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Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density

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Summary

1. Understanding the consequences of environmental change on populations is an essential prerequisite for informed management of ecosystems and landscapes. In lieu of quantifying fitness effects directly, which is often difficult, behavioural functional responses provide insight into how animals balance trade-offs, and into thresholds in responses to environmental change.

2. Here, we explore this principle using the response of moose *Alces alces* L. to roads and restricted-access tracks as a case study. Because roads are associated with the conversion of conifer to mixed deciduous–conifer forest that provides better foraging opportunities, moose in Ontario favour areas of moderate road density at a landscape scale. At a finer scale, however, moose avoid roads. These opposing effects indicate a cost–benefit trade-off. We quantified behavioural responses of moose to roads using road-crossing rate. An expected distribution of crossing rates was derived from correlated random walk null model simulations.

3. Moose exhibited a seasonally variable, nonlinear functional response in road-crossing rate at the within seasonal range scale. A pronounced response to roads was observed when road density reached approximate thresholds of 0·2 and 0·4 km km^{-2} in summer and winter respectively. Road-crossing rate was proportional to road density, though crossing rates were higher in summer than winter. Crossing rates were best explained by the interaction between mean movement rate and road density. Seasonal differences in road-crossing rate arise from seasonal differences in movement rate and seasonal range area, but not road density within seasonal ranges. Within the protected park, moose did not appear to respond to tracks. Our analysis implies that for the majority of the landscape outside of protected areas the response of moose to roads is pronounced.

4. *Synthesis and applications*. Identifying thresholds in nonlinear responses to landscape modification is a key management objective as they represent transition zones where small changes can have disproportionately large effects on wildlife populations. We establish these thresholds for moose and roads, but find no response to tracks, implying that the effects of tracks can be mitigated by restricting access to them. We discuss the implications of this work on the problem of moose–vehicle collisions.

Key-words: Canada, correlated random walk, movement model, Ontario, protected areas, response to roads, road density

Introduction

Modifications to the environment, such as development (e.g. road building, urbanisation), may result in a complex mix of both positive and negative effects on plant and animal populations across a wide range of temporal and spatial scales (Saunders, Hobbs & Margules 1991; Forman & Alexander 1998; Fahrig & Rytwinski 2009). The net lifetime benefit or detriment of these modifications to an individual will depend on the interplay between species ecology and landscape context. Effective management of populations requires an understanding of how the trade-offs between costs and benefits resulting

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from environmental change vary in time and space, how organisms balance the resulting competing demands, and the relative effectiveness of competing management strategies in achieving management goals (McDonald-Madden *et al.* 2010). For example, to prioritize alternative land management practices and predict the consequences of these decisions on populations of conservation concern, it is essential to understand the long-term dynamics of the trade-offs resulting from these policies. Of particular importance from a management perspective may be identifying potential thresholds in responses to development density, beyond which negative effects outweigh possible beneficial effects.

Although fitness measures (survival and reproduction) may represent the gold standard for quantifying cost-benefit trade-offs resulting from environmental change, these are often difficult and time-consuming to quantify in natural populations. Alternatively, behavioural responses may be useful indicators of these trade-offs and thresholds because many of the fitness effects are likely to be mediated through behavioural effects (e.g. habitat attraction or avoidance, vigilance). Specifically, quantifying how the expression of a behaviour changes across a gradient of environmental change intensity (i.e. a functional response in behaviour) can provide insight into the cumulative effects of environmental change (such as development) on a population. Here, we explore this principle by examining the response of moose *Alces alces* L. to roads.

Roads, and the vehicles that travel on them, are one of the most pervasive and significant forms of anthropogenic disturbance (Forman & Alexander 1998) and result in a wide variety of direct and indirect effects on wildlife populations. Direct effects include mortality from vehicle collisions (Pickles 1942; Groot *et al.* 1996; Seiler 2005; Fahrig & Rytwinski 2009; Soluk, Zercher & Worthington 2011), loss of habitat and habitat fragmentation (Forman & Alexander 1998; Saunders *et al.* 2002), visual and audio disturbance (Forman & Deblinger 2000; Kociolek *et al.* 2011), chemical pollution and dust (Watanabe *et al.* 2011), and alterations to the physical environment (Trombulak & Frissell 2000). Indirect effects can include changes to population distribution and abundance (Fahrig *et al.* 1995; Fahrig & Rytwinski 2009), reduced genetic flow across landscapes (Keller & Largiader 2003), edge effects (Saunders, Hobbs & Margules 1991), facilitating the spread of invasive species (Saunders, Hobbs & Margules 1991; Forman & Deblinger 2000), altered hunting pressure (Basile & Lonner 1979; Frair *et al.* 2007) and human–wildlife interactions resulting from increased human access to landscapes (Trombulak & Frissell 2000), behavioural changes that influence vigilance or foraging (Kerley *et al.* 2002), and population-level effects (Gibbs & Steen 2005). Indirect and direct effects can also interact to further influence wildlife distribution and abundance (Kramer-Schadt *et al.* 2004; Kociolek *et al.* 2011).

Some beneficial effects of roads include creating prey refugia (Hebblewhite *et al.* 2005), habitat alternations that increase forage (Bowman *et al.* 2010) or feeding opportunities for scavengers (Beckmann & Shine 2011). Areas in proximity of roads may, however, be attractive sinks (Mumme *et al.* 2000; Nielsen, Stenhouse & Boyce 2006) if increased mortality rates on roads offset any potential benefits. While some species may benefit from roads, most road effects on wildlife populations are negative (Fahrig & Rytwinski 2009). Effective management and conservation of populations affected by roads require an understanding of the many direct and indirect effects that roads and traffic have on these populations.

Behavioural responses to roads are likely to be dependent on landscape context and occur at a variety of spatial and temporal scales. Moose in Ontario, for instance, favour areas of moderate road density at a landscape scale because roads are associated with the conversion of conifer forest to deciduous forest, which provides access to better forage and browse (Rempel *et al.* 1997; Bowman *et al.* 2010). At a finer scale, although moose avoid roads (Dussault *et al.* 2007), they will cross them when moving from one area to another. Opposing effects at different scales may imply that responses to roads may be complex and vary as a function of road density (i.e. that there may be nonlinear functional responses to roads).

Functional responses with respect to habitat features are traditionally defined in terms of changes in habitat preference as a function of changing habitat availability (Mysterud & Ims 1998) or, more broadly, conditionally on the availability of all habitats to the animal (Aarts *et al.* 2008; Beyer *et al.* 2010; Matthiopoulos *et al.* 2011). Here, we apply the functional response concept to road-crossing behaviour, substituting the sample of availability (which is not meaningful in the context of road crossings) with the expected distribution of road crossings given a null movement model. Thus, we quantify a functional response representing the nonlinear change in relative road-crossing rate as a function of road density within the seasonal range. We then use these functional responses to quantify thresholds in behavioural responses of moose to increasing road density.

Materials and methods

Sampling of moose occurred in two study areas in southern Ontario, Canada (Fig. 1): Algonquin Provincial Park (APP; 45°35′N 78°21′W) and Wildlife Management Unit 49 (WMU; 45°30′N 79°46′W). APP is a 7650 km^2 area protected from hunting and development (though limited commercial logging and some aboriginal harvest is permitted) and is used for recreation. WMU is a mixture of private and public lands managed to support multiple uses including, for example, commercial forestry, residential homes, recreation and hunting. Regulated hunting of moose in WMU is permitted for a 10-day period in October each year. Both areas are low elevation (<600 m) and are characterized by a mixture of coniferous and deciduous woodland interspersed by lakes and wetlands, although WMU

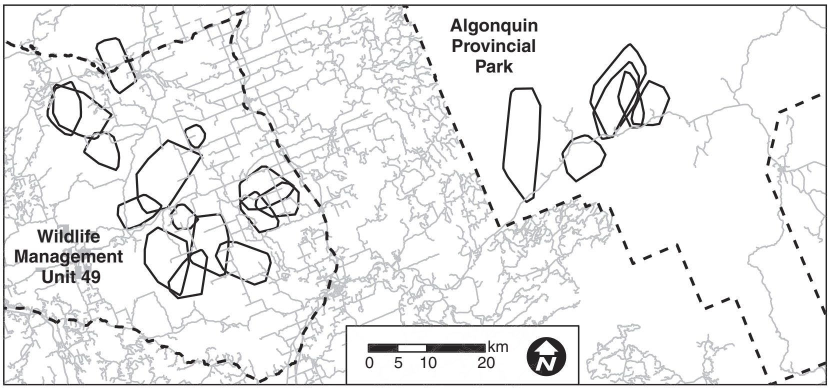

Fig. 1 . Examples of summer ranges of moose (100% minimum convex polygons; solid black lines) in two study areas: Algonquin Provincial Park (western dashed line) and Wildlife Management Unit 49 (eastern dashed line). The two areas differ in road density (grey lines).

also contains numerous private residences and some developed and agricultural land. Moose habitat availability is broadly comparable between study areas (Lowe, Patterson & Schaefer 2010). The density of roads is much lower in APP (0·03 km km^{-2}) compared to that in WMU (0·59 km km^{-2}). The study region is characterized by warm summers (mean July temperature 17·6 °C and rainfall 8·9 cm) and cold winters (mean January temperature −11·2 °C and snowfall 30·8 cm; Environment Canada). To examine seasonal effects on movement behaviour, we distinguish between a snow and ice 'winter' season (10 December–28 April) and a snow-free 'summer' (29 April–9 December) season.

Global positioning system (GPS) telemetry collars (GPS 3300; Lotek Wireless Inc., Newmarket, ON, Canada) were fit to 42 adult, female moose (22 in APP, 20 in WMU) in January 2006 ($n = 38$) and February 2007 ($n = 4$). Methods used to capture and collar moose are outlined in detail in Lowe, Patterson & Schaefer (2010). All fieldwork procedures relating to the handling and monitoring of moose were approved by the Trent University Animal Care Committee and the Ontario Ministry of Natural Resources. Moose were captured using a net gun operated by helicopter (Bighorn Helicopters Inc., Cranbrook, BC, Canada). Captured moose were administrated a nerve block (2% lidocaine, with 1:100 000 epinephrine) and a vestigial canine tooth was extracted for ageing (Matson's Lab, Milltown, MT, USA) (Murray *et al.* 2012). Spatial locations were collected at 2-h intervals until March 2008, or until the animal died or the collar failed. Most individuals were tracked for over 2 years (see Table S1, Supporting information), although six collars suffered technical failure. Success rates for acquiring locations were generally high (mean, 97·9% among all moose). Locations were deleted from the data set if they represented unrealistic or obviously erroneous movements, such as movement distances >6 km in a 2-h interval followed by a return to the vicinity of the previous location. Consecutive locations in the time series ($X_1, \ldots, X_T$, where T is the total number of locations) were joined with straight lines to create movement 'paths' for each moose in each season. The extent of seasonal ranges were calculated based on the telemetry data using 100% minimum convex polygons (MCP).

The road-crossing frequency of movement paths was quantified based on geometric intersections of the path with permanent, public, two-lane roads (Ontario Road Network, Ontario Ministry of Natural Resources; Fig. 1), which excluded narrow, private or secondary roads such as logging tracks. The response of moose to restricted-access tracks that might be used by park staff or occasional logging activity was also evaluated, although this analysis was restricted to APP as private tracks outside the park are not mapped. Seasonal data for each moose were retained for analysis only if the MCP contained roads, the moose was followed for the full duration of the season, and the success rate of acquiring scheduled locations was at least 80% (3 of 42 moose had fix rates lower than 80% as a result of collar malfunction), resulting in 86 moose-seasons among 24 moose (seven in APP, 17 in WMU).

An expected distribution of road crossings was calculated based on simulated movement paths using a correlated random walk (CRW; Turchin 1998) null model, which captured both directional persistence and spatial autocorrelation properties of real movement paths. CRWs represent movement paths as a series of step lengths (the Euclidean distance between two consecutive locations) and turn angles (the angular difference between the vectors X_{t-1}toX_t and $X_t$toX_{t+1}). CRWs ($N = 1000$) corresponding to a particular moose and season were simulated based on the empirical step length and turn angle distributions of that moose in that season, using the seasonal MCP as a reflective boundary to constrain the simulated paths to the observed seasonal range. Step lengths and turn angles were not included in empirical distributions if missed locations meant the time interval between consecutive locations was >6 h. Simulations were initialized at the first observed moose location in that season, and the number of simulated steps matched the number of steps in the observed moose path for that season.

The probability density (P_r) of the observed road-crossing rate (cr) for a given moose and season was calculated based on the cumulative distribution function of the expected distribution of road crossings derived from the CRW simulations (D). Specifically, P_r is calculated as the position of cr in the ordered list of all D, divided by the total number of observations in D and cr (1001 in this analysis). If ties occur (i.e. if cr is identical to one or more values in D), the median ranked position among all ties was used. The value of P_r, which is always in the range [0,1], is a measure of the response of moose to roads (hereafter referred to as the 'road response index'). A road response index of 0 indicates a greater road-crossing frequency than expected from the null model, a value of 0·5 indicates the observed crossing frequency matches the median-crossing frequency based on the null model, and a value of 1 indicates a lower road-crossing frequency than expected from the null model.

We modelled the functional response, the change in road response index as a function of road density, using a Gompertz function (Winsor 1932), selected because of its flexible, nonlinear form with only three parameters: $y = \beta_1 \exp(-\beta_2 \exp(-\beta_3 \mathrm{rd}))$, where rd represents road density, and the β parameters were estimated from the data using nonlinear least squares regression ('nls' library; R Development Core Team 2010). To evaluate evidence for an effect of season, we also fit the model $y = (\beta_1 + \beta_2 se)\exp(-(\beta_3 + \beta_4 \mathrm{se})\exp(-(\beta_5 + \beta_6 \mathrm{se})\mathrm{rd}))$, where se is a binary indicator variable corresponding to season. As the two models were nested, we evaluated evidence for the effect of season using a likelihood ratio test. The null hypothesis that there was no functional response and that moose crossed roads in proportion to road density was indicated by a road response index of 0·5, constant across all road densities (i.e. $y = 0{\cdot}5$). We used a likelihood ratio test to contrast the functional response models to this null model.

We modelled the observed daily road-crossing rate of each moose in each season (cr) as a function of road density in the seasonal range (rd), season (se), mean movement rate (mr) of that moose in that season, moose age (age), seasonal range area (ra) and study area (sa: APP or WMU). Competing generalized linear models (GLMs) were ranked using Akaike's Information Criterion (AIC; Burnham & Anderson 2001). Intercept terms were omitted because the expected road-crossing rate is 0 when covariates are 0.

Results

The response of moose to roads varied as a function of road density (Fig. 2a). We found greater support for the Gompertz model that included season compared with the model that pooled seasons (likelihood ratio test, $\chi^2 = 18 \cdot 6$, d.f. =3, $P < 0{\cdot}01$) or the null model of no relationship between the road response index and road density (likelihood ratio test, $\chi^2 = 149$, d.f. = 6, $P < 0{\cdot}01$). Thus, there was a seasonally variable, nonlinear relationship between road density within the seasonal range and road-crossing behaviour of moose relative to the null model (simulated CRWs). At high road densities, moose crossed roads much less frequently than predicted by the null model, but at very low road densities moose crossed roads more frequently than expected. This functional response with road density was more acute in summer than in winter. In winter, the threshold in road density at which the response to road density became pronounced (identified as the shoulder point on the fitted curves where the slope of the tangential line equals 1) was *c.* 0·4 km km^{-2}, whereas in summer this decreased to *c.* 0·2 km km^{-2} (Fig. 2a).

Road-crossing rate increased with increasing road density for both simulated and observed paths in both seasons, although road-crossing rates were higher in summer than in winter for both simulated and observed paths (Fig. 2b). Mean movement rates were higher in summer (mean, 80·5 m h^{-1}) than in winter (mean, 49·1 m h^{-1}; ANOVA, $F(1,84) = 85{\cdot}7$, $P < 0{\cdot}01$). Similarly, seasonal range area was greater in summer (mean, 37·3 km^2 ± 20 · 5 SD) than in winter (mean, 23·4 km^2 ± 17 · 5 SD; ANOVA, $F(1,84) = 11{\cdot}4$, $P < 0{\cdot}01$). The density of roads in summer and winter ranges, however, was not significantly different (0·32 ± 0·26 SD and 0·42 km km^{-2} ± 0 · 26 SD, respectively; ANOVA, $F(1,84) = 3{\cdot}54$, $P = 0{\cdot}064$).

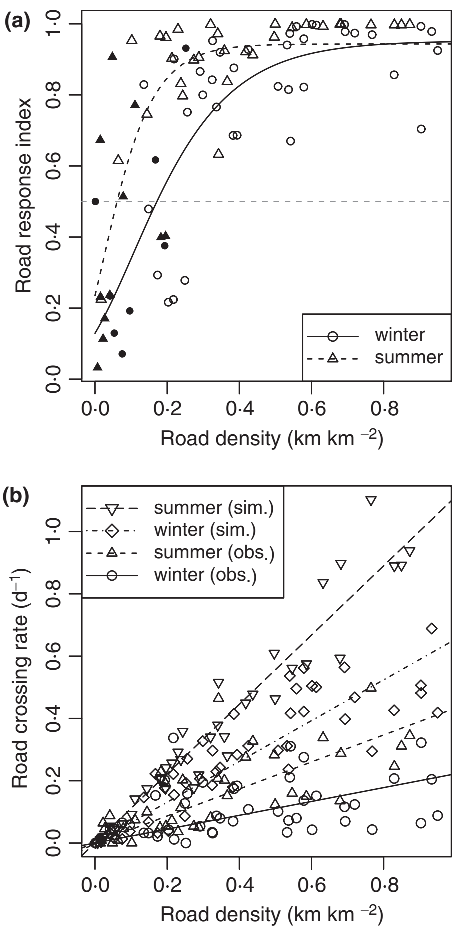

Fig. 2. (a) Functional response in road-crossing behaviour relative to road density. Road-crossing frequency of each moose in each season (N = 42, 2 years) was evaluated relative to the distribution of road-crossing frequency in simulated correlated random walk movement paths (see Materials and methods). The road response index is the rank position (expressed as a proportion) of observed road-crossing rate relative to the simulations. The functional response was quantified using competing Gompertz model. The highest ranked model included an effect of season whereby the functional response in summer (dashed line and circles) is more pronounced than in winter (solid line and triangles). Solid symbols identify moose in Algonquin Provincial Park, and open symbols moose in the Wildlife Management Unit. (b) Absolute road-crossing rates were strongly correlated with road density in both summer and winter, and for both observed and simulated movement paths.

The highest ranked model of observed road-crossing frequency included road density, mean movement rate and an interaction between the two (Table 1). Competing models lacking this interaction had substantially less support than the highest ranked model. For instance, ΔAIC (the difference between the highest ranked model and another model) for the full model containing all five covariates, but no interactions was 28·7. Competing models that combined the road density and movement rate interaction term with other covariates performed similarly to the highest ranked model (ΔAIC $< 3{\cdot}0$), but failed to explain enough of the variance to overcome the penalty for greater model complexity in the AIC calculation (Table 1).

Observations of individual moose among seasons may not be independent. We also fitted, therefore, generalized linear mixed models (GLMM) that included a moose identifier as a random effect, using the 'lmer' function in the 'lme4' library in R (R Development Core Team 2010). Model rankings and inferences were the same for the GLM and GLMM models (Table 1). We report the coefficient values from the GLM model as the value of the GLMM is questionable given the low number of samples within each level of the random effect (range, 1–5 samples). The coefficients and standard errors (SE) for the top ranked model, $\beta_1\mathrm{mr} + \beta_2\mathrm{rd} + \beta_3(\mathrm{mr} \times \mathrm{rd})$, where mr is mean seasonal movement rate and rd is road density, were as follows: $\beta_1 = 4{\cdot}21 \times 10^{-4} \pm 1{\cdot}82 \times 10^{-4}$ SE, $\beta_2 = -9{\cdot}60 \times 10^{-2}$ $\pm 4{\cdot}89 \times 10^{-2}$ SE and $\beta_3 = 6{\cdot}26 \times 10^{-3} \pm 9{\cdot}18 \times 10^{-4}$ SE (Fig. 3).

Within the protected park, moose did not appear to respond to tracks as there was no clear relationship between the road (track) response index and track density and most response index values fell within the 95% confidence intervals of the expected distributions (Fig. 4). Neither of the two full Gompertz models could be fit to these data (parameter estimation failed because of a lack of a clear trend in the data), so slightly simpler versions of the Gompertz models ($y = \beta_1\exp(-\beta_2\exp(-\mathrm{rd}))$ and $y = (\beta_1 + \beta_2\mathrm{se})\exp(-(\beta_3 + \beta_4\mathrm{se})\exp(-\mathrm{rd}))$ were fit. We found greater support for the null model than either of the simplified Gompertz models (likelihood ratio tests, $\chi^2 = 1{\cdot}95$, d.f. = 2, $P = 0{\cdot}38$ and $\chi^2 = 3{\cdot}90$, d.f. = 4, $P = 0{\cdot}42$, respectively), indicating no relationship between the road (track) response index and track density.

Table 1. The top ranked models of observed seasonal moose ($N = 42$) road-crossing rate as a function of mean seasonal movement rate (mr), road density (rd), seasonal range area (ha), moose age (age) and the factors study area (sa) and season (se). The interaction term mr * rd represents the model $\beta_1 mr + \beta_2 rd + \beta_3(mr \times rd)$. Competing models are ranked in ascending order of AIC values, and ΔAIC represents the difference in AIC between each model and the highest ranked model. Each generalized linear model (GLM) was also fit as a generalized linear mixed model (GLMM) using a moose identifier as a random effect to evaluate whether lack of independence among observations changed model rankings or inferences. The last two models listed are reference models: a full model containing all five covariates but with no interaction terms, and a model with movement rate and road density covariates with no interaction term

Model	AIC (GLM)	Δ AIC (GLM)	ΔAIC (GLMM)
mr * rd	−206·9	0·0	0·0
mr * rd + ha	−206·0	1·0	0·9
mr * rd + age	−204·9	2·0	2·0
mr * rd + sa	−204·0	2·9	3·5
mr * rd + sa + se + age	−201·8	5·1	5·6
mr + rd + sa + se + age	−178·2	28·7	28·9
mr + rd	−170·7	36·2	38·4

Discussion

Moose exhibited a functional response in road-crossing behaviour at the scale of seasonal ranges. The response to roads, measured relative to expected road-crossing frequencies from the null movement model, varied as a nonlinear function of road density and was more acute in summer than in winter (Fig. 2a). At road densities higher than *c.* 0·2 km km^{-2} in summer or 0·4 km km^{-2} in winter, for instance, moose crossed roads much less frequently than expected relative to the null model, whereas below these thresholds moose exhibited much less consistent patterns ranging from a strong avoidance of crossing roads to a strong crossing tendency. These thresholds closely agree with behavioural responses of elk *Cervus elaphus* L. to use of areas near roads, with thresholds for elk apparent at road densities of 0·25–0·5 km km^{-2} (Frair *et al.* 2008).

This functional response must be interpreted, however, in the context of absolute road-crossing rates (Fig. 2b). At the lowest road densities, in which a seasonal range might only include a short segment of road near the boundary of the seasonal range, it may only require a few (e.g. <5) road crossings by a moose to exceed the crossings expected by the null model as many of the simulated paths would cross roads rarely or not at all. Conversely, at the higher road densities where moose cross roads much less frequently than expected based on the null model, the moose are nevertheless crossing roads frequently relative to the moose at low road densities (Fig. 2b). Thus, it is important to evaluate functional responses in the context of both relative and absolute crossing rates.

Our models indicated that the strongest predictor of road-crossing rate was the interaction between road density and movement rate. Higher road densities and faster movement rates both resulted in higher crossing rates, but there was also an interaction between these variables indicating that higher movement rates may result in part from more frequent road encounters. We found little evidence that seasonal range area, season, moose age or study area offered additional explanatory power for moose road-crossing frequency, indicating that the observed seasonal differences may arise primarily from seasonal effects on movement rates.

Animals are subject to competing demands and motivations. For instance, foragers must choose a behavioural strategy that is an adaptive compromise between predation risk avoidance and foraging (Sih 1980) when these behaviours cannot occur concurrently (Fortin, Boyce & Merrill 2004). Because behaviour that mitigates predation risk reduces the time available for other fitness enhancing

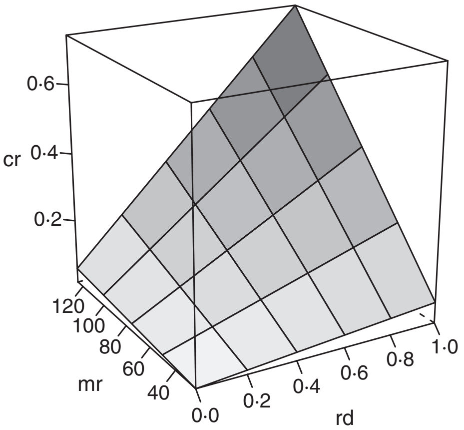

Fig. 3. Daily road-crossing rate (cr) modelled as a function of moose movement rate (mr), road density (rd) and the interaction between movement rate and road density.

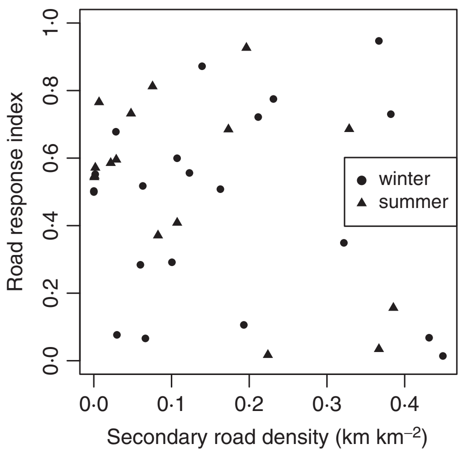

Fig. 4. Response in track (restricted-access road) crossing rate relative to track density for each moose in each season. The top ranked model to these data is the null model, indicating that moose do not appear to exhibit a response to tracks. Due to the absence of tracks in the Wildlife Management Unit, only moose from inside Algonquin Provincial Park are featured in this analysis.

behaviours (Lima & Dill 1990), and predation risk can vary in time and space, animals must manage behavioural time budgets to minimize risk while maximizing fitness: an optimization problem. Functional responses arise because these types of trade-offs can vary along a continuous environmental gradient (Mysterud & Ims 1998). The functional response in road-crossing behaviour we observed is consistent with the risk-disturbance hypothesis (Frid & Dill 2002), whereby anthropogenic disturbance plays a similar role to predation risk in influencing prey behaviour. In the case of road crossing, risk could be based on direct encounter of traffic, on the expectation of encountering traffic based on previous experience, on the risk of encountering predators that may use roads as travel routes (James & Stuart-Smith 2000; Eriksen *et al.* 2009), or on risk arising from traffic noise impeding the detection of natural predators. In the park where moose were protected from hunting, we observed that moose did not avoid tracks that could also serve as efficient travel routes for wolves, implying that avoidance of predators is less plausible than disturbance due to traffic or encounters with humans as an explanation for moose avoidance of roads.

There is an apparent contradiction in our results. We found that mean movement rate is the strongest predictor of road-crossing rate, and that mean movement rates are higher in summer than winter. We might expect, therefore, that the response to roads would be least pronounced in summer. Yet, the functional response to roads is instead stronger in summer. This arises because seasonal ranges are larger in summer than winter, providing greater opportunity for road crossings in the simulated paths (see Fig. 2b). Thus, despite the fact that moose cross roads at a higher rate in summer than winter, proportionally they still cross roads less frequently than expected based on the null model. An alternative explanation might have been that moose ranges contract or shift in winter into areas with fewer roads, thereby reducing moose winter road-crossing frequency and resulting in a less pronounced winter road response index score. Although we did find that road densities were somewhat lower in winter ranges than summer ranges the effect was weak (not statistically significant). We suggest there is probably also limited opportunity for moose to relocate to areas of lower road density, either because they do not exist or because they are already occupied. Thus, we conclude the stronger response to roads in summer was driven more by summer range expansion than by lower winter range road densities, and ultimately may arise from greater human use of the road network in summer.

The road density thresholds and mean seasonal range sizes can be used to identify areas in the landscape where responses to roads were most pronounced. For instance, the majority of the landscape outside of APP is characterized by areas in which moose response to roads is expected to be strong (Fig. 5). Roads appear to be a pervasive and important source of disturbance to moose outside of protected areas in this region. Although we found no evidence of a response to restricted-access tracks, this analysis was limited to the park where they are comprehensively mapped. Outside of the park, where moose are hunted, the response to roads may be different. Further research is needed to understand how behavioural responses of moose to roads may influence fitness, predation risk dynamics (Kunkel & Pletscher 2000), dispersal, and genetic flow.

Pregnancy and calf survival rates are high in our study area (83% and 62% respectively; Murray *et al.* 2012), and the majority of adult females we followed had calves. We note, therefore, that the inferences of our study relate primarily to adult female moose with calves and that the road-crossing behaviour of males, dispersing juveniles and females without calves may be different. Furthermore, the

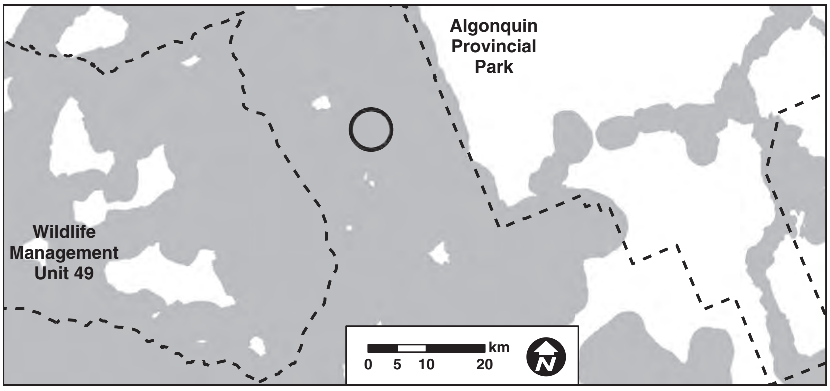

Fig. 5. Landscape characterization of areas where moose are expected to cross roads much less frequently than expected in summer (grey) relative to the null movement model (a correlated random walk), based on an estimated road density threshold of 0·2 km km^{-2} (see Results). The other areas (white) have lower road densities where moose would be expected to show a less extreme or neutral response to roads. The open circle depicts the average summer range size (37·2 km^2) of moose. Only a fraction of the landscape outside of Algonquin Provincial Park (western dashed line) contains potentially road-neutral areas (white).

road response index is derived from both the moose road-crossing frequency and the distribution of crossing frequencies based on the movement model simulations and is, therefore, a relative measure of the change in response to roads as a function of road density. Although we cannot infer behavioural motivation directly from this metric (Beyer *et al.* 2010), it provides a useful quantification of animal responses to roads. The movement model is a simple but biologically meaningful null model in that it captures several aspects of real movement paths: directional persistence and realistic (empirically based) step length and turn angle distributions, while being constrained within the seasonal range. Thus, the road response index provides insight into the road densities at which there is strong divergence between the observed and expected road-crossing frequencies.

There are both general and specific management implications arising from this work. First, we provide a general method for quantifying thresholds in the response of animals to road density. Such thresholds are particularly important from a management perspective (Groffman *et al.* 2006) as they define clear targets and limits for planning and development, and because they help to quantify what constitutes suitable habitat. Although a portion of landscapes are often maintained in a relatively undeveloped state (parks, reserves and conservation areas), the majority of landscapes are managed under a multi-use management paradigm in which development and human use is supposed to be balanced with the stewardship of natural resources, including wildlife populations. In this context, achieving balance requires understanding when anthropogenic effects have pronounced effects on wildlife populations. Nonlinear responses to landscape modification are identified as a key management objective (Groffman *et al.* 2006) to understand when small changes in management may have disproportionately large effects on populations. As one of the largest terrestrial mammals in Canada, moose may be among the most sensitive mammalian species to roads and, therefore, may be a useful umbrella species to guide management. This study also demonstrates that thresholds can be seasonally variable and that defining such limits must be based on animal movement and habitat availability at the most sensitive time of year. Although the functional response is stronger in summer than winter, and absolute road-crossing rates are higher, moose may be more sensitive to disturbance in winter when they are energetically stressed and the cost of movement is higher.

A specific management recommendation emerging from this work is that the response to roads appears to be driven by traffic intensity, not predator avoidance, as there was no evidence of avoidance of tracks within the park. Thus, if roads do need to be created for forestry or management access, restricting public access to them could greatly mitigate the impact of human disturbance on moose. Perhaps more importantly, it is recognized that in several areas in North America and Scandinavia moose constitute an important road safety hazard, with many collisions each year resulting in death or injury of humans and moose, as well as substantive property damage (Björnstig *et al.* 1986; Child, Barry & Aitken 1991; Joyce & Mahoney 2001; Seiler 2004). A long-standing issue is how best to manage moose populations to reduce collision risk, and our results provide important insight into how road density influences road-crossing behaviour. Indeed, we show that despite a nonlinear behavioural functional response to road density indicating that at higher densities moose cross roads less frequently than expected, absolute road-crossing frequencies are seasonally variable but linearly proportional to road density (Fig. 2b) across the range of road densities in our study area (0–1 km km^{-2}). The collision risk of vehicles with moose, however, is a function of both road-crossing frequency and the abundance of moose and vehicles. Thus, one objective of future work is to understand how moose density is related to road and traffic density. Mitigative measures such as roadside vegetation management, wildlife fences or wildlife-crossing structures (see Clevenger, Chruszcz & Gunson 2001; Rea 2003) can be implemented in problematic areas.

This work demonstrates that the response of moose to roads is complex, varying seasonally and as a function of road density. We observed a functional response in road-crossing behaviour in relation to road density, and an interaction between seasonal variation in movement rates with road density. Disturbance effects are often evaluated as constant effects, ignoring variations in response with respect to changes in density or intensity of disturbance factors. Quantifying functional responses is important for developing a more mechanistic understanding of the consequences of development. Functional responses also provide a framework for understanding apparently contradictory research findings (e.g. negative effects in some areas or at some scales, positive in others). Considering average responses across a wide range of road densities may obscure the fact that the strength of the response to roads by animals changes depending on landscape context. Failure to consider functional responses could lead to erroneous inferences regarding the consequences and management of environmental change.

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Supporting Information

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

Table S1. Dates of monitoring and survival outcomes of moose.