variables for traffic volume had nearly three times the weight of evidence as the next best model (Table 2). For day-time SSFs, the model with variables for traffic volume classes had nearly two times the weight of evidence as the next best model (Table 3). For the night-time SSFs, there was substantial model uncertainty with two models having nearly identical weights (Table 3). Thus, we calculated model averaged coefficients by weighting coefficients for each model by the model weight (Burnham & Anderson 2002; Table 4). For all RSF models, there was substantial individual variation in coefficient values contributing to large standard errors (Table 5), but bears consistently responded to certain variables. During the day, bears selected areas further from high and medium traffic volume roads. At night, bears selected to be further from high- and medium traffic volume roads (Table 5). For SSFs, there was again high individual variation, leading to high standard errors for model coefficients, with few variables consistently selected among bears (Table 4). During the day, bears avoided crossing roads of all traffic types but with greater avoidance of roads with higher levels of traffic. At night, bears selected to cross low traffic volume roads at greater frequency than random, with this covariate being one of the only variables consistently selected among bears (Table 4).

Discussion

We documented a strong behavioural response by grizzly bears to road traffic. Bears avoided medium- and high-volume roads but used low-volume roads when available and crossed these roads more frequently. This response was consistent between night and day, when accounting for other habitat characteristics, but nearly all of the roads in the study area were classified as low traffic at night, indicating a direct response to daily traffic patterns. Furthermore, while we documented high individual variation in habitat selection among bears, traffic volume variables were consistently selected. This indicates that although responses to habitat were individual in nature, the response to roads was not. These findings highlight the importance of using detailed representations of human road-use when characterizing habitat selection and movement by large mammals. Past human-use models have used distance from towns and/or industrial features as relative indices of human use of roads (Apps *et al*. 2004; Roever, Boyce & Stenhouse 2010). None of these variables were reliable predictors of traffic volume in any of our models, and relying on such indices could lead to false assumptions about the importance of traffic.

Grizzly bears in areas less populated by humans are most active during the day (Boyce *et al*. 2010) and there is typically no daily pattern to their use of roads (Roever, Boyce & Stenhouse 2010). Our results indicate that vehicular activity drives a clear shift in these patterns. Past studies have documented similar shifts, with disproportionate use of roads during the night and have attributed these patterns to differences in human use (McLellan & Shackelton 1988; Mueller, Herrero & Gibeau 2004; Waller & Servheen 2005). However, our study is the first to provide a mechanistic basis for this finding. Proximity to roads, particularly during times of greater human activity increases nutritional and psychological stress in some large mammals (Wasser *et al*. 2011). In addition, displacement of wildlife from preferred areas can lead to substantial energy loss (Houston, Prosser & Sans 2011), suggesting these behavioural responses could lead to decreased productivity at the population level.

The strong response of bears to traffic in our study area highlights the nuanced relationship between bears and roads. Past studies have shown grizzly bears to prefer areas with road densities below 0·6 km km^{-2} (Mace *et al*. 1996), and this value has been adopted for management targets by many jurisdictions. Road density on private land in our study area far exceeded this threshold, whereas density on public land was below this level. However, many bears in this area occupied private land exclusively, and private land was selected over public land (Northrup, Stenhouse & Boyce 2012). The fact that roads on areas of public land designated as core grizzly bear habitat in Alberta (Alberta Sustainable Resource Development 2008) have a greater behavioural effect than the higher density of roads in secondary habitat is quite remarkable and can only be explained by the human use of these roads. The majority of roads on private land received little traffic, and this traffic was highly predictable, evidenced by the small differences in traffic between WE and WD, relative to the public land (see Appendix S1, Supporting information). Furthermore, road and trail use in the public land in our study area is predominantly

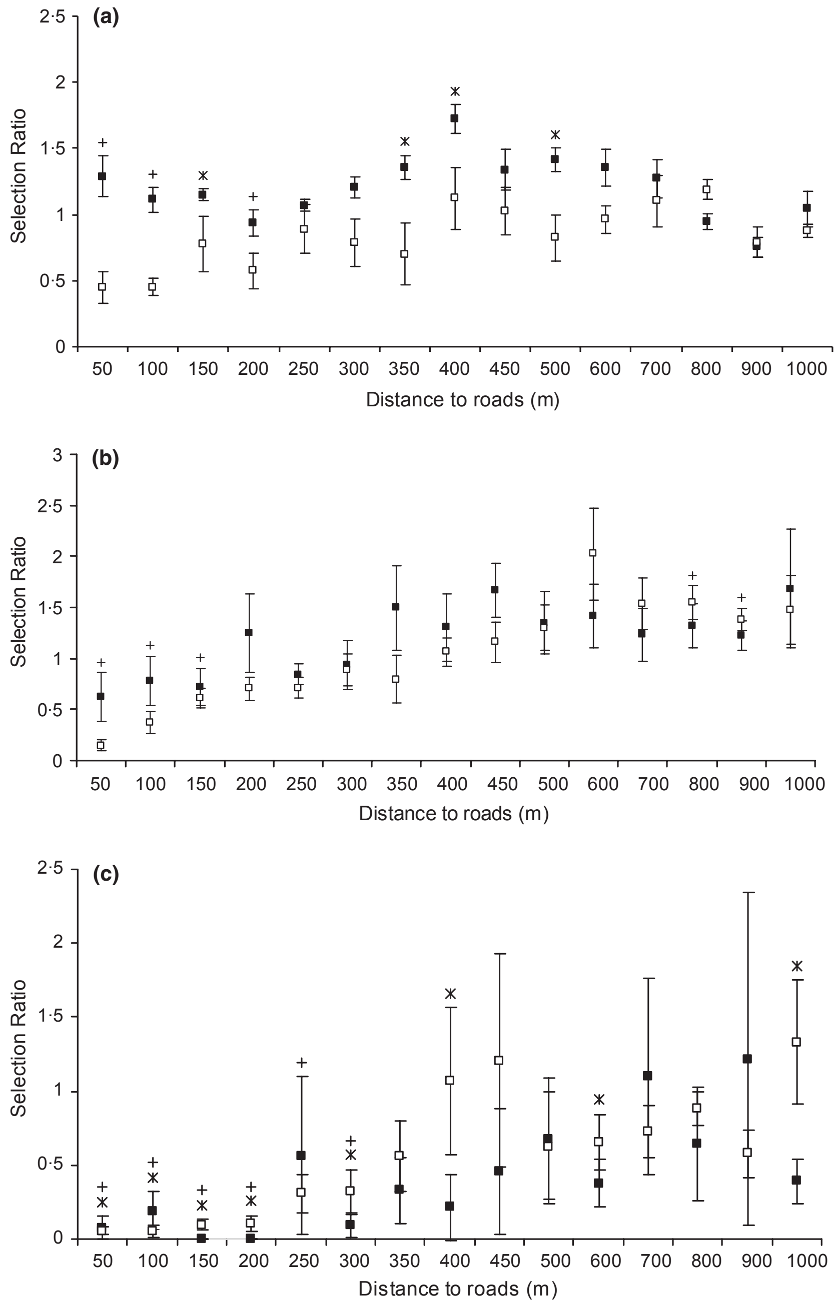

Fig. 2. Mean and standard errors of selection ratios for distance to road bins by day (□) and night (■) for (a) low-volume roads (<20 vehicles per day), (b) medium-volume roads (20–100 vehicles per day) and (c) high-volume roads (>100 vehicles per day) for16 grizzly bears in south-western Alberta. * and + indicate confidence intervals that did not overlap 0 for night time and day-time selection ratios, respectively.

recreational (OHV use and hunting; S. Ciuti unpublished data). Clearly, the type and volume of human use are important determinants of wildlife responses to roads and must be a consideration in effective management of human use of roads.

Conclusions

Management of roads to protect grizzly bears has long relied on limiting road density below thresholds established for core habitat. Such an approach reduces the potential for bear–human interaction, but ignores human use of roads, which can have greater influence on bear behaviour than the road itself. Wildlife managers must account for both traffic and road density when managing wildlife in areas with roads. Limiting road density will often be insufficient or impractical. In such cases, access management can be an effective tool for wildlife managers. Importantly, gated roads in our study area had the lowest traffic volumes of all roads. While this finding is expected, it verifies that gates can work to reduce the impacts of roads on grizzly bears. Finding the balance

Table 4. Covariates and average mean (Coeff.) and standard errors (SE) for coefficients from best step-selection function (SSF) models fit to seven grizzly bears in south-west Alberta, Canada for day and night separately, averaged across all models

Covariate	Day Coeff.	Day SE	Night Coeff.	Night SE
cut	3·5E-4	5·1E-04	−2·4E-04	3·1E-04
stream	2·4E-2	0·06E	−0·01	0·04
ndvi	1·8E-4	2·6E-04	1·3E-05	1·6E-04
cti	−1·4E-2	0·07	0·02	0·05
edge_e	−5·9E-4	2·7E-03	−2·6E-03	1·7E-03
edge_i	1·3E-3	6·9E-04	4·1E-05	5·9E-04
tri_lwm	0·03	0·02	−4·7E-04	0·01
age	1·7E-4	1·1E-04	8·1E-05	7·2E-05
shrub	−0·03	0·25	−0·07	0·28
herb	−0·49	0·28	−0·01	0·18
x_barren	−0·68	0·54	0·12	0·31
d_low	1·9E-4	2·3E-04	9·3E-05	1·0E-04
d_med	3·0E-4	2·4E-04	−4·7E-05	5·8E-05
d_high	1·7E-4	1·8E-04	−5·3E-05	5·0E-05
x_low	−0·43	0·55	0·22	0·07
x_med	−0·71	0·48	0·03	0·13
x_high	−1·14	0·73	0·05	0·41
d_rds	–	–	6·0E-05	1·0E-04
cross	–	–	0·26	0·07
cross_traff	–	–	2·1E-04	2·1E-04

Land cover variables above are in reference to treed land cover.

Table 5. Covariates and average mean (Coeff.) and standard errors for coefficients (SE) from best resource selection functions (RSF) model fit to 12 grizzly bears in south-west Alberta, Canada for day and night separately

Covariate	Day Coeff.	Day SE	Night Coeff.	Night SE
cut	−6·4E-4	2·0E-4	−5·6E-4	1·6E-4
stream	−0·03	0·04	−0·06	0·03
ndvi	3·3E-5	1·06E-4	−3·1E-5	8·4E-5
cti	−0·14	0·05	−3·0E-3	0·04
edge_e	−2·4E-3	1·8E-3	−3·3E-3	1·3E-3
edge_i	−4·9E-4	4·5E-4	−1·3E-3	4·6E-4
tri	−0·02	07·1E-3	−0·02	7·0E-3
age	1·3E-4	8·4E-5	2·9E-6	7·1E-5
shrub	−2·79	160·55	−1·31	32·16
herb	−0·71	0·31	−0·16	0·20
barren	−3·19	73·06	−0·24	0·24
d_low	0·08	0·07	3·7E-3	0·04
d_med	0·29	0·08	0·13	0·07
d_high	0·19	0·08	0·24	0·12

Land cover variables above are in reference to treed land cover.

between managing road density and traffic will be a difficult task. Roads with higher traffic volume should contribute more towards density thresholds than roads receiving less traffic. Alternatively, thresholds could be set for the proportion of roads in core habitat that receives more than some set volume of traffic, for example, in our study area, bears avoided roads receiving >20 vehicles per 24 h period. This finding could be used as the basis for a management guideline; core habitat should have road densities below 0·6 km km^{-2} with the majority of these roads receiving fewer than 20 vehicles per 24 h period.

As resource extraction industries continue to develop in wild lands in North America, the accompanying road networks will put a strain on wildlife populations. In addition to industrial traffic, recreational users become accustomed to using roads, and strong resistance is likely to ensue when attempting to close roads. Thus, limiting the types and volumes of road-use will become a crucially important tool for reducing the impacts on wildlife. We recommend that access management should be required for any activity that includes the construction of new roads.

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References

Adams, L.W. & Geis, A.D. (1983) Effects of roads on small mammals. *Journal of Applied Ecology*, **20**, 403–415.

Alberta Sustainable Resource Development (2008) *Alberta Grizzly Bear Recovery Plan 2008–2013*. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta.

Apps, C.D., McLellan, B.N., Woods, J.G. & Proctor, M.F. (2004) Estimating grizzly bear distribution and abundance relative to habitat and human influence. *The Journal of Wildlife Management*, **68**, 138–152.

Archibald, W.R., Ellis, R. & Hamilton, A.N. (1987) Response of grizzly bears to logging truck traffic in the Kimsquit River valley, British Columbia. *International Conference on Bear Research and Management*, **7**, 251–257.

Benn, B. & Herrero, S. (2002) Grizzly bears and mortality in Banff and Yoho National Parks, 1971–98. *Ursus*, **13**, 213–221.

Boyce, M.S., Pitt, J.A., Northrup, J.M., Morehouse, A., Knopff, K.H., Cristescu, B. & Stenhouse, G.B. (2010) Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2213–2219.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference. A Practical Information-theoretic Approach*, 2nd edn. Springer Verlag, Berlin.

Carr, L.W. & Fahrig, L. (2001) Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology*, **14**, 1071–1078.

Cattet, M.R.L., Caulkett, N.A. & Stenhouse, G.B. (2003) Anaesthesia of grizzly bears using xylazine-zolazepam-tiletamine or zolazepam-tiletamine. *Ursus*, **14**, 88–93.

Chruszcz, B., Clevenger, A.P., Gunson, K.E. & Gibeau, M.L. (2003) Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology*, **81**, 1378–1391.

Ciarniello, L., Boyce, M.S., Seip, D.R. & Heard, D.C. (2009) Grizzly bear population ecology: comparison of a wilderness versus heavily roaded landscape. *Wildlife Biology*, **15**, 247–265.

Dyer, S.J., O'Neil, J.P., Wasel, S.M. & Boutin, S. (2001) Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management*, **65**, 531–542.

Fahrig, L. & Rytwinski, T. (2009) Effects of roads on animal abundance: an empirical review. *Ecology and Society*, **14**, 1–20.

Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D. & Wegner, J.F. (1995) Effect of road traffic on amphibian density. *Biological Conservation*, **73**, 177–182.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring, or opportunity? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2233–2244.

Forman, R.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, **29**, 207–231.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004) Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, **41**, 201–212.

Franklin, S.E., Stenhouse, G.B., Hansen, M.J., Popplewell, C.C., Dechka, J.A. & Peddle, D.R. (2001) An integrated decision tree approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. *Canadian Journal of Remote Sensing*, **27**, 579–592.

Gibeau, M.L., Clevenger, A.P., Herrero, S. & Wierzchowski, J. (2002) Grizzly bear response to human development and activities in the Bow River watershed, Alberta, Canada. *Biological Conservation*, **103**, 227–236.

Hebblewhite, M., Percy, M. & Merrill, E.H. (2007) Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. *The Journal of Wildlife Management*, **71**, 2026–2033.

Hood, G.A. & Parker, K.L. (2001) Impact of human activities on grizzly bear habitat in Jasper National Park. *Wildlife Society Bulletin*, **29**, 624–638.

Houston, A.I., Prosser, E. & Sans, E. (2011) The cost of disturbance: a waste of time and energy? *Oikos*, **121**, 597–604.

Johnson, C.J., Boyce, M.S., Schwartz, C.C. & Haroldson, M.A. (2004) Modeling survival: application of the Andersen-Gill model to Yellowstone grizzly bears. *The Journal of Wildlife Management*, **68**, 966–978.

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L. & Boyce, M. S. (2006) Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *The Journal of Wildlife Management*, **70**, 347–357.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J. & Zuuring, H. (1996) Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology*, **33**, 1395–1404.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd edn. Kluwer Academic Publishers, Dordrecht.

Mattson, D.J., Knight, R.R. & Blanchard, B.M. (1987) The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research and Management*, **7**, 259–273.

Mazzerolle, M.J. (2004) Amphibian road mortality in response to nightly variations in traffic intensity. *Herpetologica*, **60**, 45–53.

McLellan, B.N. (1989) Dynamics of a grizzly bear population during a period of industrial resource extraction II. Mortality rates and causes of death. *Canadian Journal of Zoology*, **67**, 1856–1860.

McLellan, B.N. & Shackelton, D.M. (1988) Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology*, **25**, 451–460.

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.

Mueller, C., Herrero, S. & Gibeau, M.L. (2004) Distribution of subadult grizzly bears in relation to human development in the Bow River watershed, Alberta. *Ursus*, **15**, 35–47.

Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217–229.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B. & Munro, R.H.M. (2002) Modelling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelations seriously. *Ursus*, **13**, 45–56.

Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M. L. & Jevons, S. (2004) Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation*, **120**, 101–113.

Northrup, J.M., Stenhouse, G.B. & Boyce, M.S. (2012) Agricultural lands as ecological traps for grizzly bears. *Animal Conservation*, **14**, 369–377.

Oxley, D.J., Fenton, M.B. & Carmody, G.R. (1974) The effects of roads on populations of small mammals. *Journal of Applied Ecology*, **11**, 51–59.

Roever, C.L., Boyce, M.S. & Stenhouse, G.B. (2008) Grizzly bears and forestry I: road vegetation and placement as an attractant to grizzly bears. *Forest Ecology and Management*, **256**, 1253–1261.

Roever, C.L., Boyce, M.S. & Stenhouse, G.B. (2010) Grizzly bear movements relative to roads: application of step selection functions. *Ecography*, **33**, 1–10.

Rowland, M.M., Wisdom, M.J., Johnson, B.K. & Kie, J.G. (2000) Elk distribution and modeling in relation to roads. *The Journal of Wildlife Management*, **64**, 672–684.

Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *The Journal of Wildlife Management*, **73**, 1052–1061.

Spellerberg, I.F. (2002) *Ecological Effects of Roads*. Science Publishers, Enfield.

Stathopoulos, A. & Karlaftis, M. (2001) Spatial variations of real-time traffic data in urban areas. *Transportation Research Record: Journal of the Transportation Research Board*, **1768**, 135–140.

Townshend, J.R.G. & Justice, C.O. (1986) Analysis of the dynamics of African vegetation using the normalized difference vegetation index. *International Journal of Remote Sensing*, **7**, 1435–1445.

Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.

Turchin, P. (1998) *Quantitative Analysis of Movement*. Sinaur Associates, Sunderland.

Vos, C.C. & Chardon, J.P. (1998) Effects of habitat fragmentation and road density on the distribution pattern of the Moor frog *Rana arvalis*. *Journal of Applied Ecology*, **35**, 44–56.

Waller, J.S. & Servheen, C. (2005) Effects of transportation structure on grizzly bears in Northwestern Montana. *The Journal of Wildlife Management*, **69**, 985–1000.

Wasser, S.K., Keim, J.L., Taper, M.L. & Lele, S.R. (2011) The influence of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology and the Environment*, **9**, 546–551.

Whittington, J., St. Clair, C.C. & Mercer, G. (2004) Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society*, **9**, 4.

Wielgus, R.B., Vernier, P.R. & Schivatcheva, T. (2002) Grizzly bear use of open, closed, and restricted forestry roads. *Canadian Journal of Forest Research*, **32**, 1597–1606.

Wilson, R.E. (2008) Mechanisms for spatio-temporal pattern formation in highway traffic models. *Philosophical Transactions of the Royal Society. Series A*, **13**, 2017–2032.

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Appendix S1. Modelling and predicting road traffic.

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