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Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings

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ABSTRACT

Globally, human activities impact from one-third to one-half of the earth's land surface; a major component of development involves the construction of roads. In the US and Europe, road networks fragment normal animal movement patterns, reduce landscape permeability, and increase wildlife-vehicle collisions, often with serious wildlife population and human health consequences. Critically, the placement of wildlife crossing structures to restore landscape connectivity and reduce the number of wildlife-vehicle collisions has been a hit-or-miss proposition with little ecological underpinning, however recent important developments in allometric scaling laws can be used to guide their placement. In this paper, we used cluster analysis to develop domains of scale for mammalian species groups having similar vagility and developed metrics that reflect realistic species movement dynamics. We identified six home range area domains; three quarters of 102 species clustered in the three smallest domains. We used $HR^{0.5}$ to represent a daily movement metric; when individual species movements were plotted against road mile markers, 71.2% of 72 species found in North America were included at distances of ≤ 1 mi. The placement of wildlife crossings based on the $HR^{0.5}$ metric, along with appropriate auxiliary mitigation, will re-establish landscape permeability by facilitating wildlife movement across the roaded landscape and significantly improve road safety by reducing wildlife vehicle collisions.

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1. Introduction

The activities of humans around the world impact an estimated one-third to one-half of the earth's land surface (Vitousek et al., 1997). Accompanying nearly all human habitat alteration is the construction of roads. The cumulative effects of road systems include their virtual footprint (Bissonette, 2002) which extends beyond the road surface and has been estimated to impact about one-fifth of the land mass of the contiguous US (Forman, 2000). To put the problem into perspective, the US has a mean road density of 0.75 km/km^2 (1.2 mi/mi^2); the mean road density in Germany, France, and England is 2.5 times greater and in Japan 4 times greater (Forman et al., 2003). Clearly, the environmental impacts of roaded networks are a global problem.

Roads have direct effects including animal mortality (Haines et al., 2006; Ramp et al., 2005; Roe et al., 2006; Roger et al., 2007), habitat loss (Ewers et al., 2006; Nielsen et al., 2006), habitat degradation (Nyström et al., 2007), and fragmentation (Mata et al., 2005), as well as indirect effects on ecological patterns and processes, including barrier effects (Bhattacharya et al., 2003), loss of connectivity (Clevenger and Wierzchowski, 2006), and reduced permeability (Spellerberg, 2002; Bissonette and Storch, 2003; Forman et al., 2003;

Altrichter and Boaglio, 2004). Both direct and indirect effects impact animal movement (Jaeger et al., 2005). Spatial linkage, accomplished by animal movement, is critical because the arrays of resources that are essential to population viability are usually distributed heterogeneously across habitat networks (Merriam, 1998). The ability of animals to move has profound impacts on ecological phenomena and processes, including individual fitness, population structure, life history strategies, foraging dynamics, and species diversity (Addicott et al., 1987; Bowne and Bowers, 2004). Significantly, movement dynamics represent one of the most significant knowledge gaps in animal ecology (Bennetts et al., 2001; Paradis et al., 2002; Trakhtenbrot et al., 2005). Although barrier effects (Ng et al., 2004) vary widely with different types of roads, the combined effects of road geometrics; e.g., road type, width, fences,) and traffic volume (Kaczensky et al., 2003; Fahrig et al., 1995) and speed (Knight et al., 1995; Seiler, 2005) present significant problems to animals, resulting in fragmented habitats, disconnected resource networks, non-permeable or semi-permeable landscapes (Bissonette, 2002), and most critically, isolated populations (Burnett, 1992; Wang and Schreiber, 2001; Kattan et al., 2004; Seiler and Folkeson, 2006).

Effective mitigation that employs wildlife crossings involves both their placement and spacing. Crossings usually are placed on roads at hotspot locations where animals tend to be hit (Clevenger et al., 2003; Clevenger and Waltho, 2005). The spacing between crossings has been a hit-or-miss proposition, largely lacking a solid ecological basis, perhaps in part because the idea of landscape permeability traditionally has not been viewed from an animal perspective. We have either ignored an explicit assessment of spacing or operated with the scale-free tacit assumption that one 'spacing' fits all species. It is profitable to think about permeability as a scale concept; i.e., the ability of species of all sizes to move relatively freely across the landscape during their daily activities. Connectivity as we define it refers to an anthropocentric view of the landscape. It may be obvious to suggest that a mouse does not have movement characteristics similar to a moose, but the point is clear: animal vagility is scaled and differs from species to species (Bowne and Bowers, 2004) according to allometric scaling functions (Kleiber, 1961; McNab, 1963; Lindstedt et al., 1986), suggesting that the spacing of crossings can be determined by the scaling properties of species movement.

1.1. Scaling domains

Landscape permeability is improved when the location of crossing structures allows all species and individuals in a community to cross roads safely at will. Clearly, spacing appropriately-designed crossings at shorter distances apart will allow most species in the community to use the structures. However, it is unreasonable from a management perspective to attempt to space wildlife crossing structures for each individual species. Some grouping of species is desirable. Hence, an important first task is to translate movement distances characteristic of a community of species into useable, data-based scaling domains. To the extent that: (a) similarities in home range sizes exist for groups of species; and (b) there are recognizable and measurable differences be-

tween groups, it should be possible to determine an effective scale domain (Wiens, 1989) that reflects the range of normal movements characteristics of each group. Here we use scale domain to refer to a range of species movement distances that are similar, so that several species can be considered as belonging to a particular domain. Home range area is perhaps the best indicator of normal animal movement (Moorcroft and Lewis, 2006). Using home range data, cluster analysis (McCune and Mefford, 1999) can be used to identify and group species with similar movement dynamics into home range scale domains.

1.2. Ecological neighborhoods

Ecological neighborhoods are defined for individual species by three properties: (a) an ecological process (e.g., inter-patch movement); (b) a time scale relevant to the process; and (c) an organism's activity during that time period (Addicott et al., 1987). Characteristically for mobile organisms, the ecological neighborhood for a given process is the region within which that organism is active. Indeed, Addicott et al., 1987, p. 343) suggested that "for neighborhoods..., the most appropriate indicator of activity may be a measure of net movement of individuals... One (*such indicator*) is the direct measurement of dispersal distances". Migratory movements involve larger neighborhoods. Another measure involves daily movements. Most daily movements by animals are relatively short; long-distance movements are typically rare and seasonal (Harestad and Bunnell, 1979; Bowman et al., 2002). Both can be indexed and scaled to home range area. Recent developments in allometry provide the connection between home range area and movement metrics.

1.3. Allometric scaling

Allometric scaling has had a long history in ecology and has been a particularly successful tool for investigating animal movements. The general form of the scaling equation is: $Y = aX^b$ (Kleiber, 1961; Lindstedt et al., 1986). McNab (1963) showed that among mammals, a power law relationship (scaling exponent) existed between home range area (HR) and body weight (explanatory variable). Recently, Wolff (1999) and Sutherland et al. (2000) demonstrated that body size of mammals was linearly related to dispersal distance when both variables were expressed on a $\log_{10}$ scale and corrected for bias (Sprugel, 1983). Bowman et al. (2002) showed that dispersal distance (response variable) was actually more closely related to home range area ($R^2 = 0.74$) than to body size ($R^2 = 0.60$). Further, they found that when body size effects were removed, the slope of the relationship of the residuals of dispersal distance regressed against the residuals of home range area was not significantly different from 0.50 ($F = 31.6$, df = 1, 32, $P = 3.2 \times 10^{-6}$, SEE = 0.54), a result with very important ramifications. The significance is this: dispersal distance is a linear measure, while home range area is a squared linear measure. Because $X^{0.5}$ is equal to $\sqrt{X}$, and because X in the scaling equation is equal to home range area, taking the square root of the home range area yields a linear dimension of home range, allowing dispersal distance to be related to home range size by a single scaling constant and with the

same unit of measurement. Additionally, the relationship is linear and proportional (isometric, slope = 1). Bowman et al. (2002) found that median dispersal distance (MedDD) was related to home range size (HR) by the metric: MedDD = 7 ($\sqrt{HR}$). The linear home range metric (linear distance = $\sqrt{HR}$ = $HR^{0.5}$) is itself also a scaled measure of animal vagility. Home range area estimates for many species are readily available in published literature (McNab, 1963; Harestad and Bunnell, 1979; Sutherland et al., 2000) enabling: (a) the identification and assignment of species to clustered movement domains; and (b) the development of scaled movement metrics based on ecological neighborhoods. These are the essential conceptual elements for deciding the scaled placement of wildlife crossings of appropriate type and configuration to promote landscape permeability.

We addressed the problem of placing crossings by answering two questions. Is it possible to develop scaling domains based on normal movements of animals across their home ranges? Can ecologically relevant metrics that characterize movement distances be developed? Below we show how domains of scale can be developed from sound home range data and we use the ideas of ecological neighborhoods and allometry to develop a daily animal movement metric. When considered together, these developments provide the ecological basis for spacing wildlife crossings effectively.

2. Materials and methods

2.1. Home range data

Bowman et al. (2002) developed their home range dispersal relationships for mammals from data given in Harestad and Bunnell (1979). Other sources of home range data are available, but the Harestad and Bunnel data are well-known, accepted by ecologists, and are the data that have been used to advance the allometric scaling of mammals (Kelt and Van Vuren, 2001). We used the Harestad and Bunnell data and augmented those with the species home range list given in Appendix 7 of Holling (1992). The Holling data increased the number of species for which reliable home range data were available. Only data for species with at least five replicates were used in the Holling data. Some species do not occur in North America, but were included because: (1) the data related to their home range areas were reliable, and (2) they provided a reasonable sample size from which to develop reliable dispersal distance domains. Elimination of duplicate entries left reliable home range area estimates for 102 species. These data represent widely distributed species from around the world, but animals in any local community are likely to fall into one of the six distance domains.

2.2. Clustering

To detect minimally arbitrary breaks (scale domains) in the data, we applied the hierarchical polythetic agglomerative clustering method included in the PC-ORD software package (McCune and Mefford, 1999) to the home range data, using the conventional Euclidean distance measure and Ward's linkage method as the sorting strategy. We used Euclidean distance because it is one of the simplest measures (parsi-mony) and is conceptually equivalent to the linear distance (sum of squares of the distance) between any two measures. The shorter the distance, the more similar the measures and the more likely the species involved will be included in a group. Ward's minimum variance method avoids distortion and is well suited to the Euclidean distance measure (McCune and Grace, 2002).

PC-ORD's cluster analysis generates a clustering matrix and a dendrogram of the species groups. We used several analytical tools to identify the optimal arrangement of species among classes, including visual inspection of the dendrograms and sequential application of multiple response permutation procedures (MRPP) (McCune and Mefford, 1999; McCune and Grace, 2002) to successive cluster configurations. These methods indicated little change in cluster structure (within-group dispersion and among-group separation) until six classes emerged. Finer clustering levels artificially subdivided classes of similar species, and coarser clustering levels aggregated species with dissimilar characteristics. Silhouette widths (Rousseeuw, 1987) were calculated to identify misclassified species; there were none. The wolverine (*Gulo gulo*) was identified as an outlier and removed from the dataset prior to clustering.

2.3. Ecological neighborhoods

After the natural breaks were detected, we calculated different movement metrics based on two ecological neighborhoods for each of 102 mammalian species: one based on a linear measure of home range area ($HR^{0.5}$) to represent shorter daily movements, and one based on median dispersal distances ($7 * HR^{0.5}$) to represent longer, less frequent dispersal events. Both transformations represent different ecological neighborhoods for individual species. We then plotted frequency distributions of the species scaled by both the median dispersal distances and the linear home range distances against both km and mile road markers. Finally, we compared the options for spacing wildlife crossings and present the scaling for large mammals in North America that are most likely to be involved in serious animal vehicle crashes.

3. Results

We used cluster analysis (McCune and Mefford, 1999) to identify six home range area (ha) domains (Fig. 1). Almost of the species clustered in the smallest home area range domain. Although our data set was drawn from many communities, it includes small terrestrial mammals as well as larger ranging carnivores (foxes, wolves, lynx, coyotes, grizzly bears, and mountain lions) and ungulates (deer, elk, bighorn sheep, pronghorn antelope, and moose). Even with these larger species, the species community was skewed to smaller scale domains (Fig 2). The three rightmost groups (vertical lines A, B, C) in the dendrogram are clearly distinct and different. Fig. 2 shows that the species represented by the group "D" are more similar to each other than the species in groups "C" or "E." There was little discernable difference when more groups were considered. When we compared the number of species by movement neighborhood against a typical km road marker, clear patterns emerged (Fig. 3a). When the linear
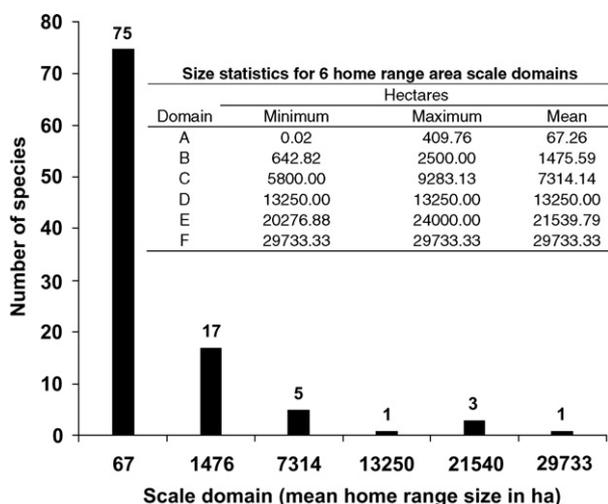
Fig. 1 – Distribution of 102 species among six home range area scale domains.
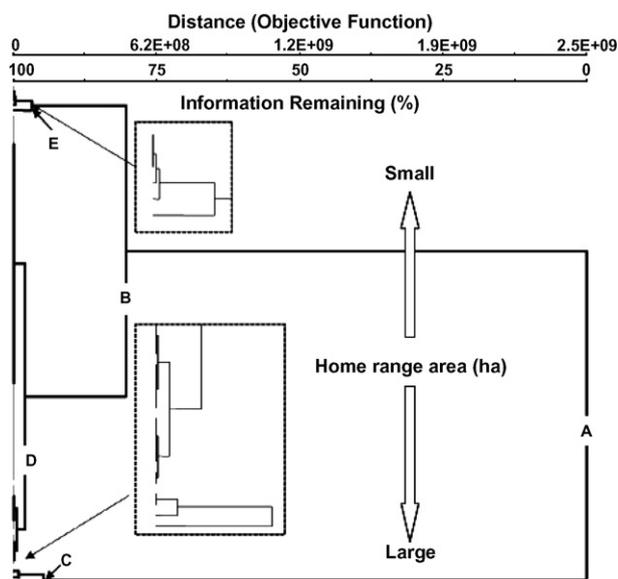
Fig. 2 – Dendrogram of 102 mammalian species. The two groups with the smallest home ranges are relatively similar to each other. The two groups with the largest home ranges (wolverine excluded) are also relatively similar.

Fig. 3 – Linear distance ($HR^{0.5}$) and median dispersal ($7 * HR^{0.5}$) ecological neighborhoods for (a) 102 mammalian species by km marker, and (b) 72 North American mammalian species by mile marker.

home range metric was plotted, 74.0% of species were included in distances of ⩽2 km. If median dispersal distances were used as the movement metric, only ∼38.2% of species was included in distances of ⩽2 km. When we plotted the linear distance metric against the km markers using only the 72 species in the data set found in North America (not shown), 52.1%, 9.6% and 16.4% of the species (total = 78.1%) were included in distances of ⩽2 km or less. When we used the dispersal distance metric, 24.7%, 10.9%, and 12.3% (total = 47.9%) were included in distances of ⩽2 km.

Roads in the United States are measured in mile markers. When we plotted the frequency distribution of the linear distance metric for the 72 species found in the US against mile markers spaced at 0.5, 1, 2, 3, 4, 5, 10, and >10 mi, 71.2% of the species were included at distances of ⩽1 mi. When the

dispersal distance metric was plotted, only ∼43.8% was included at distances of ⩽1 mi (Fig. 3b). This line of evidence strongly suggests that community-wide landscape permeability is largely governed by surprisingly short daily movement distances. Clearly, crossings located according to a median dispersal distance criterion would be too far apart to allow frequent movement across roads for most species in the community. Inexpensive crossing tubes, pipes, and small culverts with drift fences and other associated mitigation structures may be sufficient for successful movement of smaller animals as well as for reptiles and amphibians that tend to move over short distances. Mata et al. (2005); p. 403) showed that structural aspects of crossing structures most influenced the species that used the structures: they showed that 'circular and adapted culverts were used selectively by small mustelids, amphibians, reptiles and small mammals'. Even larger ungulates and carnivores, which in the United States are most likely to cause serious injuries or human death if involved in wildlife-vehicle collisions, scale between 0.5 and 6.0 mi when the linear home range metric is used (Table 1).

4.   Discussion and conclusions

Wildlife-vehicle crashes involving large terrestrial mammals tend to result in greater vehicle damage and greater potential

Table 1 – Home ranges of large mammals in North America and derived ecological neighborhoods for wildlife crossing placement

Species	HR (ha)	$HR^{0.5}$ (mi)	$7 * HR^{0.5}$ (mi)
Black-tailed deer *O.[a] h. columbianus*[a]	59[b]	0.5[c]	3.3[c]
California black-tailed deer *O. h. californicus*[a]	79	0.6	3.9
White-tailed deer *O. virginianus*[a]	196	0.9	6.1
Mule deer *O. hemionus hemionus*[a]	285	1.1	7.4
Pronghorn antelope *Antilocapra americana*	1061	2.0	14.2
Moose *Alces alces*	1215	2.2	15.2
Elk *Cervus canadensis*	1293	2.2	15.6
Bighorn sheep *Ovis canadensis*	1433	2.4	16.5
Black bear *Ursus americanus*	2413	3.1	21.4
Grizzly bear *Ursus arctos*	9283	6.0	41.9

a Genus = Odocoileus.
b Rounded to nearest ha.
c Rounded to nearest 0.1 mi.

for human injury and death than smaller animals, and are a greater safety risk on the road (Forman et al., 2003). It appears that to achieve the level of landscape permeability that will help insure the health of large mammal populations (e.g., deer, moose, elk, and bear) and minimize dangerous wildlife-vehicle crashes, placement of crossings of appropriate type and design informed by linear home range distances would be the best, albeit the more expensive, choice. For example, placing wildlife crossings for white-tailed deer and mule deer (by far the most frequently hit animals on North American roads) at about 1 mi (1.6 km) apart in hotspot areas where these animals cross the road frequently and are often hit by vehicles, would certainly improve highway safety and help insure ease of movement, improving landscape permeability for >71% of the species. Using the MedDD values of 6.1–7.4 mi to space the crossings for these deer species will result in much fewer crossing structures; it is difficult to see how movement would be facilitated other than in those areas. Connectivity, not permeability would be achieved. Similar arguments can be made for all species in general. Using scaling domains identified by cluster analysis and informed by species ecological neighborhoods provides a sound conceptual underpinning to improve landscape permeability and highway safety and, coupled with local information about migration pathways, areas of local animal movement across roads, hotspots of animal vehicle crashes, as well as carcass data provide an ecologically sound approach to inform the placement of animal crossing structures.

Often, given fiscal constraints, local topography, or other reasons, it may not be possible to place crossings based strictly on the isometric scale extents we have identified. In these cases, although closer would appear to be better, widening the spacing between crossings may be the only practical alternative. When fiscal constraints are paramount, placing crossings in areas of high wildlife kill becomes especially important. Significantly, hotspots of wildlife-vehicle accidents and of carcasses appear not only to be clustered, but are often restricted to certain routes and not others in a road network. For example, Kassar (2005) reported that in Utah with ~9500 km (~5900 mi) of state highways, 54.6% of 24,210 deer vehicle collisions occurred on only ~1001 km, (~622 mi) or 10.5% of total state route highway miles (10 of

248 routes). This makes what may seem at first a huge problem, more tractable. When municipalities begin to address the problem of wildlife road mortality at the state, province, or other large administrative scale extent, it would seem prudent to first prioritize areas for mitigation based on hotspot data. Often, hotspots of serious wildlife road mortality are relatively short stretches of road. When this is the case, the placing of crossings at distances that will be effective becomes less problematic. Even placement that is twice or three times the isometric distances we suggest should be effective, if crossings are placed where wildlife actually cross the road. Complete permeability in real world roaded landscapes may not be achieved. Often it may be possible to only partially reduce the barrier effect. Although limited movement across roads may be sufficient to insure genetic mixing, it may not prevent population isolation and decline. Only subsequent monitoring will determine if the mitigation was effective. If not, reconsideration of additional crossings is warranted.

4.1.   Caveats

4.1.1.   Home range size estimations

Clustering techniques, such as the one used in this research, simply group similar clusters based on specified criteria; in this paper all measurements derive from published home range data. The home range of an animal is an area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Home range area is a measure that implicitly assumes that the animal uses all parts of its range. This clearly is not the case. However there are some home range measurement techniques that quantify actual space use; e.g., those using the center of activity such as the Kernel method (Mohr, 1940; Worton, 1987), and nonparametric methods; e.g., where area used is determined by GPS Cartesian coordinate spatial locations and analyzed with map software metrics that measure not only the extent of the area used by the animal but also concentrations of activity within the home range. One of the oldest and most commonly used methods is the minimum convex polygon home range estimator (Mohr, 1947). It estimates only area of use, similar to the data used by Harestad and Bunnell (1979). A clearer and more concise measure of resource use can be

obtained by following an animal's movement trajectory (Aebischer et al., 1993; Bissonette et al., 1994), and assessing what resources it is using, but this is seldom done and multi-species data sets are unavailable. An advantage of following animal trajectories is that daily movement distances could be estimated. Home range size varies over time for individuals and for populations and is correlated with resource availability and distribution. The values we used are the best representative values available for the species. Individual home ranges will no doubt vary around these mean values.

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