



Caught in the mesh: roads and their network-scale impediment to animal movement

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Roads have a pervasive multi-faceted influence on ecosystems, including pronounced impacts on wildlife movements. In recognition of the scale-transcending impacts of transportation infrastructure, ecologists have been encouraged to extend the study of barrier impacts from individual roads and animals to networks and populations. In this study, we adopt an analytical representation of road networks as mosaics of landscape tiles, separated by roads. We then adapt spatial capture–recapture analysis to estimate the propensity of wildlife to stay within the boundaries of the road network tiles (RNTs) that hold their activity centres. We fit the model to national non-invasive genetic monitoring data for brown bears *Ursus arctos* in Sweden and show that bears had up to 73% lower odds of using areas outside the network tile of their home range centre, even after accounting for the effect of natural barriers (major rivers) and the decrease in utilization with increasing distance from a bear's activity centre. Our study highlights the pronounced landscape-level barrier effect on wildlife mobility and, in doing so, introduces a novel and flexible approach for quantifying contemporary fragmentation from the scale of RNTs and individual animals to transportation networks and populations.

In a world dissected and heavily impacted by roads, road ecology has emerged as an important applied ecological discipline (Forman and Alexander 1998). Networks of roads cover entire landscapes, and their impacts extend from individuals and their surroundings to the scale of populations, landscapes and the ecological processes associated with ecosystem functions (Tikka et al. 2001, Gibbs and Shriver 2002, Rytwinski and Fahrig 2012). Furthermore, policies implemented at network scales, i.e. at levels comprising the collection of multiple roads forming a web, have the potential of vast and far-reaching impacts (Turner 2006, Selva et al. 2011). Thus, ecologists are encouraged to study the higher-order environmental impacts, not only local effects (Balkenhol and Waits 2009, van der Ree et al. 2011, Manel and Holderegger 2013).

Local barrier effects are constituents of large-scale fragmentation caused by transportation networks (Jaeger et al. 2005). Yet, effects quantified at the individual road level cannot readily be extrapolated to the network scale. For example, network configuration could modulate ecological impacts (e.g. effects of gridded versus parallel configuration on fragmentation and mortality; Jaeger et al. 2006), but is not captured fully by studies taking place solely at a local scale (Jaeger et al. 2006, Coffin 2007, Roedenbeck 2007).

Similarly, assessment of the impact of network-caused fragmentation on meta-population dynamics requires direct study at the landscape-scale. Although studies on gene flow and genetic diversity can address questions related to barrier effects and network-caused fragmentation at a large spatial scale (Simmons et al. 2010, Proctor et al. 2012), they are constrained by the time needed for genetic effects to appear in wild populations (especially for long-lived species, Anderson et al. 2010) and do not capture individual space use. It is also worth noting that typically only a small fraction of a population is transient at any given time. Many individuals in wild populations maintain home ranges for most of their life, it is thus important to not only focus on the impediment to long-distance migration and dispersal, but also on the constraints that fragmentation poses to resident movements and the configuration of home ranges within the population (Morales et al. 2010, Poessel et al. 2014).

When it comes to animal movements, ecologists have primarily studied roads as local barriers (Riley et al. 2006, Sawaya et al. 2014, Proctor et al. 2015, Wilson et al. 2015). We think two primary challenges have hindered the move up and across scale: 1) the conceptual focus on the process of crossing or not-crossing linear barriers and 2) the scope of the empirical data typically used to study wildlife movements. In this article, we suggest solutions to both of these challenges to population- and network-scale assessment of barrier effects, which we then implement using an empirical example.

The first challenge concerns the need to move the conceptual perspective beyond individual roads as linear barriers to animal movement. We can view landscapes cut up by road networks as habitat mosaics (Jaeger 2000). These mosaics are composed of individual segments, hereafter referred to as road network tiles (RNT) or simply ‘tiles’. This is analogous to the basic setup in island biogeography (MacArthur and Wilson 1967): the road network represents the inhospitable habitat or ‘sea’, surrounding and separating more or less habitable tiles (‘islands’). Each tile in a network is surrounded by roads (or other potential non-habitat for terrestrial animals, e.g. rivers and oceans) and has its own set of biotic and abiotic characteristics, such as geometry, size, habitat composition, biodiversity and factors directly related to human impact. This conceptualization as a mosaic made up of individual tiles already forms the basis for the calculation of effective mesh size in road ecology (Jaeger 2000, Moser et al. 2007), a geometric measure of fragmentation that relates to the size of un-dissected tiles in the mosaic created by road networks. The multiple-fragment perspective has proven useful for examining other aspects of environmental impacts of road networks, for example to monitor ecosystem degradation (Roch and Jaeger 2014) and to measure the structural diversity of landscapes (Walz 2015). In terms of wildlife mobility, the conceptual representation of road networks as a collection of more or less isolated tiles allows us to move from quantifying the resistance to crossing from one side

of a road to the other, to quantifying the extent of isolation between tiles in the network (Fig. 1).

The second challenge concerns access to empirical information about individual movements at the level of populations and road-networks. Telemetry applications (e.g. GPS or VHF tags) remain the primary means for obtaining animal movement and space-use data (Cagnacci et al. 2010). GPS telemetry in particular has the potential to yield copious amounts of precise relocation data for tracked individuals (Hebblewhite and Haydon 2010). Nevertheless, the demand on resources and the nature of field implementation usually mean that a) only a small fraction of a population can be equipped with tracking devices (Hebblewhite and Haydon 2010) and b) selection of the tracked sample of individuals is usually not random and may therefore not be representative of the population (Millsbaugh and Marzluff 2001, Hebblewhite and Haydon 2010). In short, the empirical information used for movement analyses matches the scale of a few individuals and roads (Dyer et al. 2002, Riley et al. 2006, Gagnon et al. 2007), not populations and road networks. During the past two decades, non-invasive genetic sampling – the collection of hair, feathers, scat and other material left behind by animals, followed by DNA extraction and genetic analysis – has emerged as a popular alternative or complement to intensive individual-based monitoring (Taberlet et al. 1999, Mills et al. 2000). Genetic sampling can yield individual-based data at the population and landscape level, which are

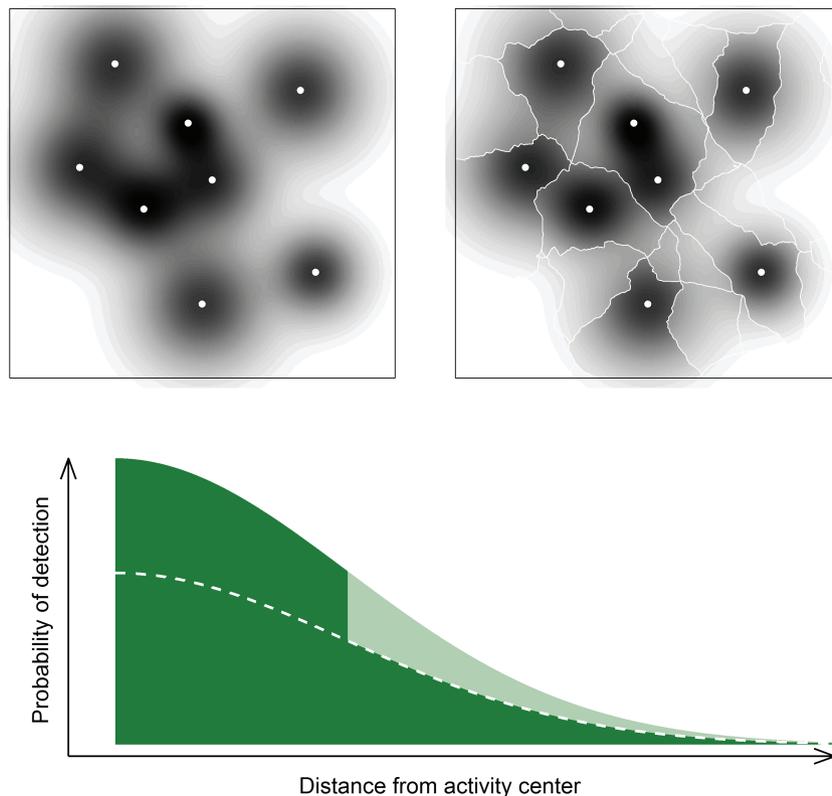


Figure 1. Illustration of the spatial process of DNA deposition and the corresponding detection process. Due to its inherent link with home range use, probability of detection is a decay function of distance from the individual’s activity centre (bottom panel). Resistance to movements beyond the network tile that contains an individual’s activity centre is modelled as an additional drop in the detection function. Top panels show the utilization distribution (darker: higher density) for the same hypothetical population (white dots: individual activity centres), with (right) and without (left) a road network.

in turn used to study a variety of natural phenomena associated with wild populations and communities, including abundance and population dynamics, which were formerly reserved for studies involving physical mark–recapture (Boulanger et al. 2008, Mondol et al. 2009, Cubaynes et al. 2010). Genetic methods have already proved useful for exploring road effects at both local and landscape scales (reviewed by Balkenhol and Waits 2009), although when applied within road ecology, the focus has remained on quantifying barrier effects on local genetic connectivity (Sawaya et al. 2014, Wilson et al. 2015).

In this study, we estimate the contemporary network-level effect of roads on space use by a large carnivore. We do so by tapping into the individual-based spatial information contained in genotyped DNA samples of brown bears *Ursus arctos* collected across the species' range in Sweden. Using spatial capture–recapture analysis, we 1) introduce an approach for quantifying the network-scale barrier and fragmentation effect of roads and 2) demonstrate that road-induced impediment of movements across the landscape can be pervasive even for notoriously mobile and wide-ranging species.

Methods

Spatial capture–recapture model

We use spatial capture–recapture (SCR) analysis as a starting point for developing our model. Traditional capture–recapture (CR) models estimate detection probability, thereby controlling for the biasing effect of imperfect detection on focal parameters in ecological investigations, such as presence/absence, abundance and survival (Williams et al. 2002). Recently developed SCR models expand CR models by accounting for the fact that both ecological and observation processes are patently spatial (Efford et al. 2009b, Royle et al. 2013). Common to all SCR models is that they include a functional expression for the declining probability of detection with increasing distance from the centre of an individual's activity (activity centre, AC), a latent variable. The probability p of detecting individual i at detector j in a grid of detectors can, for example, be modelled as a half-normal function of the distance d between the detector and the individual's centre of activity (Fig. 1; see also Efford et al. 2009b)

$$p_{ij} = p_0 \exp(-d_{ij}^2 / 2\sigma^2) \quad (1)$$

Where p_0 and σ are the magnitude and scale parameter, respectively.

Typical SCR models allow for, and in fact estimate, the presence of individuals that remained undetected during sampling. If z is the true state of an individual (present: $z = 1$; absent: $z = 0$), observations y (detection: $y = 1$; non-detection: $y = 0$) of individuals at any given detector follow a Bernoulli distribution with probability $z_i p_{ij}$ (shown here for a single time step).

$$y_{ij} | z_i \sim \text{binomial}(1, z_i p_{ij}) \quad (2)$$

For detailed information about spatial capture–recapture models and their various uses and permutations see for example Royle et al. (2013).

The goal of our analysis is to estimate the tendency of an individual to stay within the habitat tile in a road network that contains its AC. We make two adjustments to the basic SCR model described in Eq. 1 and 2. First, to simplify the model and because we are not interested in estimating abundance or density, we make individual presence conditional on having been detected at least once. This removes z (Eq. 2) from the formulation of the likelihood

$$y_{ij} \sim \text{binomial}(1, p_{ij}) \quad (3)$$

Second, we add parameter ω to the detection function. The resistance parameter ω signifies the change in an individual's use of the state–space (and consequently its probability of being detected) outside the tile in which the individual's AC is located. We provide D as an indicator variable that specifies whether the current location j is inside ($D = 0$) or outside ($D = 1$) the tile that contains the AC of individual i

$$\text{logit}(p_{ij}) = \text{logit}(p_0 \exp(-d_{ij}^2 / 2\sigma^2)) + \omega D \quad (4)$$

Negative ω indicates resistance against using areas outside an individual's home tile, or in other words the degree of isolation between the tiles created by the road network. Quantitatively, ω is a biologically meaningful, probabilistic expression of the resistance to moving beyond one's home tile, controlled for declining utilization as distance from the AC increases (Fig. 1). We allow ω to depend on individual attributes (e.g. gender) and landscape characteristics (e.g. network region, Fig. 2), but it could also be made a function of tile characteristics, temporal and spatial covariates, or subject to random effects.

The logit transformations on both the left and right side of Eq. 4 are used to ensure that overall detection, after adding the effect of barriers, remains bound by 0 and 1. The resistance parameter ω is realized as an additive effect on overall detection at any given distance d . Equation 4 is thus a logistic equation where the entire half-normal function (Eq. 1) represents the intercept value (at a given distance d). The logit transformation on the right side of the equation then serves to retain the value of the original half-normal component, when accounting for the link function on p . Alternatively; the change in detection probability could be incorporated directly into the half-normal function:

$$p_{ij} = p_0 \exp(-d_{ij}^2 (1 - \hat{\omega} D) / 2\sigma^2), \quad \text{where } \hat{\omega} \leq 0 \quad (5)$$

Here, the resistance parameters is denoted $\hat{\omega}$, as the quantitative realization differs from that in equation 4. For our analysis, we chose Eq. 4, as it signifies a simple proportional change in p on a logit scale and makes incorporation of both additive effects and possible interactions between multiple barrier types straightforward (see Eq. 6 below).

Empirical example

We obtained brown bear non-invasive genetic sampling data from Rovbase 3.0 (<www.rovbase.no/>), the Scandinavian large carnivore monitoring data base (Norwegian Environment Agency and Swedish Environmental Protection Agency 2014). Although non-invasive genetic sample collections have been taking place in Sweden since 2001, we limited our analysis to survey bouts conducted in 2006, 2010, 2012

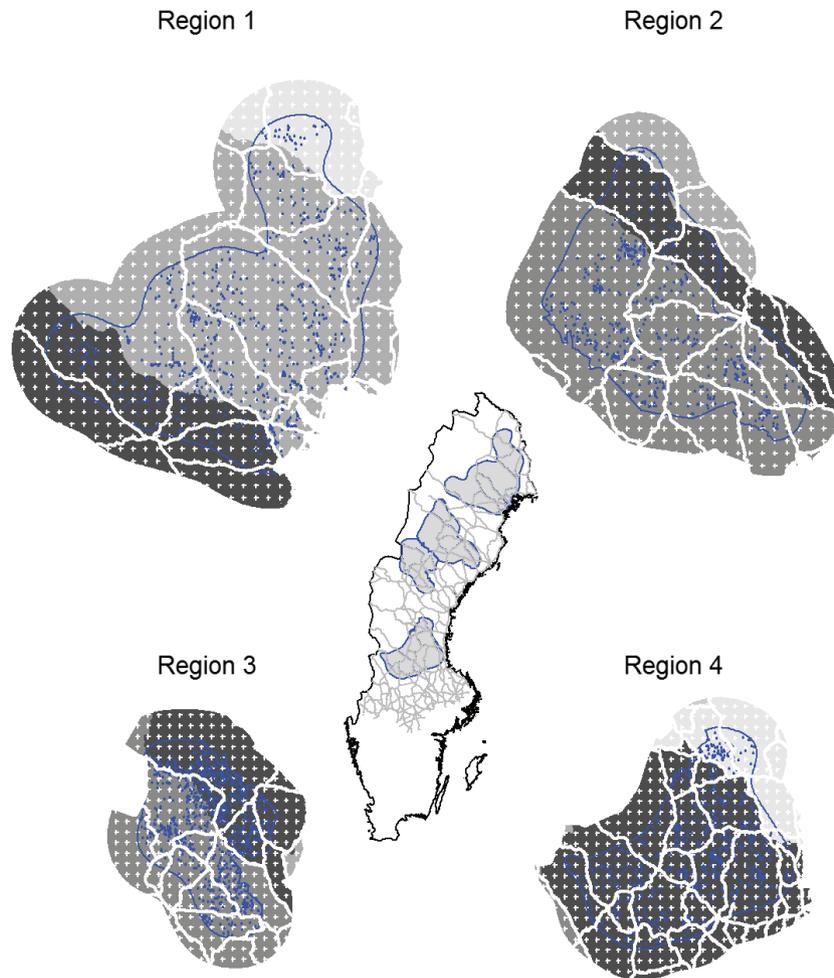


Figure 2. Configuration of four study regions dissected into tiles by the network of primary roads (white lines) within the Swedish brown bear range. Detection areas (blue outline, 'detector array') within each region were delineated based on non-invasive genetic sampling locations (blue dots) and are surrounded by an additional 30 km buffer of available habitat. White crosses indicate the centres of 10×10 km grid cells of the habitat mask. Within the detection areas, habitat grid cells coincide with detector grid cells. Variable grey shading distinguishes polygons delineated by major rivers that transect the study regions.

and 2014, to ensure close temporal proximity between each bout and to stay in the context of the contemporary road network structure. Each survey targeted a different management region, delineated primarily by county boundaries. After each survey bout, suspected brown bear scats were subjected to DNA extraction and amplification using 6–8 microsatellite primers and a sex-specific primer to confirm species, determine sex and assign genotypes (individual). For a description of the sample collection procedure and genetic analysis, see Bellemain et al. 2005, Kindberg et al. 2011.

The collection area ($\sim 105\,000$ km²) covers large swaths of managed boreal forest in a rolling landscape (elevation range 0–1189 m a.s.l.). Only a fraction (1.2%) of the collection area exceeded the tree line (~ 700 m a.s.l.) (Van Bogaert et al. 2011). The area is interspersed with bogs ($\sim 16\%$) and water bodies ($\sim 7\%$). Other land cover types such as build-up and agricultural land, and barren habitat are rare (all below 2% of the collection area). Land cover composition and terrain characteristics are comparable between the four survey regions. Geographic attributes of the management units are given in the Supplementary material Appendix 1 Table A1.

Detector grid

We delineated the focal search area within each survey region by estimating the 75% bivariate normal kernel based on all non-invasive sample locations collected during the respective survey bout. This approach excluded areas on the periphery of the search area that yielded fewer samples; although it omitted some of the data, the approach ensured that most of the area included in the analysis was actually searched. We then imposed an artificial 10×10 km detector grid across the extent of each focal area, following Bischof et al. (2016). Each year's sampling period started on Aug 21 and continued for up to 13 weeks. Sample collection was opportunistic and mainly performed by hunters and other volunteers (Kindberg et al. 2009). The sampling period included the start of the moose hunting season with more than 200 000 Swedish hunters participating. In principle, all areas in the study area were open to hunting by organized teams during the hunting season.

To avoid confounding between spatial variation in effort and density, variable effort should be accounted for in SCR models (Efford and Fewster 2013). Using simulations

(see description near the end of the Methods section and Supplementary material Appendix 1 Fig. A5), we found that even substantial variation in the proportion of cells in the detector grid that are searched had little impact on mean parameter estimates in a basic SCR model. Nonetheless, we took additional steps to account for possible differences in detection probability across detector cells. We allowed the magnitude parameter p_0 of the detection function to vary between regions. In addition, we modelled a single annual detection occasion to reflect the fact that we had little information about the temporal structure of searches or sample deposition by bears. As highlighted by Efford et al. (2009b), in SCR models, density estimates can be derived from observations accumulated during a single time interval if individuals can be detected at multiple detectors. Following Efford et al. (2009b) and because the actual search path taken in a given grid cell was unknown, detection location of DNA samples within the focal period were projected to the nearest active detector location (detector grid centre). We used the binary proximity model for detection (Efford et al. 2009a), where detection or non-detection of an individual at a detector is indicated as the outcome of a Bernoulli trial, with the possibility of detecting the same individual at multiple detectors. The Bernoulli observation model has also been highlighted as the favoured model by Royle et al. (2013), even when the sampling scheme produces encounter frequencies (e.g. number of scats from an individual found in the same detector grid cell). Finally, we included road network tile ID as a random effect on detection probability, thereby accounting for spatial heterogeneity in search effort and detectability. This was based on the rationale that the probability of detection in a given detector cell depends not only on attributes of individual bears in the population, but also on location-specific attributes at that grid cell. Road tiles within the network are not searched with equal effort and may not be used by bears with equal intensity (aside from barrier effects). Including tile ID as a random effect can help to at least partially capture and thus control for the resulting heterogeneity in detection probability. Finally, individual space use, including home range size, influences detection probability at a given detector. We accounted for this source of heterogeneity by including individual bear ID as a random effect on the scale parameter σ . See below for a description of the model fitted during the analysis, together with the implementation of strata, fixed effects and random effects.

Habitat mask

We modelled habitat as a raster composed of 10×10 km grid cells (same resolution as the detector grid, Bischof et al. 2016). For context, the average home range sizes for adult bears in our study population have been estimated at 217–280 km² for females and 833–1055 km² for males (Dahle and Swenson 2003), suggesting a sufficient resolution of both the habitat grid and the detector grid (Sollmann et al. 2012, Royle et al. 2013). We excluded clear non-habitat (ocean) from the habitat mask, but, in order to avoid the circularity inherent in defining non-habitat based on assumptions about the study system, we did not impose further restrictions (Royle et al. 2013). Furthermore, brown bears

are one of the most wide spread carnivore species; their distribution covers a substantial part of the terrestrial northern hemisphere and the species occurs across an a wide range of habitats, latitudes, and elevations (Wilson and Mittermeier 2009). We added a 30 km buffer of habitat to each focal area: bears detected within the detector grid could have home range centres located anywhere within the greater habitat mask (Bischof et al. 2016). We used each sample collection region as a separate stratum in the analysis, instead of running four separate analyses. Stratification allowed for transferability of some parameters (random effect of tile on p , random effect of individual on σ , sex effect on σ), thereby increasing overall precision. Additional benefits of a stratified approach in SCR models are discussed in Royle et al. (2013).

Road network

We obtained road network data from the Swedish Transport Administration (Trafikverket I2014/00764). The Swedish Transportation Administration classifies all state owned road segments in Sweden into four quality classes based on several parameters such as maintenance history and thematic characteristics (e.g. road width, traffic volume, speed limits, number of lanes, etc.; Swedish Transport Administration 2008). We extracted all roads of the highest quality class from the Swedish National Road Database (NVDB quality class 1). These roads include all major connective paved roads on the national and the regional level, and have relatively high traffic volumes (Swedish Transport Administration 2008). We used road polylines to cut each study area polygon into a mosaic of tiles (RNTs, Fig. 2). For each mask and detector cell, we then identified the RNT that contained the cell. This information was used in the model to 1) estimate the random effect of RNT on detection and 2) determine the effect on detection when a detector cell is located within the same versus a different tile than the predicted activity centre of a given individual.

Roads may follow distinct landscape features such as rivers, and resistance to leaving an individual's home tile in a transportation network may be confounded by fragmentation due to other causes. We therefore created another mosaic layer, with tiles delineated by major rivers (catchment areas > 5000 km²) and included a corresponding resistance parameter in the model. We used the Water Information System for Europe (WISE) 'Large rivers and large lakes' database from the European Environmental Agency to extract the river data. Density of major rivers ranged from 0.018 to 0.033 km km⁻² between the management units (Supplementary material Appendix 1 Table A1).

The equation that describes the detection process (Eq. 4) can be generalized to allow for additive effects of K different causes of fragmentation (index k), such as for example roads, railroads, and rivers:

$$\text{logit}(p_{ij}) = \text{logit}(p_0 \exp(-d_{ij}^2 / 2\sigma^2)) + \sum_{k=1}^K \omega_k D_k \quad (6)$$

Although not done in our example, Eq. 6 can be easily extended to allow for interaction between barrier types. We only included major rivers that dissected the study area (Fig. 2) completely, but less restrictive approaches (e.g. least

cost path distances) could also be used to account for barriers that do not split the landscape into a mosaic of tiles.

Fitted model

The model finally fitted during analyses was:

$$\text{logit}(p_{i,j}) = \text{logit}(p_{0,i,j} \exp(-d_{ij}^2 / 2\sigma_i^2)) + \omega_{road,sex_i,region_j} D_{road,i,j} + \omega_{river,sex_i,region_j} D_{river,i,j} \quad (7)$$

Potential differences in resistance parameters between regions and sexes are incorporated as strata, shown as indices on ω_{road} and ω_{river} in Eq. 7. Fixed effects of sex and individual random effects ϵ on the scale parameter σ are included as follows:

$$\text{logit}(\sigma_i) = \sigma_0 + \beta_{sex} sex_i + \epsilon_i \quad (8)$$

The sex of individual i is indicated by sex_i (0 for males, 1 for females). The magnitude parameter p_0 (with intercept α_0) is estimated separately for the sexes and regions (as strata) in the model, and includes a random effect ϵ of the road network tile in which a given detector cell is located

$$\text{logit}(p_{0,i,j}) = \alpha_{0,sex_i,region_j} + \epsilon_j \quad (9)$$

Model implementation

We implemented the model in program JAGS (Plummer 2003) via the R2jags package (Su and Yajima 2012) in R (<www.r-project.org>). Uniform or flat priors were used for all unknown parameters. Probabilities were sampled on the logit scale, therefore their priors were informative after inverse-logit transformation. We ran three chains for 7500 iterations with an initial burn-in of 5000 iterations. Chains were thinned by retaining parameter values from every fifth iteration to reduce the influence of autocorrelation. We assessed convergence to a stationary distribution using trace plots for model parameters to ensure adequate mixing and by using the Gelman and Rubin diagnostic (R-hat; Gelman 1996). We summarized posterior distributions of the unknown parameters by their means and 95% credible intervals. Aside from the primary parameters estimated by the model (Supplementary material Appendix 1 Table A3), each model iteration also led to predictions of the grid cell that contained the AC of each bear. The most common grid cell among all iterations can be interpreted as the most likely position of the AC given a half-normal detection probability (with increasing distance from the AC) and the pattern of detections and non-detections across available detectors (cells). Alternatively, the coordinates of grid cell locations containing a bear's AC over multiple iterations can be used to derive individual's predicted AC location. This latter approach should be applied cautiously, as it could lead to unrealistic location estimates if predicted AC positions are non-contiguous across the habitat grid. We note also that, within the Bayesian model, the predicted AC location for individuals with a single sample (or multiple samples from the same RNT) still inform the estimate of key parameters, as the AC does not necessarily have to fall into the same tile as the sample, and the pattern of non-detections throughout the detector grid is as much a result of the configuration of

detections as the pattern of non-detections. R code for model implementation in JAGS, together with an example dataset are provided in the Supplementary material Appendix 2–4.

Validation

We conducted three additional analyses, in order to assess model performance and sensitivity to violation of assumptions. First, we extracted model-predicted AC locations (a latent variable estimated by the model) for individual bears. We calculated average latitude and longitude of estimated AC locations over all MCMC iterations for each bear and compared these visually with DNA sample positions.

Second, we generated simulated data for a range of values for the resistance parameter ω (–2 to 0), with σ and p_0 set to 10 and 0.75, respectively. Simulations entailed drawing a random spatial sample of 'true' AC locations (150 individuals) and realizing detection throughout a 10 × 10 km detector grid based on aforementioned parameters. We then fit the model to each simulated data set (60 simulations for each value of ω), using 2000 iterations (thinned by 3), following a burn-in of 5000 iterations. Parameter estimates generated by the model were then plotted against true parameter values for visual comparison.

Finally, to evaluate the effect of variable (detector cells are either searched or unsearched) and unknown search effort on SCR models, we generated subsampled versions of a simulated spatial capture–recapture data set with known values for σ , p_0 (conditional on a detector cell having been searched), and density (the parameter of primary interest in most SCR studies). This resulted in 1600 datasets with the proportion of detector grid cells that was searched ranging from 0.25 to 1. We fit standard SCR models to each dataset using function `secr.fit` in R package `secr` (Efford 2015), to evaluate the effect of spatially heterogeneous search effort (and thus p_0) on estimates of σ , density, and their associated confidence interval widths.

Data deposition

Data available from Rovbase 3.0 (Scandinavian Large Carnivore Database) free online access: <www.rovbase.no> (Norwegian Environment Agency and Swedish Environmental Protection Agency 2014).

Results

A total of 3231 samples from 1169 individual bears (673 male, 496 female) fell within the search regions considered for the analysis (Supplementary material Appendix 1 Table A2). On average, 2.76 samples were associated with each individual, but the number of samples varied widely between individuals (SD: 2.52; range: 1–20). Of 403 individuals with more than one detection, 106 (26.3 %) were detected in multiple RNTs. Only a single individual was detected in two different (adjacent) regions and thus two different years.

All key parameters exhibited satisfactory mixing and convergence, with all \hat{R} -values below the commonly accepted threshold of 1.1 (Supplementary material Appendix 1 Table A3, Fig. A6). Predicted AC locations corresponded well with the spatial configuration of sample locations associated with a given individual (Supplementary material Appendix 1 Fig. A8). The median distance between model-predicted ACs and the nearest road was 8.4 km, but varied between regions (Supplementary material Appendix 1 Table A2, Fig. A7). Model-predicted values of the resistance parameter ω for simulated data exhibited satisfactory correspondence with true parameter value that these simulations were based on (Supplementary material Appendix 1 Fig. A4).

Brown bears were significantly less likely to be detected outside of the road mosaic tile in which their AC was predicted to be located, even when taking into account the gradual decline in detection probability with increasing distance from the AC (Fig. 3). This was the case across all four study regions and for both sexes, with the exception of males in region 1 and females in region 2, where estimates of ω (the resistance parameter in the detection function,

Eq. 4, 6) were also negative, but where the 95% credible interval overlapped zero (Supplementary material Appendix 1 Table A3, Fig. A9). Major rivers that transected detection regions (Fig. 2) posed additional resistance to movement in regions 1 and 3 (for both males and females), but such an effect was not detected in regions 2 and 4 (Supplementary material Appendix 1 Table A3).

Model-predicted estimates of σ (the scale parameter in the detection function, Eq. 4, 5) ranged from 6 km (95% CI: 5.6–6.6) for female bears to 11 km (95% CI: 10–12.1 km) for males (Fig 3), with σ significantly smaller for females than males ($\beta_{sex:female} = -0.61$, 95% CI: -0.72 to -0.49). In addition, the model revealed pronounced individual heterogeneity in σ ($\epsilon_{individual} = 0.37$, 95% CI: 0.33–0.42), as well as heterogeneity in detection among RNTs ($\epsilon_{tile} = 0.36$, 95% CI: 0.1–0.58). Detection models, like the half-normal detection function used here, imply a model of space usage, due to the assumed link between the probability of detecting an individual at a particular location and its proportional use of that location. For the half-normal detection function, home range size can be obtained from the scale parameter σ using the χ^2 -distribution with 2DF (Royle et al. 2013).

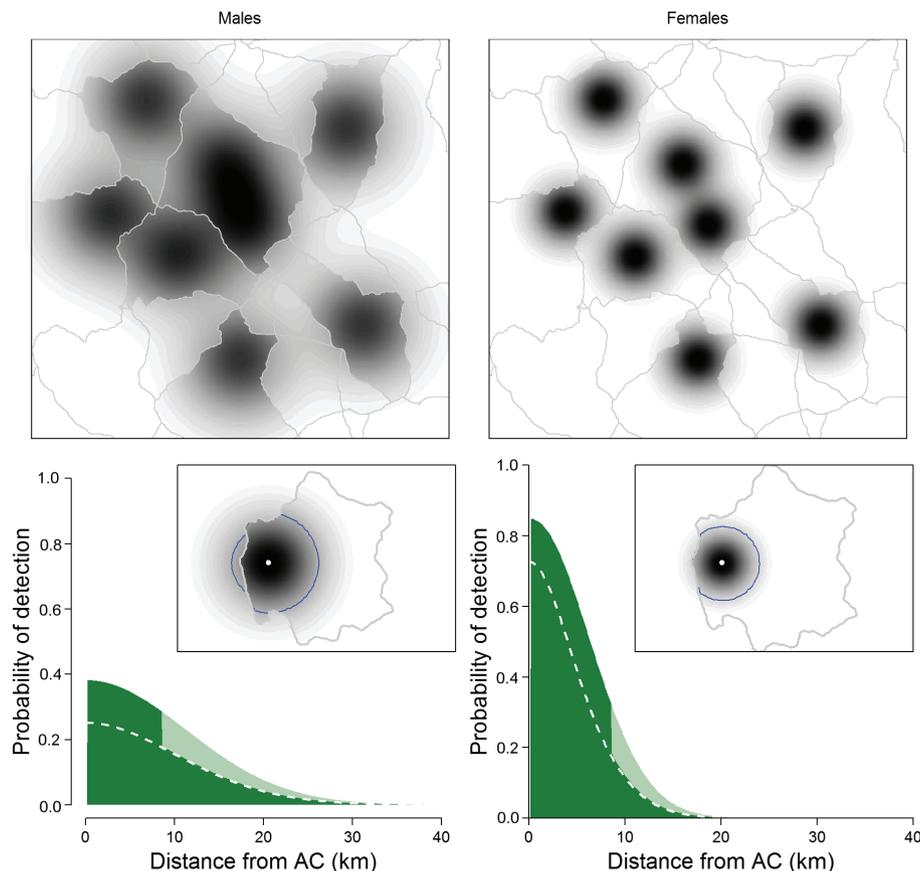


Figure 3. Results from the spatially-explicit capture–recapture model that estimates propensity of staying within the road network tile (RNT) which contains an individual’s activity centre, or, conversely, the resistance to using areas outside the home tile. Top panels provide a spatial illustration of the overall effect of barriers on the utilization distribution for male and female brown bears, based on model predicted parameters, shown in the same road network and for a hypothetical distribution of individuals to facilitate comparison. Bottom panels show detection curves based on non-invasive genetic sampling. Barrier effects are manifested as an additional drop (from the edge of the curve to the dashed white line) in the half-normal detection function, which corresponds to the declining area use with increasing distance from the home range centre. The drop in detectability due to the resistance effect was illustrated at the median distance between activity centre and the closest road (8.4 km). Insets give a spatial illustration of the estimated barrier effect on the utilization distribution associated with a single activity area and RNT (95% kernel isocline marked with a blue line).

Average home range sizes calculated from our estimates of σ ranged from 682 km² (95% CI: 593–829 km²) for females to 2305 km² (95% CI: 1914–2770 km²) for males.

Discussion

Road networks divide the landscape into tiles that both accommodate and isolate wildlife. Road impacts are scale-transcending, and in this study, we have quantified the extent of isolation between the constituent tiles at the network level. It is not surprising that roads pose barriers to the movements of small, relatively slow-moving species, such as small mammals (Rondinini and Doncaster 2002), reptiles (Shepard et al. 2008), amphibians (Vos and Chardon 1998), and insects (Keller and Largiader 2003). More startlingly, transportation networks can impede movements also in populations of large and highly mobile species like the brown bear (Proctor et al. 2012, 2015). This is particularly noteworthy, as brown bears are one of the most wide-spread carnivores, and because the species occurs across an impressive range of habitats, latitudes and elevations (Wilson and Mittermeier 2009). In short, most of Fennoscandia is potential habitat for bears, and there are no serious topographic barriers to their movements in Sweden, with the exception of large rivers, reindeer husbandry areas (Schregel et al. 2012), and areas densely populated by humans (Nellemann et al. 2007). Yet, depending on region and sex, we found that brown bears had up to 73% lower odds of being detected outside the RNT in which their predicted activity centre was located than within (Fig. 3–4, Supplementary material Appendix 1 Fig. A9). These estimates were produced while accounting for the declining probability of detection with increasing distance from the activity centre and controlling for potential additional barrier effects due to major rivers. Both sexes exhibited significant reductions in the probability of being detected outside of their ‘home’ tile, despite the smaller home range size of females (Blanchard and Knight 1991, Dahle and Swenson 2003).

That females bears have smaller home ranges than males was confirmed by our analysis, manifested as a lower value of the scale parameter σ for females ($\beta = -0.61$, 95% CI: -0.72 to -0.49). Although our home range size estimates are between 2–3 times larger than home range sizes reported in the same study area by Dahle and Swenson (2003), these authors conceded that their estimates were likely biased low by a factor of 1.5–2, due to low frequency of earlier telemetry relocations. More importantly, our estimates are based on unimpeded movements, i.e. before the resistance coefficient has been accounted for. In other words, home range estimates derived from intercept values of σ refer to ideal home ranges that are not fully realized due to barrier effects by the transportation network and other obstacles. We note here the functional similarity between our measure of resistance and the accessible habitat measure proposed by Eigenbrod et al. (2008): both capture the extent to which fragmentation restricts the utilization of space by individuals in a network of linear barriers.

Apparent from the spatial configuration of non-invasive genetic samples, roads in our study system do not pose impenetrable barriers to movements of brown bears per se.

However, with the caveat that ours is a ‘natural experiment’ lacking randomization, it appears that roads between tiles in the transportation network do impair movements.

A number of studies have explored the effect of roads (often in conjunction with fencing) on gene flow in wildlife, including large carnivores (Riley et al. 2006, Garroway et al. 2011, Breyne et al. 2014, Sawaya et al. 2014). Although near complete isolation is required for population divergence via genetic drift (sensu Laurance et al. 2009), even impeded movement can lead to deleterious effects, including genetic differentiation (Riley et al. 2006, Wilson et al. 2015). The graded, yet pronounced isolation between tiles in the road network in our study areas can have consequences for the behaviour, social organization, life history, and ultimately population dynamics and persistence of bears and other affected large mammals. For example, being ‘trapped’ in a habitat tile within a road mesh inherently implies that access to resources is constrained. Consequently, an animal will have to adjust its habitat selection behaviour to cope with restricted resource availability (Mysterud and Ims 1998, Lele et al. 2013). Road isolation effects likely hamper or guide dispersion and migration (Forman and Alexander 1998), which can alter the social structure of a population and negatively impact reproduction, survival (Mansergh and Scotts 1989), and genetic diversity (Epps et al. 2005, Schregel et al. 2012). In addition, denser road networks (i.e. smaller habitat tiles) imply increased human access into wildlife habitat, which typically increases human-induced wildlife mortality (Kerley et al. 2002, Nielsen et al. 2004, Switalski and Nelson 2011, Steyaert et al. 2016) and, presumably, human-wildlife conflict. The propensity for individuals to remain in their home tile can also have far-reaching indirect ecological consequences. For example, hampered animal movement can limit nutrient translocation within and between ecosystems (Schmitz et al. 2010), and impede dispersal of plant species that rely on zoochory (Forman and Alexander 1998, Suárez-Esteban et al. 2013) which can decrease floral diversity on vast spatial scales (Ozinga et al. 2009).

Metapopulation dynamics are similarly impacted, as roads may staunch the flow of individuals and genes required for recolonization or maintenance (Mladenoff and Sickley 1998, Epps et al. 2005, Garroway et al. 2011). Bear populations in Norway depend to a large part on an influx of bears from neighbouring Sweden (Bischof and Swenson 2012, Bischof et al. 2016) – re-colonization and source-sink dynamics are liable to be impeded since movements, regardless of their trajectory, have to occur across multiple tiles first in the Swedish and then the Norwegian road network. Genetic patterns emerge from animal movements across the landscape. Both, landscape genetic approaches (Balkenhol and Waits 2009) and the approach we described here transcend spatial scales, but complement each other in terms of the time it takes for focal effects to become manifested. Space use is liable to respond quickly and remain highly fluid, whereas effects on genetic patterns are expected to take longer to manifest but be more long lasting. As Balkenhol and Waits (2009) noted, integrating landscape genetic approaches with field based methods will increase our understanding of the consequences of behavioural responses to road networks, as well as provide a stronger basis for developing strategies for mitigation.

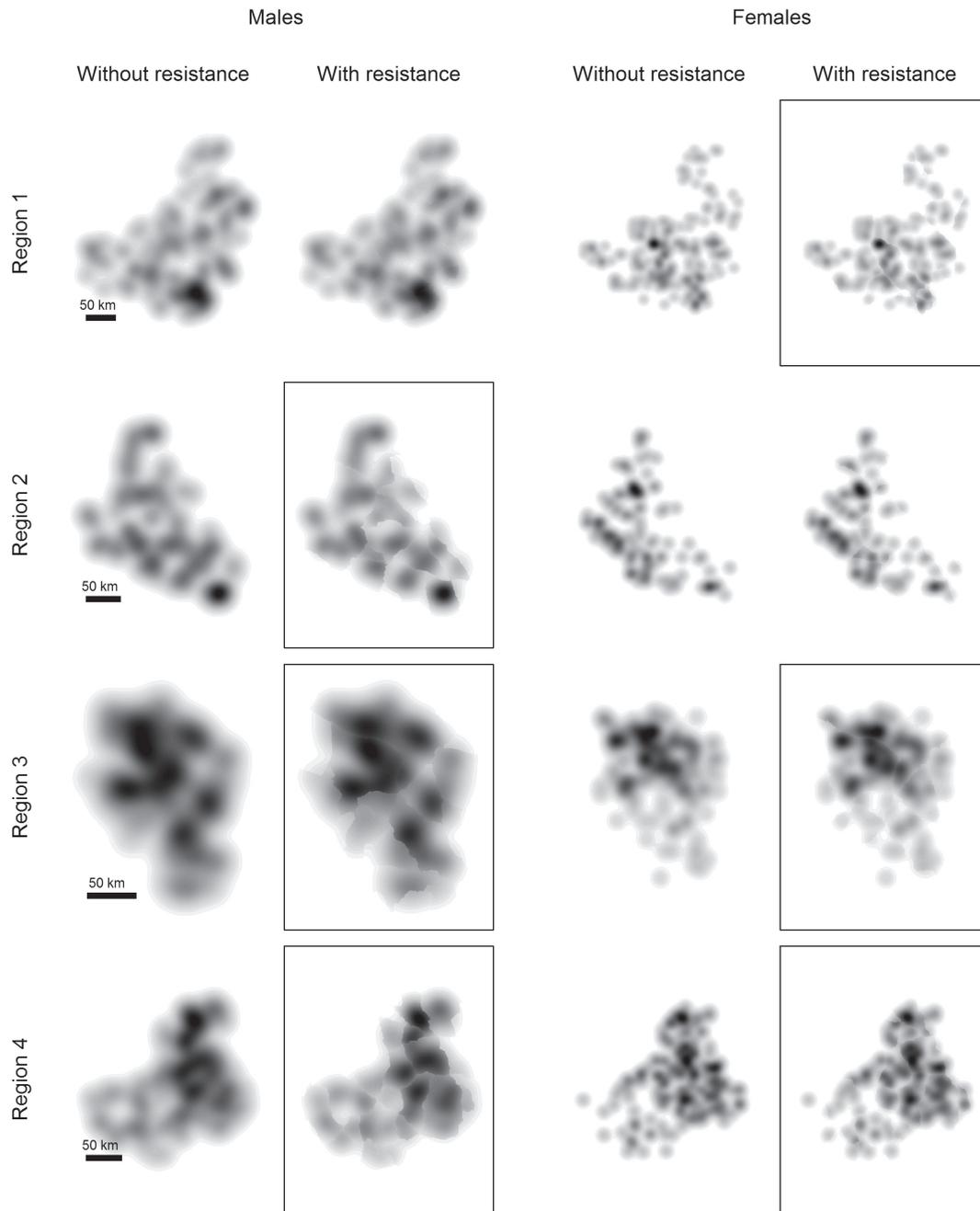


Figure 4. Illustration of resistance effect based on predicted activity centre (AC) locations and utilization distributions for male and female bears in four road network regions in Sweden. Darker areas signify greater utilization by bears detected during non-invasive genetic sampling. Resistance to moving beyond the road network tile containing a bears' AC is apparent in an abrupt drop in utilization (clear edges between darker and lighter shaded areas). Region/sex combinations with significant barrier effects are marked with boxes around plots. Note that landscape-level resistance effects are somewhat masked in the illustration due to overlapping AC locations and utilization distributions of multiple bears.

Although we assessed network-scale fragmentation due to roads, our model can be readily adapted to evaluate isolation or resistance to movements at smaller scales as well. Tiles in the mosaic likely differ in the extent to which they isolate their inhabitants from the surroundings. Characteristics of each tile (e.g. size and habitat) or the roads surrounding it (e.g. traffic volume and structural parameters) may explain variation in the degree of isolation across space. Incorporating tile specific attributes could help answer applied questions about the role of network configuration (Jaeger et al. 2006)

and the extent to which wildlife mitigation projects, such as road crossing structures and fencing (van der Grift et al. 2013), modulate the resistance to leaving one's home tile. At larger spatial scales, the model could be used to relate geometric measures of fragmentation due to linear barriers, such as effective mesh size (Jaeger 2000, Moser et al. 2007) or accessible habitat (Eigenbrod et al. 2008), with the species-specific measure of isolation derived in our study. We contrasted the degree of isolation experienced by male and female brown bears within the Swedish road network.

Additional attributes (e.g. age and reproductive status), if available, can be incorporated in the model to explore potential causes for individual variation in the propensity to stay within one's home tile. Similarly, if vital rates are known or estimable, these could be used to evaluate the fitness effects of fragmentation caused by transportation networks, which in turn could lead to predictions for population dynamics.

In two out of eight sex-region combinations included in our study, the credible intervals for the resistance effect overlapped zero (Supplementary material Appendix 1 Table A3). Without additional information, attempts at explaining this finding would be purely speculative. Be that as it may, it is worth pointing out again that barrier effects are liable to be context-specific, even within populations and transportation networks. Intrinsic attributes (such as phenotypic traits, energetics, etc.) and extrinsic factors (such as traffic volume, habitat configuration, historic and current levels of human disturbance, etc.) are liable to influence the magnitude of realized resistance to crossing linear structures such as roads. As touched on above, incorporating such attributes as potential predictors into analyses of barrier effects could help investigators to explain heterogeneity in fragmentation across scales of space and biological organization.

Our approach is not a panacea for assessing barrier effects and fragmentation. The large spatial and demographic scope comes at the cost of spatial and temporal detail: often only a few relocations per individual are available and, depending on environmental conditions and study design, there can be substantial uncertainty in the timing of sample deposition. Telemetry studies can yield a vast amount of information for every individual monitored, and are able to assess the behavioural mechanisms from which larger scale patterns ultimately emerge. This has repercussion also for active management, especially site selection and impact assessment of mitigation structures such as wildlife crossings and fences. We concur with the recommendation to combine genetic approaches with tracking data (Balkenhol and Waits 2009). Our approach not only complements information obtained from more detailed individual-based studies but can also be used to guide the selection of areas for targeted intensive study (for example by identifying regions or RNTs) where resistance effects are particularly conspicuous. Conversely, our approach allows the assessment of larger scale effects of multiple local mitigation actions: e.g. successful implementation of a system of wildlife crossings should be reflected in a reduction of the resistance parameter across the network or parts thereof.

For simplicity and computational efficiency, the model used in our analysis was conditional on having detected an individual at least once. The unobserved ecological process – i.e. the distribution of all individual ACs within the habitat mask, not only those detected during sampling – can be easily incorporated into the likelihood by adding Eq. 2. Such a hierarchical version of our model would 1) allow estimation of various model parameters as they apply to the entire population (detected and undetected) within the study area and 2) help assess the potential role barrier effects may have in biasing estimates of key parameters, such as density, in SCR models.

One of the primary goals of road ecology is to help planners make informed decisions that can mitigate the negative ecological effects of road networks (Balkenhol and

Waits 2009). This includes quantification of road impacts and assessment of the potential effect of mitigation actions. Roads affect species differently (Fahrig and Rytwinski 2009, Rytwinski and Fahrig 2012) and consequently mitigation of such effects has to be species specific as well (Balkenhol and Waits 2009, van der Grift et al. 2013). The approach showcased here is applicable to other species and systems, requiring only minor adjustments (e.g. reduced grid size for species with smaller average movement distances). Finally, the conceptual approach, in combination with parameters derived from fitting the model to empirical data, opens the door for targeted simulations at multiple spatial scales. Such simulations could for example be used to compare the predicted impacts of alternative network configurations (Jaeger et al. 2006) or forecast the effect of expansion of the road network.

Conclusions

To our knowledge, this is the first study to estimate the network-level effect of road-caused fragmentation on contemporary wildlife movements. In doing so, we have broken from the traditional approach of artificial and problematic inflations of scale by attempting to extrapolate from local barrier effects (Coffin 2007, Balkenhol and Waits 2009). Transportation networks do not only dissect/split individual habitat patches, they cut up entire landscapes and as such are expected to have broad-scale effects (Balkenhol and Waits 2009). This should provide ample motivation to quantify the impact of roads and mitigation efforts at multiple spatial scales, from local road segments to the network-level. Similarly, roads impact populations and communities, not only individual animals. The emergent properties at the population level that result from changed movements and interactions of individuals may remain hidden if only a small portion of a population is being studied. A shift towards exploring effects at the network and population scales has begun (Manel et al. 2003, Simmons et al. 2010, van der Ree et al. 2011) and examples of such effects are now accumulating (Mladenoff and Sickley 1998, Gibbs and Shriver 2002, Robinson et al. 2012). We are witnessing an increasing utilization of survey methods that can yield individual based data over large expanses, such as non-invasive genetic monitoring and camera trapping, in combination with analytical methods that can exploit the spatial information in these data. These developments now let ecologists capture the ecological impacts of transportation networks at large spatial scales and at the level of populations. Finally, we note that the RNT is an intuitive unit for analysing and modelling the effects of road networks. This is partly because the size of an RNT is a function of road density: with increasing landscape fragmentation and anthropogenic disturbance, the size of the study unit decreases, resulting in a corresponding increase in spatial detail during analysis. Furthermore, an understanding of road networks as mosaics of habitat tiles links barrier effects with concepts in research on habitat fragmentation, the leading agent of anthropogenic environmental change (Lindenmayer and Fischer 2006), thereby offering ecologists a larger set of tools and broader perspective for tackling critical problems in road ecology.

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Supplementary material (Appendix ecog-02801 at <www.ecography.org/appendix/ecog-02801>). Appendix 1–4.