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Thresholds in landscape connectivity and mortality risks in response to growing road networks

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Summary

1. The ecological footprint of a road may extend for several kilometres with overlapping effects from neighbouring roads causing a nonlinear accumulation of road effects in the landscape. Availability of preferred habitat, spatial dependencies between roads and habitat types, and fidelity to traditionally used areas further confound our ability to predict population-level responses of animals to growing road networks.

2. To isolate these effects, we developed an individually based movement model using elk *Cervus elaphus* L. as a model system. Empirically derived movement rules redistributed elk under different amounts of preferred habitat (clearcuts), road densities, and road development schemes. We tracked potential mortality risk (given time spent near roads) and emigration rates (given declining accessibility of foraging habitat).

3. Design of the road network accounted for up to 30–55% difference in mortality risk and emigration rates, with the largest differences occurring at intermediate road densities (1–1·5 km km^{-2}) when road effects began to saturate the landscape. Maintaining roads in association with clearcuts caused a decline in habitat accessibility equivalent to replacing 50–75% of these foraging patches with conifer forest. A nine-fold difference in potential emigration was observed after varying elk tolerance for declining habitat accessibility despite holding local movement biases constant.

4. Elk responses to growing road networks were non-linear, exposing thresholds for road density that were reflected in the home range occupancy patterns of a large sample of elk in the region.

5. *Synthesis and applications*. Our approach provides a means of scaling-up complex movement decisions to population-level redistribution, separating the confounding effects of landscape context from road effects, and exposing thresholds in connectivity and mortality risks for wildlife caused by infrastructure growth. Our model indicated that road densities ≤ 0·5 km km^{-2} yielded the highest probability of elk occurrence where elk were hunted (and sensitive to roads), but dis-associating roads from foraging habitats or managing human access to roads may maintain effective elk habitat at substantially higher road densities.

Key-words: habitat bias, movement model, random walk, road density, road ecology

Introduction

A growing and increasingly pervasive network of roads extends the reach of humans, and the deleterious effects of their activities, into wildlife habitat. Road construction increases mortality risk for wildlife as a result of collisions with vehicles (Lode 2000), and fundamentally alters the amount and arrangement of habitat patches (Andrews 1990). The unwillingness or inability of individuals to cross roads can lead to population isolation (Epps *et al.* 2005; Riley *et al.* 2006), and reduced population viability. Even within 'connected' populations, road-related mortality can alter the demographic structure of populations (Steen & Gibbs 2004) or create localized population sinks (Nielsen, Stenhouse & Boyce 2006). Importantly, roads influence habitat quality in areas adjacent to the road proper (Barnes *et al.* 1991; Nellemann *et al.* 2003), extending the ecological footprint up

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to several kilometres from the road surface (Forman 2000). As a result, road effects can saturate a landscape even at relatively low road density (Forman *et al.* 2003). Non-linearities arise from landscape asymmetries (i.e. effects differ on either side of a road) and spatial redundancies (i.e. overlap of neighbouring road effects), which complicates the task of scaling-up localized animal responses to the cumulative effect of a road network on animal populations (Rowland *et al.* 2000; also see review by Forman *et al.* 2003). Nevertheless, knowledge of critical shifts in population responses to growing road networks is necessary to ensure species persistence and functional ecosystems in an increasingly human-dominated world (Forman 2000; Boutin & Hebert 2002; Groffman *et al.* 2006).

Reductions in species abundance correlate to increases in road density for a variety of species (Reijnen, Foppen & Veenbaas 1997; Apps *et al.* 2004; Ripley, Scrimgeour & Boyce 2005). Mechanisms underlying reduced abundance include elevated mortality on or along roads (a numerical response, e.g. Gratson & Whitman 2000), and avoidance of areas near roads (a functional response, e.g. Nellemann *et al.* 2003). Documenting mortality is straightforward, but behavioural responses are constrained, in part, by the availability of suitable alternate habitat (Gill, Norris & Sutherland 2001) and the fidelity of some species to traditionally used areas. As the abundance of habitat unaffected by roads declines, animals remaining in the landscape have no choice but to use habitats close to roads or encounter roads more frequently as they search for resources. Thus, consideration of animal behaviour in the broader landscape context is required to infer how numerical and behavioural responses affect the spatial structure of animal populations as roads proliferate.

Further, because road effects accumulate in a nonlinear manner, critical thresholds in species responses to road density may exist. Threshold values are likely to depend on the overall amount of favourable habitat (Andrén 1994; Groffman *et al.* 2006), the spatial design of the road network (Rowland *et al.* 2000), and the extent of road effects. Such variation potentially underlies contrasting animal responses in different landscape contexts (e.g. Rempel *et al.* 1997; Rowland *et al.* 2000; Rothley 2002; Jepsen & Topping 2004). Empirically demonstrating the effects of road density, landscape context, range fidelity, and their interactions on animal distributions would be difficult to achieve without experimentation, and such experiments are feasible for only a limited number of species. Simulation models provide a useful alternative, and a movement-based approach is appealing for several reasons. First, movement models account for habitat accessibility contingent upon starting location and movement constraints, such as an unwillingness to move towards roads. In contrast, statistical models of animal distribution patterns may predict high animal use in areas that remain unused by animals due to intervening barriers or inhospitable habitats (Matthiopoulos 2003). Secondly, advances in the study of animal movement make available relatively simple and transparent models based on a random walk process (Turchin 1998). To date, movement models applied to road effects have focused largely on dispersal success (Schippers *et al.* 1996; Zollner & Lima 2005; Kramer-Schadt *et al.* 2004; Revilla *et al.* 2004; but see also Gibbs & Shriver 2002). Yet, road networks may also impede routine movements, and maintaining suitable, accessible, and safe habitat for regular movements may be as or more critical to the structuring and persistence of populations than successful dispersal (Van Dyck & Baguette 2005).

Herein, we use a random walk framework to understand the interacting effects of road network density and design, amount of critical habitat, and animal behaviour on potential changes in the distribution of non-dispersing animals as road networks grow. We parameterized our model for elk *Cervus elaphus* L., a useful model species because they are subject to increased incidental mortality from roads via legal hunting and illegal poaching (McCorquodale, Wiseman & Marcum 2003; Frair *et al.* 2007), and they tend to avoid roads throughout their geographic range (Witmer & deCalesta 1985; Czech 1991; Jones, Hudson & Farr 2002). Yet, elk distributions demonstrate a high degree of variation in response to road density in different ecological settings (Millspaugh 1999; Rowland *et al.* 2000; Roloff *et al.* 2001). We collected movement data using Global Positioning System (GPS) collars on adult, female elk in the Rocky Mountain foothills of Alberta, Canada, over a period of four summers. From these data, we developed movement rules that redistributed elk across test landscapes where we controlled road density, network design, habitat amount, and elk tolerance of declining habitat accessibility caused by roads. We measured the proportion of time animals spent near roads to infer mortality risk based on a previous study of elk survival in the region (Frair *et al.* 2007). We also estimated the proportion of animals expected to abandon areas given trade-offs between declining habitat accessibility and assumed levels of home range fidelity. Our goal was to find critical thresholds in elk responses to growing road networks, and quantify the relative effects of network design under alternative landscape contexts.

Materials and methods

The movements and habitat selection of 23 adult-female elk were studied from 2001 to 2004 in a ~2800 km^2 area in the lower foothills, natural subregion (Beckingham, Corns & Archibald 1996) of the Rocky Mountains of Alberta, Canada (52°27′ N, 115°45′ W; Fig. 1), where approximately 1000 elk occurred (Allen 2005). The area ranged in elevation from 870 to 1800 m above sea level and was predominantly forested (~84% of total area) by lodgepole pine *Pinus contorta* Dougl. ex Loud, white spruce *Picea glauca* [Moench] Voss, aspen *Populus tremuloides* Michx. and balsam poplar *Populus balsamifera* L. Foraging habitats for elk included clearcuts (regenerating after timber harvest; 8·9% of the total area), natural meadows (2·6%), and herbaceous utility corridors (0·6%; Beyer 2004).

Land use was dominated by timber harvest and gas exploration. Thus, roads were either closely associated with the location of primary foraging habitat for elk (clearcuts) or placed largely at random with respect to clearcuts (gas industry roads). We focused on maintained, gravel roads open to public travel year-round, which were related to

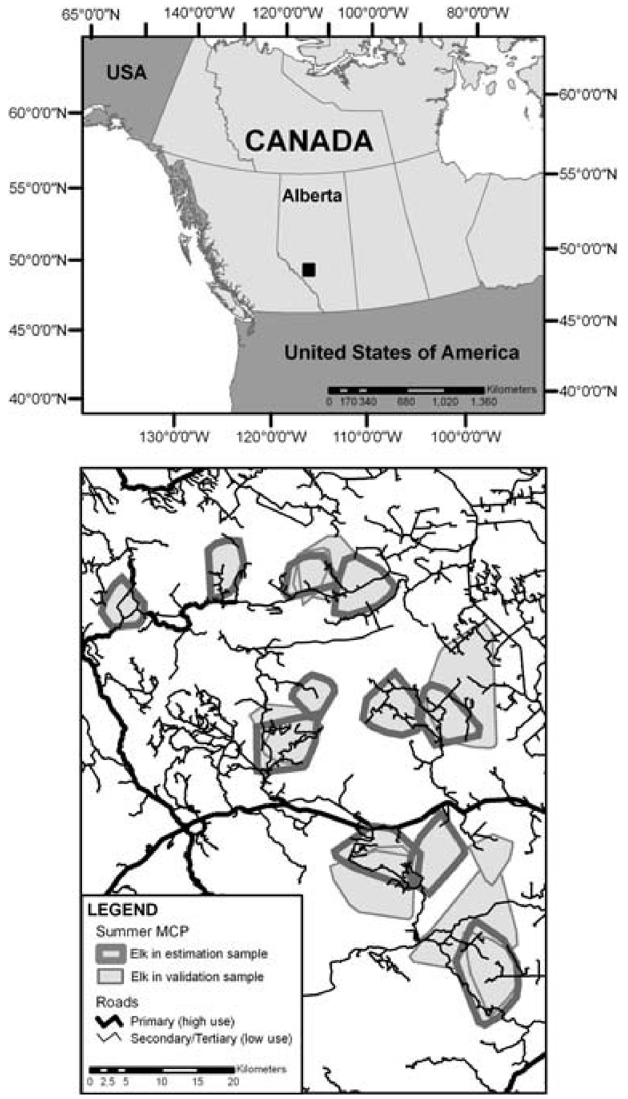

Fig. 1. Location of study area (black rectangle; top) in the lower foothills of the Rocky Mountains, Alberta, Canada. Distribution of monitored elk and roads, 2001–2004 (bottom).

elk survival in an associated study (Frair *et al.* 2007). Our GIS layer for roads (provided by Alberta Sustainable Resources Development) was updated annually using TM imagery, and field-validated. For each 30-m cell in our landscape and each year, we derived the proximity to the nearest road for comparison to elk locations.

Details of collar deployment and performance are provided elsewhere (Frair *et al.* 2004, 2005). For this study, we retained 2-h interval locations collected during summer only (June–September) to avoid any confounding effects of the regulated autumn hunt or winter snow conditions on elk movements. There was no regulated hunt of female elk during the autumn; however, First Nations people hunted year-round, and 67% of the female elk harvest occurred during June–September (Frair *et al.* 2007), coincident with the time frame of this analysis. Movement characteristics and selection of vegetation types were derived from 11 individuals having largely non-overlapping home ranges, with the remaining 12 animals withheld for model validation (Fig. 1). These animals occupied areas where road density ranged 0·13–0·88 km km^{-2} (Supplementary Material Table S1). We derived step length (SL), the straight-line displacement between consecutive 2-h locations, and turn angle (TA), the angular difference between two consecutive steps (3 consecutive locations), using Hawth's Tools (www.spatialecology.com). On average, 879 (± 47 SE) step lengths and 735 (± 50 SE) turn angles were recovered per animal.

MODEL DEVELOPMENT AND VALIDATION

We took a pattern-oriented approach (Grimm *et al.* 2005) to model development by adding increasingly detailed movement behaviour until elk were redistributed 'correctly' with respect to road and habitat features. For each formulation, we compared the proportion of simulated vs. empirical elk locations occurring within 11 road proximity intervals and six general classes of vegetation. We stopped adding complexity when the 95% CI for simulated and real elk overlapped throughout the range of observed road proximities and vegetation types.

Common to all formulations, we randomly selected 100 actual elk locations as starting points, and used the specified model (see sections to follow) to produce 100 realizations of simulated paths. Movement decisions were made at 2-h intervals for 1440 time steps (120 days). Simulated movements were constrained to occur within existing home range boundaries by rejecting steps that intercepted the boundary, and drawing another step according to the model specified.

Simple Random Walk (SRW)

Data were pooled across individuals to yield the population distribution of SL (range 0–6308 m, median = 154 m, n = 11 671) and TA (mean vector direction = 0·38°, n = 9983). Random and independent draws from the SL and TA distributions identified the potential displacement, i.e. distance and direction, a simulated elk would move at each time step. The 95% CI from simulations overlapped the empirical elk distribution throughout the range of road proximities, but tended to deviate when ≤ 250 m from a road (Fig. 2a). However, simulated elk redistributed randomly with respect to vegetation types (Fig. 2a).

State-Based Random Walk (SBRW)

Separate SRW models were produced depending upon animal state. Empirical SL < 50 m were considered 'inactive' with remaining displacements classified as 'foraging' or 'travelling' using an individual-specific scale criterion ($r_{\max}$; see Frair *et al.* 2005). When SL < $r_{\max}$, we considered the animal to be foraging, otherwise it was travelling. Thus, three possible SL and TA distributions were identified (Table 1). To predict which state a simulated animal was in at each time step, we correlated empirical state (for our 11 animals) to time of day and local environmental covariates using binomial time series models (XTLOGIT; Stata 8·2). Time of day was fit as a sine wave, and environmental covariates included vegetation type, degree slope, aspect, predation risk (see Frair *et al.* 2007), proximity of trail/pipeline, and proximity of road. Time of day explained the most variation, although elk were likely to remain inactive in areas of higher predation risk and northeast-facing slopes, to forage in cutblocks and on steeper slopes, and to travel when ≤ 50 m of a trail or 300 m of a road (Supplementary Material Table S2; see also Frair *et al.* 2005). For our simulations, the probability of a given animal state at

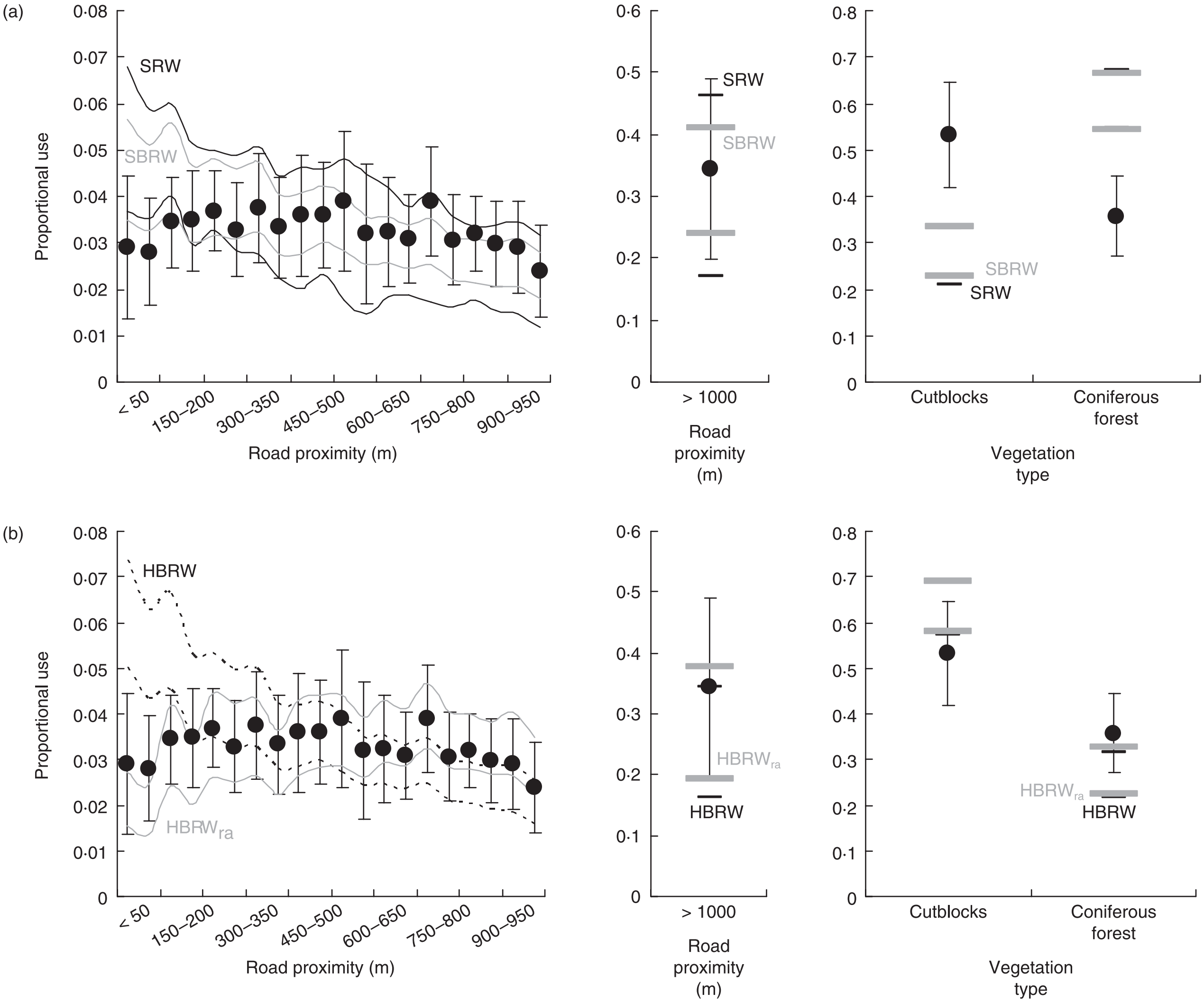

Fig. 2. Distributions of empirical elk (filled symbols showing mean with 95% CI; n = 11 671 locations, n = 11 elk) and simulated elk (95% CI only) in the Rocky Mountain foothills, Alberta Canada, with respect to road proximity and the two most abundant habitat types. The results from a Simple Random Walk (SRW, dotted black line) and State-Based Random Walk (SBRW, grey line) are shown in (a), with the Habitat-Biased Random Walk (HBRW, dotted black line) and the Road-Adjusted Habitat Bias ($\mathrm{HBRW_{ra}}$, grey line) shown in (b).

Table 1. Step length and turn angle distributions by behavioural state for 11 adult female elk in the central Rocky Mountain Foothills, Alberta, Canada, 2001–2004. For turn angles, the circular mean direction with 95% confidence interval in degrees and vector strength is given. Superscripts indicate tests of uniformity and unimodality for the turn angle distributions following Batschelet (1981)

	Step length (m)			Turning angle (°)			
State	*n*	Mean (SE)	Range	*n*	Mean	95% CI	Strength
Inactive	2383	24·7 (13·9)	0·0–50·9	2041	184·0*†	160·9–207·2	0·076
Foraging	5791	203·8 (159·6)	51·0–1241·4	4900	344·4*	Bimodal	0·018
Travelling	2289	899·6 (616·2)	201·0–6308·1	1953	4·8*†	346·5–23·1	0·097

*reject hypothesis of uniformity at $P < 0{\cdot}05$.
†accept alternative hypothesis of unimodality at $P < 0{\cdot}001$.

time t and location x, y was chosen randomly (uniform distribution) but weighted probabilistically by the P_{active} and P_{forage} values from the logistic models (Supplementary Material Table S2). Random and independent draws from the appropriate SL and TA distributions identified the potential displacement. Despite habitat associations with movement state, the SBRW redistributed elk similarly to the SRW (Fig. 2a) but with tighter confidence intervals due to autocorrelation induced by periodicity in behavioural states. Results did not differ for a simpler SBRW model that predicted elk state as a function of time of day only (Supplementary Material Table S2).

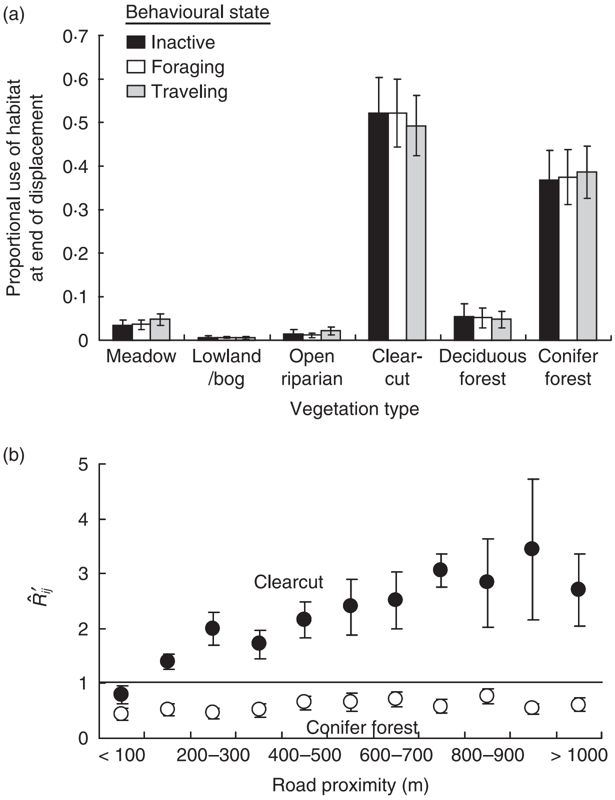

Fig. 3. Parameterization of the habitat bias using empirical data from 11 elk (n = 11 671 locations) in the Rocky Mountain foothills of Alberta, Canada, 2001–2004. Proportional use (mean ± SE) of each vegetation class is shown for the end-points of inactive (black), foraging (white), and travelling (grey) displacements (a). Resource selection ratios ($\hat{R}'_{ij}$; mean ± SE; see text), pooled across behavioral states, capture variation in end-point choices as a function of vegetation type and road proximity (b). $\hat{R}'_{ij} = 1$ indicates use proportional to availability

State-Based and Habitat-Biased Random Walk (HBRW)

To the SBRW model (based on time only), we added a habitat bias that oriented displacements toward favourable habitats. To do so, we first determined that the vegetation type underlying the end-point of empirical elk displacements, i.e. the location at time $t + 1$, did not differ depending upon behavioural state (Fig. 3a). We pooled all displacements to create a single habitat bias using resource selection ratios following Manly *et al.* (2002: 47) as:

$$\hat{R}'_i = \frac{\sum_{k=1}^{n}(y_i/x_i)}{n},$$

where y_i was the frequency of use of vegetation type i by individual k, and x_i was the availability of type i sampled randomly within the minimum convex polygon range of individual k (using a 1:1 sampling ratio; Supplementary Material Table S3). We divided each $\hat{R}'_i$ by the maximum observed ($\hat{R}'_{\text{clearcut}} = 2{\cdot}32$), which rescaled values from 0 to 1 and represented the relative probability of use of the location at the end-point of each potential displacement (P_{enduse}). Cover types not used by elk (e.g. water) were assigned $P_{\text{enduse}} = 0$. After drawing a potential step, P_{enduse} was compared to a random P value, with steps rejected at a rate of $1 - P_{\text{enduse}}$. Following rejection, another displacement was randomly drawn from the appropriate distribution.

The HBRW model redistributed elk well with respect to vegetation types, but caused greater disparity between the simulated and empirical distribution of elk ≤ 250 m of a road (Fig. 2b). Ultimately, $\hat{R}'_{ij}$ were derived separately for each vegetation type and road proximity to create a road-adjusted habitat bias (HBRW$_{\text{ra}}$). Notably, elk became increasingly selective for clearcuts with increasing distance away from roads, and consistently avoided conifer forest regardless of road proximity (Fig. 3b). The HBRW$_{\text{ra}}$ model achieved our goal of overlap between the empirical and simulated elk distributions throughout the range of vegetation types and road proximity values (Fig. 2b).

For validation, we ran the HBRW$_{\text{ra}}$ model for 12 elk, withheld during model development, which used areas > 1 km from a road 15% more and cutblocks 10% less on average than the elk used for model parameterization. The model achieved overlap in the 95% CI of empirical and simulated animals throughout the range of habitat types and road proximity intervals (Supplementary Material Fig. S1), and was sufficient for our application.

RESPONSES OF ELK TO LANDSCAPE CONDITIONS

For our simulation experiments, we focused on a landscape equivalent to the average elk home range (10 × 10 km), and developed scenarios relying on existing road and vegetative conditions. We quantified elk responses to road densities ranging from 0·1 to 2·33 km km^{-2} following two network designs – gas roads (independent of clearcuts) vs. forestry roads (associated with clearcuts) – and three habitat amounts (5%, 10% and 20% of the landscape clearcut). Both road networks began by building-up the long-term, primary access roads in the area (Scenarios 2–3, road density 0·10–0·31 km km^{-2}, see Supplementary Material Fig. S2). To increase road density further, we added either gas roads alone (Sc. 3a–e, 0·63–2·08 km km^{-2}), or the full extent of forestry roads (Sc. 4, 0·92 km km^{-2}) followed by gas roads (Sc. 4a–c, 1·34–2·33 km km^{-2}; Supplementary Material Fig. S2). Gas roads capitalized on existing infrastructure but were otherwise developed independently of clearcuts. To test elk sensitivity to the amount of preferred habitat (clearcuts), we used these same road networks after randomly reforesting 50% and 75% of the clearcuts leaving 11% and 5% of the landscape cut (Supplementary Material Fig. S2). Under each clearcut amount, baseline conditions were simulated considering that no roads occurred within 1 km of any cell in the landscape. We randomly selected 100x,y coordinates as start locations, set the initial time to midnight and initial behavioural state to inactive, and moved individuals for 120 days. Steps intercepting the landscape boundary were replaced with another randomly drawn step depending upon elk state.

Four outputs were quantified, starting with the proportional use of areas at different distances from roads. Secondly, setting mortality risk > 1 km from a road = 0, we converted the use of areas ≤ 1 km of a road to the per-location mortality hazard for elk j under scenario k as:

$$H_{jk} = \sum_{l=1}^{10} nh/N,$$

where the frequency of locations (n) occurring in road distance bin l (in 100-m intervals) was multiplied by the relative mortality hazard (h) associated with use of that distance bin, and N was the total number of locations for the animal. The mortality hazard, h, was calculated as $e^{-1\cdot5059x}$ following Frair *et al.* (2007), where x was the midpoint of each 100-m bin expressed in kilometres.

Thirdly, we quantified habitat accessibility by the number of potential displacements evaluated before an acceptable end-point

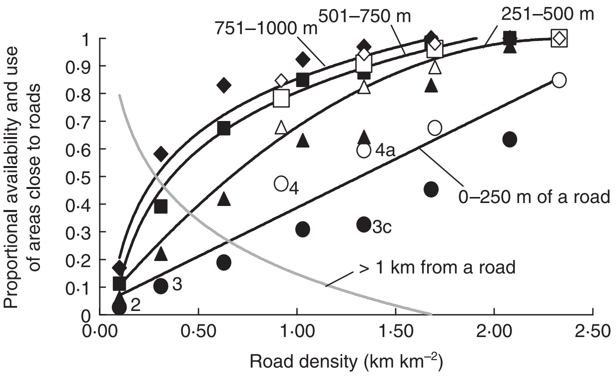

Fig. 4. The proportion of land area available to (lines) and used by simulated elk (symbols) within 0–250 m (circles), 251–500 m (triangles), 501–750 m (squares), and 751–1000 m (diamonds) of a road given an increasing road density when 20% of the landscape was cut. The proportion of area occurring > 1 km from a road is also shown (grey line). Open symbols indicate the 'roads associated with clearcuts' design, and filled symbols the 'roads independent of clearcuts' design. Scenario labels (e.g. 4, 4a) facilitate cross-referencing with Supplementary Material Fig. S2.

was identified. Landscape-level habitat accessibility for elk *j* in scenario *k* was:

$$A_{jk} = \left(\sum\nolimits_{t=25}^{1440} a_t/N\right)^{-1},$$

where the number of displacement attempts (*a*) at each time step (*t*) when the animal was actively moving was averaged over the total number of displacements (*N*). To avoid confounding boundary and road effects, we calculated *A* within the core 8 × 8 km of the landscape only. Finally, we allowed individuals to emigrate from the landscape when the number of attempted steps (*a*) within the core area exceeded a set tolerance level, because choosing not to return to areas difficult to access would shift home ranges away from core areas. We tracked the number of animals remaining in the landscape as a function of different tolerances for *a*.

Results

SIMULATED ELK REDISTRIBUTION AND MORTALITY

The extent of areas > 1 km from a road decayed rapidly as road densities increased, leaving no refuge from road effects given road densities ≥ 1·6 km km^{-2} (Fig. 4). Non-linearities occurred in the availability of areas > 0·25 km of a road as road density increased (Fig. 4). Assuming elk stayed in the landscape, their use of areas ≤ 1 km from a road increased with increasing availability of such areas (Fig. 4). Use of areas ≤ 250 m from a road differed up to 46% depending upon the road network design (Fig. 4), and these differences were steadily reduced (to a maximum difference of 21%) by reducing clearcut amount (Supplementary Material Fig. S3).

Mortality risk (*H*) rose rapidly as roads proliferated, dependant upon clearcut amount and road network design (Fig. 5). Differences were greatest at moderate road densities and greater amounts of clearcut habitat. For a given level of road density, ≤ 38% difference in *H* was accounted for by road network design. Alternatively, to maintain any given *H*, ≤ 60% greater road density was possible when roads were developed independently of clearcuts (Fig. 5).

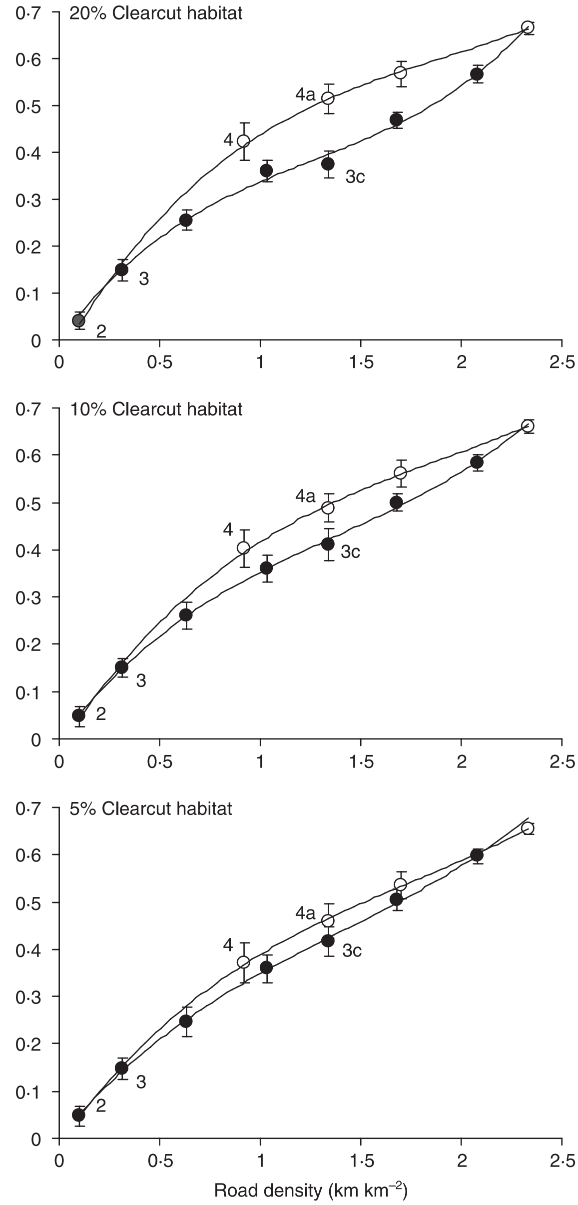

Fig. 5. The per-location mortality hazard (*H*; mean ± SD) incurred by simulated elk given an increasing road density and differing amounts of clearcut habitat. Polynomial curves were fit to the mean values observed under the 'roads independent from clearcuts' (filled symbols) and 'roads associated with clearcuts' (open symbols) designs. Scenario labels (e.g. 4, 4a) facilitate cross-referencing with Supplementary Material Fig. S2.

HABITAT ACCESSIBILITY AND HOME RANGE FIDELITY

Clearcut amount set different baselines for *A* (Fig. 6). A 17–27% drop in *A* occurred after developing the main access road, which bisected the landscape, after which a linear decline was observed with increasing road density (Fig. 6). Up to 32% difference in *A* was attributable to the design of the road network, with differences less pronounced as the

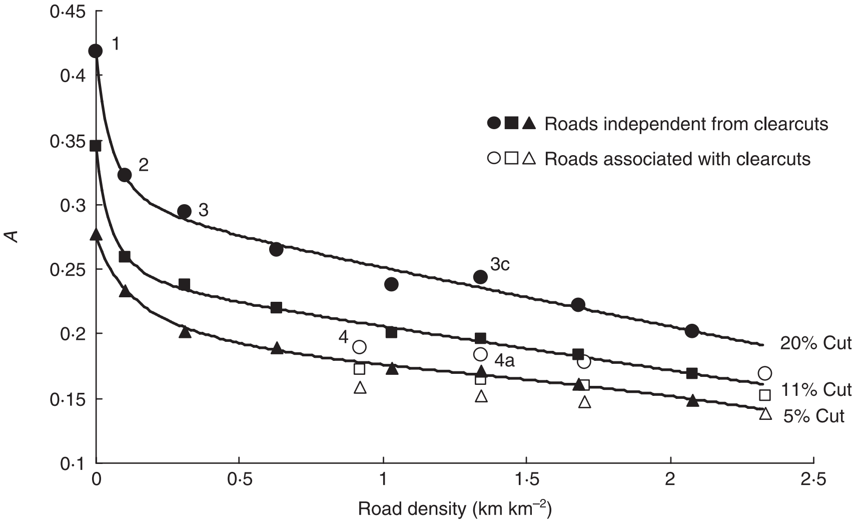

Fig. 6. Habitat accessibility (*A*), that is, the mean number of potential steps evaluated before suitable habitat is located (see text), given an increasing road density and differing amounts of clearcut habitat. Polynomial curves were fit to the mean values under the 'roads independent of clearcuts' design (filled symbols), but the 'roads associated with clearcuts' design is also shown (open symbols). Scenario labels (e.g. 4, 4a) facilitate cross-referencing with Supplementary Material Fig. S2.

amount of clearcut declined (Fig. 6). When clearcuts were abundant, developing roads in association with clearcuts caused a reduction in *A* equivalent in effect to reforesting 50–75% of the clearcuts (Fig. 6).

The potential rate of emigration was strongly affected by elk tolerance for declining habitat accessibility (Fig. 7). The majority of tolerant animals ($a \geq 40$) remained across all road densities and network designs when ≥ 10% of the landscape contained clearcuts. In contrast, intolerant individuals ($a \geq 20$) rapidly left as road density increased, with 90% emigrating at road densities ≥ 0·5 km km^{-2}, irrespective of clearcut amount. Road network design accounted for up to a 55% difference in the number of individuals retained, with the greatest effect apparent at intermediate-high habitat amounts, intermediate road densities, and intermediate tolerance levels (Fig. 7).

Discussion

Our simulations provided three general insights into potential thresholds in elk responses to increasing road densities. First, the most rapid changes in all response variables occurred at relatively low road densities, indicating a potential threshold between 0·25 km and 0·5 km of road/km^{-2} (Figs 4–7). Secondly, under some circumstances, mortality risk tended towards saturation or switched to an accelerating function of road density above ~1·25 km of road km^{-2} (Fig. 5). Thirdly, road effects saturated the landscape (i.e. no refuges > 1 km from a road) given a road density of ~1·6 km km^{-2} (Fig. 4). We compared these observations to the surrounding region, where 90% of 87 cow elk ranges occurred in areas where road density was < 0·5 km km^{-2} (the lowest threshold), and none occupied areas where road densities exceeded 1·08 km km^{-2} (approaching the mortality threshold) despite road densities exceeding 2·5 km km^{-2} in the region (J. Frair, unpublished data). These elk were exposed to general autumn hunting seasons and year-round hunting pressure by First Nations treaty rights (see Frair *et al.* 2007), probably engendering the low tolerance for increasing road density observed here. In contrast, in the adjacent Banff National Park, where elk were protected from hunting, 88% of 72 cow elk ranges occurred where road densities exceeded 1·0 km km^{-2}, with 54% exceeding densities of 2 km km^{-2} (max = 4·12 km km^{-2}; M. Hebblewhite, University of Montana, unpublished data). These observations compare closely with our predictions for animals having different levels of home range fidelity, or tolerance for increasingly encountering roads in their daily movements. In places like Banff National Park, human activity is both non-lethal and predictable, and elk have habituated to activities associated with roads (McKenzie 2001; see also Thompson & Henderson 1998). In fact, in some cases, human activities may create predation refugia for elk (Hebblewhite *et al.* 2005; Hebblewhite & Merrill 2007), with roads potentially becoming an attractive rather than a repulsive force.

To date, understanding road-related thresholds to which animal populations respond has been problematic. While general displacement from roads may be quantifiable, our results, as well as the work by Rowland *et al.* (2000), demonstrated that a broad range of population-level responses to increasing road density might arise despite a consistent pattern of local road avoidance by individuals (see also Gautestad & Mysterud 2005). Higher-order landscape and behavioural patterns limit the utility of inferences based only upon local responses to roads (e.g. Jaeger *et al.* 2005; see also Gill *et al.* 2001). The greatest utility of a model like ours lies in its ability to isolate the effects of landscape context vs. road network design on population-level redistribution patterns. While road network design is considered to be important (see Forman *et al.* 2003), logistical constraints generally preclude empirically separating local, context effects from network design effects, hindering effective management action. Contrasting the relative effects of preferred habitat amount vs. road configuration in our simulations exposed a conditional relationship between the two such that design of the road network played an increasingly

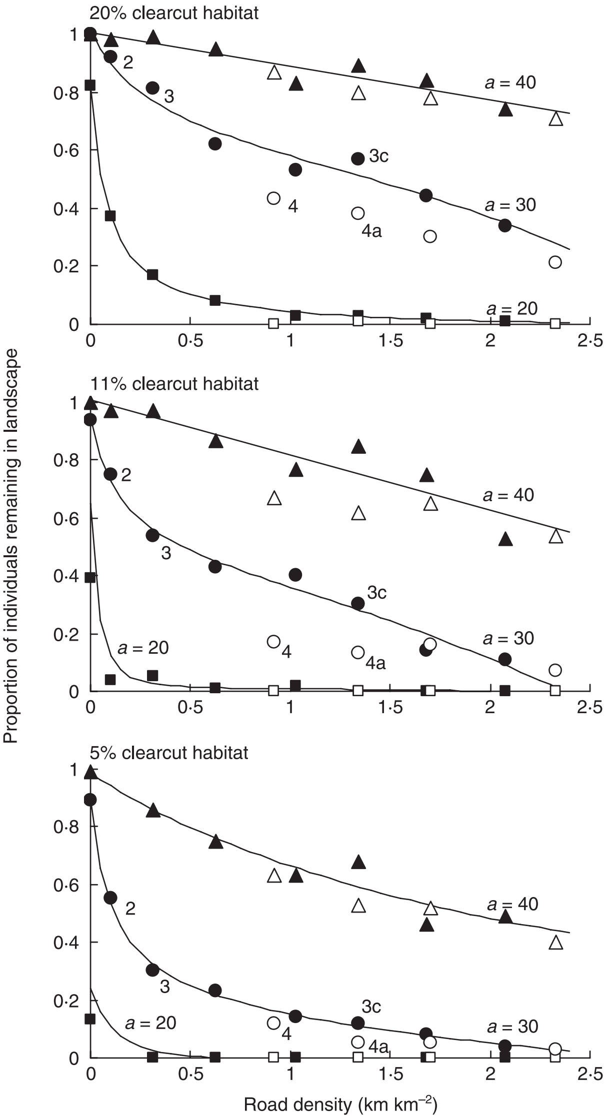

Fig. 7. The proportion of animals remaining in the landscape given an increasing road density, variation in elk tolerance for declining habitat accessibility (a; see text), and different amounts of clearcut habitat. Curves were fit to the mean values observed under the 'roads independent of clearcuts' design (filled symbols), but the 'roads associated with clearcuts' design is also shown (open symbols). Scenario labels (e.g. 4, 4a) facilitate cross-referencing with Supplementary Material Fig. S2.

important role as habitat amount increased. When foraging habitat was abundant, developing roads away from forage patches (clearcuts) created opportunities for elk to readily move among patches without encountering roads, thus reducing their mortality risk and increasing their retention in the landscape. Alternatively, when foraging patches were few, movements were constrained inordinately by baseline conditions (set by habitat amount), and elk derived little benefit from the design of the road network. Moreover, because road effects extended to 700 m and clearcuts averaged 9·4 ha in size (~346 m in diameter; Frair *et al.* 2005), roads bisecting or adjacent to clearcuts did not fragment habitat per se but essentially removed entire patches from the landscape or greatly increased the risk of using those patches, the latter potentially setting an 'ecological trap' for elk showing fidelity to traditionally used areas (Schlaepfer, Runge & Sherman 2002).

Given such complexities, how might managers maintain populations of elk while continuing to extract resources? In our simulations, the design of the road network accounted for up to 60–80% difference in the density of roads associated with a set level of elk mortality or emigration, demonstrating the potential for modified road placement (or closure) to expand road services while at the same time ensuring integrity of the ecosystem for species like elk (see also Forman *et al.* 2003). We observed the greatest differences resulting from network design at road densities of ~1·4 km km^{-2}, which exceeded the density currently tolerated by elk in this system, but large differences occurred within the upper range of currently occupied road densities (0·92–1·03 km km^{-2}), and are likely to continue, albeit to a lesser degree, at lower road densities although we did not test that here. Note that elk may become more tolerant of areas adjacent to roads should their impact be reduced by managing human use of the road network (e.g. Gratson & Whitman 2000; Cole, Pope & Anthony 2004). Aside from restricting human access to roads, our simulations indicated that simple modifications to road placement can have important benefits for animal populations. Importantly, these observations stemmed from a currently realistic rather than optimistic view of infrastructure design. Actions to protect important areas (e.g. deconstructing fallow roads within 700 m of clearcuts) would have even greater implications. Models like ours can be used to identify network designs having the least ecological footprint for species sensitive to road effects similar to elk. Even so, we emphasize that the effect of the road network design was small by comparison to the effect of increasing road density overall, and while better inclusion of wildlife values in the design of the road network may help to stem the tide of range loss, long-term persistence of animal populations will certainly require additional considerations such as setting aside road-less areas (Crist, Wilmer & Aplet 2005).

We were able to expose the above relationships and insights because our modelling approach accounted for interactive constraints created by the attractive force of foraging habitats and repulsive force of roads. Employing resource selection functions to parameterize movement biases overcame the difficulties of non-scalar elk responses to different landscape elements. However, our assumption of a static movement bias may be unrealistic across a broad range of road densities. Recent advances, such as conditional models that constrain availability based on movement potential (e.g. Fortin *et al.* 2005), and inclusion of functional responses using random effects (Gillies *et al.* 2006) may yield greater flexibility for modelling context-sensitive movement decisions. Regardless of the approach, the results of modelling efforts ultimately must be tested with natural or manipulative field experiments to gain confidence in our ability to predict the effects of infrastructure growth on wildlife populations. We suggest that the movement model presented here provided adequate realism and generality to guide such studies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary data for elk used to parameterize and validate the simulation model.

Table S2. Regression models used to predict elk state.

Table S3. Resource selection ratios used to parameterize the habitat bias.

Fig. S1. Model validation results.

Fig. S2. Landscapes used in the simulation experiment.

Fig. S3. Use of areas ≤ 250 m of a road given differing clearcut amounts.