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ORIGINAL PAPER

Forest mammal roadkills as related to habitat connectivity in protected areas

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Abstract Fragmentation of wildlife habitat by road development is a major threat to biodiversity. Hence, conservation and enhancement of habitat connectivity in roaded landscapes are crucial for effectively maintaining long-term persistence of ecological processes, such as gene flow and migration. Using multivariate statistical techniques combined with graph theoretical methods, we investigated the influence of road-crossing habitat connectivity and road-related features on roadkill abundance of forest mammals in protected areas of South Korea. Because species have different dispersal abilities and thus connectivity would differ between them, we explored three different groups of road-killed mammals, categorized as small, intermediate, and large ones. We found that in all three mammal groups, roadkills are increased on roads that intersect high-connectivity routes. Furthermore, the effect of habitat connectivity on roadkill abundance was scale-dependent. The roadkill abundances of small, intermediate, and large mammals were related with connectivity measured at scales ranging between 100 and 300 m, between 5 and 7 km, and between 10 and 25 km, respectively. Our finding with regard to scale-dependency

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highlights the importance of maintaining movement and connectivity across roads at multiple scales based on the dispersal potential of different species when planning conservation strategies for forest mammalian roadkill mitigation.

Keywords Biodiversity · Conservation · Dispersal · Graph theory · Habitat fragmentation

Introduction

Habitat loss and fragmentation due to human encroachment continue to threaten wildlife populations and diversity (Devictor et al. 2007; Forman and Alexander 1998; McKinney 2006). In particular, roads have significant adverse impacts on wild animals by increasing access for poachers (Clements et al. 2014), disconnecting them from essential habitats, restricting their physical movements, and contributing a large source of mortality by vehicle collisions (Forman and Alexander 1998; Laurance et al. 2009; Trombulak and Frissell 2000).

The mortality of animals due to vehicle collisions is well documented (Bruinderink and Hazebroek 1996), and there are a number of studies on causes of roadkill. For instance, Hussain et al. (2007) reported that traffic volume was highly correlated with animal road mortality, while Gunther et al. (1998) implicated speed as the major reason for animal–vehicle collisions. Clevenger et al. (2003) found road topography to be a significant factor explaining roadkill rates. However, few studies have addressed road mortality in various groups of mammals together (Barthelmess 2014). There have been some studies examining the influence of road and landscape features on small mammal roadkills (e.g. Clevenger et al. 2003; Oxley et al. 1974), while most previous studies concentrated on identifying important variables for large mammal roadkills (e.g. Bissonette and Kassar 2008; Bruinderink and Hazebroek 1996; Jensen et al. 2014). In addition, while some studies have shown spatial patterns in road kill frequency (e.g. Child 1998; Clevenger et al. 2001; Danks and Porter 2010), little is known about how landscape-level patterns, particularly connectivity, affect mortality (but see Girardet et al. 2015; Grilo et al. 2011). Despite efforts to restore connectivity across roads with wildlife crossing structures (Clevenger 2005), many roadkills still occur throughout the world (KNPS 2009; Spellerberg 2002). Landscape-level connectivity (i.e. the probability of movement among patches) is an important factor that needs to be considered for the distribution and the abundance of roadkills (Forman and Alexander 1998), as available habitat types and configuration of those habitats are critical factors for the existence of wildlife.

Protected forest areas often exist in a network of reserves that may be separated from each other by long distances and many roads. Movement from one habitat reserve to another may be necessary for long-term persistence of biodiversity but may also be dangerous if it involves crossing busy roads. Because species have different movement abilities, a habitat network that is perceived as well-connected for one species or a group of species may not be suitable for another species (Minor and Lookingbill 2010). Hence, explanatory factors for wildlife road-kills may vary widely between species and groups.

In this study, we evaluate the connectivity of forest networks in and around protected areas of South Korea. Then, we assess scale-dependent relationships between habitat connectivity and roadkills of forest mammals with different dispersal abilities, associated with body size, as well as effects of road-related features on roadkills. Our general hypothesis is that roadkills are more likely to occur on roads in well-connected landscapes.

Data and methods

Study area and spatial data

The study area is the southern part of the Korean Peninsula (Fig. 1), which lies between latitudes 33° and 39°N, and longitudes 124° and 131°E, and covers 96,390 km^2 (MLTM 2012). The road density in South Korea was 1.05 km/km^2 in 2009 (World Bank 2010).

Spatial data and information about the forest areas in South Korea were obtained from the 2009 national land-cover map at 30 m resolution, produced by the Korean Ministry of Environment. We performed manual editing to correct the misclassification of forest patches based on visual comparison with the 2012 high resolution aerial image provided by Daum Kakao Corp. Forest habitat patches were defined as contiguous cells using an eight-neighbor rule. The minimum size of habitat patches was an area of 1 ha, which is a rough estimate of home range size for small mammals (Wolton and Flowerdew 1985). Small patches meeting this minimum size may also act as stepping stones between larger patches for mobile mammals in fragmented landscapes. The National Transport Information Center provided the 2012 road network in vector format at a scale of 1:5000.

Roadkill data and focal species

We collected data on the distribution and abundance of road-killed forest mammals on 18 roads between 1.2 and 20.0 km in length from National Institute of Biological Resources (NIBR 2012) (Fig. 1). These surveys were periodically (at least once a week) conducted at

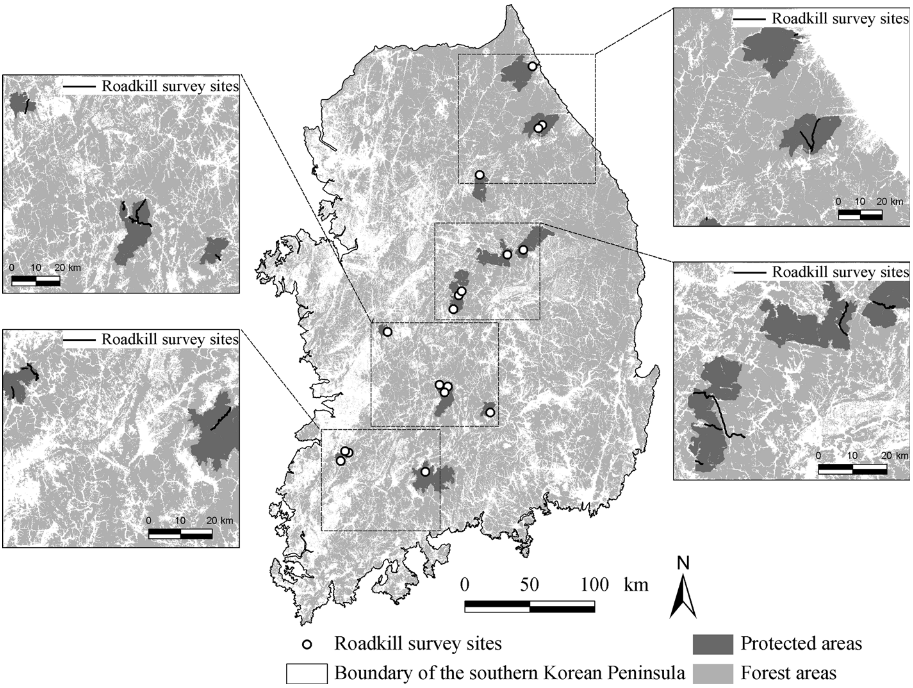

Fig. 1 The surveyed road sites (n = 18) (KNPS 2009), adjacent protected areas, and forest areas

the fixed road intervals every year from 2006 to 2012 by national park managers. All roads were paved two-lane roads, with a speed limit of 60 km/h or lower, that run through national parks.

We chose 18 focal species that had at least one individual case of roadkill at the survey sites (Table 1). Species were classified into three groups based on dispersal ability and home range size, averaged across sexes, which we obtained from published literature (Table 1; Fig. 2). The three groups approximately corresponded to small-, intermediate-, and large-bodied species. We referred these groups as small mammals, intermediate mammals, and large mammals in the present study. For analysis purposes, except large mammals, we calculated the average number of road-killed individuals of each group per year on each survey road site as dependent variables. In case of large mammals, because the number of the observed roadkills of large mammals during the seven years was too low (an average of 0.2 individuals ± 0.3 SD per road per year), we used the total number of road-killed individuals.

Measuring connectivity and road-related features

We employed a graph theoretical approach for measuring network connectivity as an independent variable (Kang et al. 2012; Koh et al. 2013; Urban and Keitt 2001). Graph theory allows broad applications in a wide range of disciplines including mathematics, social science, computer science, and landscape ecology (Hayes 2000a, b). In the methodological approach, a graph is a set of nodes (i.e. discrete habitat patches) connected by links (i.e. movement of organisms) (Minor and Urban 2008).

We calculated the edge-to-edge Euclidean distance between patches using the Graphab 1.0 (Foltête et al. 2012). The level of inter-patch connectivity was then quantified as *area-weighted flux* (AWF) (i.e. amount of dispersal or movements) (Laita et al. 2011; Minor and Urban 2007), at 12 threshold distances (0.1, 0.2, 0.3, 0.5, 1, 1.5, 3, 5, 7, 10, 15, and 25 km) to encompass a broad range of species dispersal abilities. Flux from a donor patch i to a recipient patch j is calculated as the dispersal probability between two patches (P_{ij}) multiplied by the area size (a_i) of the donor patch ($\mathrm{Flux}_{ij} = a_i \times P_{ij}$). Probability ($P_{ij}$) expresses the probabilities that an individual in the donor patch will disperse to the recipient patch. It can be approximated as negative exponential decay:

$$P_{ij} = e^{-kd_{ij}}$$

where k is a constant and d_{ij} is the distance between the patches. A dispersal probability of 0.05 corresponded to the threshold distance (i.e. separation distance beyond which a pair of patches have no link). Here, we simplified AWF by averaging the two directions, yielding an area-weighted flux (w_{ij}) for each pair of nodes. High flux between patches indicates a large number of dispersal events. Thus, a road that intersects a pair of patches with high flux between them may have a high probability of roadkill. We regarded all forest patches that were separated by highways with impassable concrete barriers, or rivers wider than 100 m, as disconnected.

For each road with associated road-kill data, we measured four variables that might affect mortality: (1) the connectivity (i.e. amount of flux) of links that intersected each road site; (2) road length; (3) slope; and (4) traffic volume. The average slope of each road site was derived from a 30 m digital elevation model (DEM). We obtained traffic volumes (i.e. vehicle counts) from the 2011 annual average daily traffic map of the Traffic Monitoring System (http://www.road.re.kr).

Table 1 Forest mammal species included in the study, and the number of road-killed mammals on 18 roads (a total distance of 140.4 km) from 2006 to 2012

Common name	Scientific name	No. of roadkill obs.	Home range size (km^2)	Dispersal distance (km)	Mammal group	References
Hedgehog	*Erinaceus amurensis*	13	0.060	0.23	Small	Morris (1988), Saether (1999)
Korean wood mouse	*Apodemus peninsulae*	15	0.002	0.10	Small	Ko et al. (2011)
Lesser Japanese mole	*Talpa wogura*	19	0.003	0.20	Small	Loy et al. (1992)
Red-backed vole	*Clethrionomys rufocanus*	14	0.001	0.10	Small	Lee (2011)
Siberian chipmunk	*Tamias sibiricus*	669	0.008	0.20	Small	Ko et al. (2011), Marmet et al. (2009)
Striped field mouse	*Apodemus agrarius*	3	0.006	0.10	Small	Lee (2011)
Ussuri white-toothed shrew	*Crocidura lasiura*	8	0.001	0.26	Small	Fontanillas et al. (2004), Long (2003)
Least weasel	*Mustela nivalis*	1	0.085	1.08	Intermediate	Chappell et al. (2013), Sheffield and King (1994)
Korean hare	*Lepus coreanus*	44	0.210	1.62	Intermediate	Bray et al. (2007), Ruhe and Hohmann (2004)
Raccoon dog	*Nyctereutes procyonoides*	80	0.690	2.40	Intermediate	Kim et al. (2008), Woo (2010)
Red squirrel	*Sciurus vulgaris*	76	0.075	1.01	Intermediate	Bryce et al. (2005), Wauters et al. (2010)
Siberian flying squirrel	*Pteromys volans*	1	0.340	2.15	Intermediate	Hanski et al. (2000)
Siberian weasel	*Mustela sibirica*	48	0.150	1.80	Intermediate	Nowak (1999), Sasaki and Ono (1994)
Water deer	*Hydropotes inermis*	51	0.320	0.78	Intermediate	Kim (2011)
Asian badger	*Meles leucurus*	5	1.240	15.00	Large	More and Good (2006), NIER (2009), Pope et al. (2006)
Leopard cat	*Prionailurus bengalensis*	17	3.165	12.00	Large	Choi et al. (2012)
Roe deer	*Capreolus pygargus*	5	0.900	10.00	Large	Danilkin (1995), Mysterud (1999)
Wild boar	*Sus scrofa*	1	3.900	10.60	Large	Boitani et al. (1994), Truvé et al. (2004)

Species were assigned to different mammal groups based on their mean home range and dispersal distance, estimated from or reported in published papers

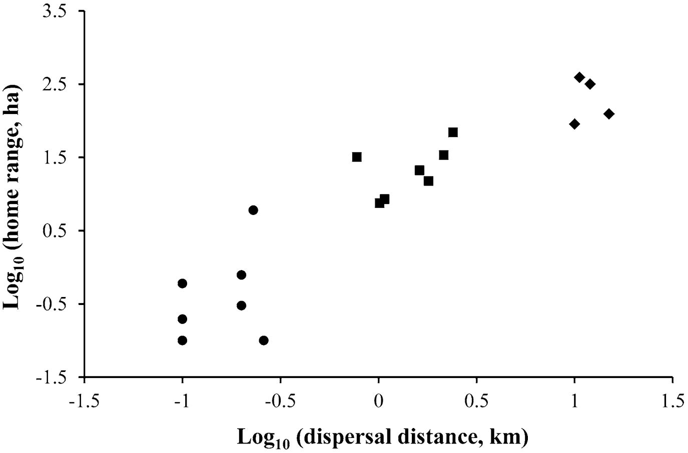

Fig. 2 Relationship between dispersal distance and home range size of mammals (small, intermediate, and large mammal groups are represented by *circles*, *squares*, and *diamonds*, respectively. These groups were used to evaluate the abundance of road-killed forest mammals using the connectivity of forest habitat and road characteristics)

Data analyses

We used generalized linear models (GLMs), using a log link function assuming a Poisson distribution, to explore the influence of connectivity (i.e. flux measures) and road characteristics on each mammal group. Some models for the large mammal group were fitted with a negative binomial distribution and a logarithmic link function to explain over-dispersion in the observed data. We implemented the Poisson and negative binomial models using the package stats (Chambers and Hastie 1992) and MASS (Venables and Ripley 2002), respectively, in R (3.1.0) (R Core Team 2015).

We generated models with all possible combinations of predictors for each mammal group. Models were ranked according to their Akaike's Information Criteria corrected for small sample size (AICc) and to the relative model likelihood value (*w*AICc) (Burnham and Anderson 2002), using the MuMIn package in R (Barton 2011). At each of the scales at which connectivity was measured, we presented the AICc value of the best model, and examined the significance of the connectivity variable if it was included in the model. In addition, across all spatial scales, we presented the most parsimonious models with ΔAICc < 2. If the models had more than two independent variables, we performed hierarchical partitioning (Mac Nally 2002) to assess the relative importance of each independent variable using the hier.part package in R (Walsh and Mac Nally 2008). All independent factors were log-transformed ($\log[x + 1]$) so as to improve normality. Before executing GLMs, we checked multicollinearity between all predictor variables by performing Pearson's correlations. The results showed that no variables were highly correlated (i.e. $|r| < 0.7$).

Results

A total of 1070 individual kills (ca. 1.09 kills per km of road per year) consisting of 18 species of forest mammals were recorded (Table 1). The result showed more roadkills for small ($n = 741$, 69.3 %) and intermediate ($n = 301$, 28.1 %) mammals than large

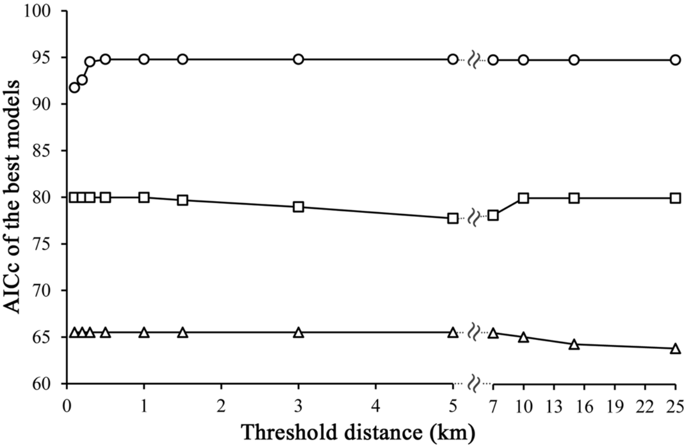

Fig. 3 A graph of AICc of the best models at each of the scales at which road-crossing habitat connectivity was measured, from 0.1 to 25 km. Scale dependent responses of roadkill abundance of small (*circles*), intermediate (*squares*), and large (*triangles*) mammal groups to the connectivity and road-related variables

($n = 28$, 2.6 %) mammals. Siberian chipmunk ($n = 669$) was the most common roadkill among the small mammals, the raccoon dogs was most common among the intermediate mammals ($n = 80$), and the leopard cat was most common among the large mammals ($n = 17$).

At threshold distances of 0.1, 0.2, and 0.3 km, the non-zero coefficients of connectivity in the models for abundance of road-killed small mammals were significant ($p < 0.05$), and the lowest AICc appeared at 0.1 km (Fig. 3). Across all threshold distances, we obtained the best model for small mammal group relating roadkill abundance to the connectivity measured at a 0.1 km scale, road length, and slope (Table 2). As determined by hierarchical partitioning, road length had the highest explanatory power (positively correlated) for the small mammal group, followed by connectivity (positively correlated) and slope (negatively correlated) (Table 2).

For intermediate mammals, the non-zero coefficients of connectivity in the models were significant at threshold distances of 5 and 7 km ($p < 0.05$), with the lowest AICc value at 5 km (Fig. 3). Like the small mammal group, the factors used in the best model were the connectivity measured at a 5 km scale (positively correlated), road length (positively correlated), and slope (negatively correlated) (Table 2). The relative importance of the three variables was nearly identical to that of the small mammal group (Table 2).

For large mammals, the non-zero coefficients of connectivity in the models were significant at threshold distances of 10, 15, and 25 km ($p < 0.05$), and the lowest AICc appeared at 25 km (Fig. 3). In contrast to the best models of roadkill abundance for small and intermediate mammal groups, connectivity was the only significant positive predictor in the best model for the large mammal group. The relative importance of connectivity variables was more than two times higher for the large mammal group than for the small and intermediate mammal groups (Table 2). Traffic volume was not included in the best models for roadkill abundance of any mammal group.

Table 2 Summary of model selection statistics for predicting the abundance of road-killed small, intermediate, and large mammals using connectivity, road length, slope, and traffic volume, showing the most parsimonious models (ΔAICc < 2) with a Poisson error distribution

Response	Model	AICc	ΔAICc	*w*AICc	Adj. r^2	Hierarchical partitioning (%)
Small mammals	Connectivity 0.1 km + length − slope	91.75	0.00	0.60	0.99	Connectivity = 30, length = 58, slope = 12
	Connectivity 0.2 km + length − slope	92.58	0.83	0.40	0.99	Connectivity = 25, length = 63, slope = 12
Intermediate mammals	Connectivity 5 km + length − slope	77.73	0.00	0.37	0.66	Connectivity = 31, length = 56, slope = 13
	Connectivity 7 km + length − slope	78.13	0.40	0.30	0.65	connectivity = 33, length = 55, slope = 12
	Connectivity 3 km + length − slope	78.95	1.22	0.20	0.64	Connectivity = 28, length = 59, slope = 13
	Connectivity 1.5 km + length − slope	79.68	1.95	0.14	0.62	Connectivity = 26, length = 61, slope = 13
Large mammals	Connectivity 25 km	63.85	0.00	0.21	0.49	
	Connectivity 25 km + length	64.09	0.24	0.19	0.56	Connectivity = 62, length = 38
	Connectivity 15 km	64.30	0.45	0.17	0.48	
	Connectivity 15 km + length	64.90	1.05	0.13	0.54	Connectivity = 58, length = 42
	Connectivity 10 km	65.07	1.22	0.12	0.45	
	Length[a]	65.51	1.66	0.09	0.19	
	Connectivity 10 km + length	65.56	1.71	0.09	0.52	Connectivity = 46, length = 54

The connectivity variables refer to road-crossing habitat connectivity quantified as area-weighted dispersal flux at different threshold distances (0.1, 0.2, 1.5, 3, 5, 7, 10, 15, and 25 km)

Adj. r^2 indicates the Nagelkerke's adjusted r^2 (Nagelkerke 1991)

[a] A negative binomial regression model was used to account for over-dispersion in the observed data

Discussion

The purpose of this study was to use the forest mammalian roadkill survey data to investigate how roadkill abundance is influenced by road-crossing habitat connectivity and road characteristics. Because species have different dispersal abilities, we explored three different groups of road-killed forest mammals, including small, intermediate, and large ones. Our results showed that, in all three cases, the effect of the habitat connectivity on roadkill abundance was scale-dependent. Also, the number of roadkills increased with the increase of the connectivity levels, showing roadkills occur mainly on roads that intersect movement routes with high connectivity. Therefore, the finding with regard to scale-dependency highlights the importance of maintaining movement and connectivity across roads at multiple scales to reduce forest mammal roadkills.

Our results showed that roadkills occur mainly on the roads intersecting the areas with high rates of inter-patch connectivity. Moreover, the level of connectivity was related to roadkill abundance in a scale-dependent way. The spatial scale of the best connectivity measure for small (0.1–0.3 km), intermediate (5–7 km), and large mammals (10–25 km) reflects the species' potential dispersal ability (Table 1). This provides an indication of the scale level for each mammal group at which connectivity conservation objectives should be set in roads through protected areas. This finding also highlights the importance of maintaining the inter-patch connectivity across roads (i.e., improving the permeability of roads) at multiple scales. A single focal species (typically a large carnivore presumed as an umbrella species) approach may not be appropriate for designing and managing multi-species networks of protected forest areas (Minor and Lookingbill 2010). Some studies also reported that optimized movements of large carnivores do not necessarily represent those of other species across a landscape (e.g. Beier et al. 2009). The present study provides further evidence that the level of connectivity for large mammals is not associated with the abundance of road-killed small mammals, implying that smaller mammals' movements may not be predicted by the level of connectivity for large mammals. Again, the movement of large mammals is feasible among protected forest areas, but it is difficult to expect the same function of the protected forest areas for small mammals. The distance between large protected forest areas is not closely connected with one another for small mammals nor do they necessarily have smaller reserves between the larger areas, which can function as stepping stones that facilitate the movement and dispersal of species. Overall, it can be concluded that separate connectivity measurements of specific groups of species, rather than a focal species, are necessary for protected areas including multi-species networks (Minor and Lookingbill 2010).

Roadkill abundances of small and intermediate mammals were a function of small-and medium-scale variation in the habitat connectivity, respectively, while roadkill abundance for large mammals was a function of large-scale variation (Fig. 3). In this regard, the hierarchical partitioning analysis identified the relative importance of habitat connectivity and road-related features and highlighted that the relative importance varied with species group based on their dispersal potential. This shows that the connectivity explained a large part of the variance over 50 % for large mammals but a medium part of the variance (i.e. about 30 %) for small and intermediate mammals. This means that the degree to which habitat connectivity is disrupted by roads is relatively more important for large mammals than for small and intermediate mammals, perhaps because of their high vagility (Sutherland et al. 2000) and low habitat specificity (Ziv 2000), resulting in a high frequency of road crossings (Forman et al. 2003).

While connectivity was an influential variable for all mammal groups, road slope was also negatively related to the vehicle collisions of small and intermediate mammals. Flat roads, especially in protected areas, are likely to promote increased speed and careless driving among motorists, increasing the likelihood of wildlife-vehicle collisions (de Carvalho et al. 2014).

Although traffic volume has been identified as the most influential variable for mammalian roadkills in several studies (e.g., Inbar and Mayer 1999; Joyce and Mahoney 2001; Trombulak and Frissell 2000), it was not an important factor in the present research. This is probably because the traffic volume is usually low at night around the national parks, and most investigated roads were small with comparatively low traffic volumes.

Among the small mammals, Siberian chipmunks were most commonly killed, followed by red squirrels. This may be because these small rodents are diurnal species that cross roads during the daytime when there are relatively high traffic volumes and speeds (Haikonen and Summala 2001). Among the intermediate mammals, raccoon dog was the most common road-killed animal. This may be associated with their relatively long-distance movement and tendency to use linear features such as roads and gutters if available (Saeki et al. 2007). The most common large mammal roadkill was the leopard cat, which has been listed as an endangered species by the Ministry of Environment of Korea since 2005. Leopard cats prefer lowland forest edges and surrounding open grasslands near rivers, which provide a great variety of microhabitats and a high diversity and abundance of prey (Choi et al. 2012; Watanabe et al. 2003). However, their habitat preferences, large home ranges, and long-distance movements may often make them wander onto roadways and become roadkill. Because of their small population sizes, road mortality is an immediate threat to the long-term survival of the species (Izawa et al. 2009).

Little is known about the effectiveness of roadkill mitigation structures, and uses of wildlife crossing structures do not necessarily equate to their effectiveness (van der Grift et al. 2015). We also acknowledge that results from the connectivity study alone are not enough to provide specific recommendations for species with high roadkill rates. To give specific recommendations for each species further research needs to be done to directly examine the effectiveness of roadkill mitigation measures. For example, van der Grift et al. (2013) has introduced a process for setting up a monitoring plan for assessing the effectiveness of wildlife crossing structures.

The roadkill data used in this study was based on the official animal carcass count survey, which has been continuously conducted by the Korea national park service. Some studies have suggested issues regarding animal carcass count surveys. For example, the time of carcass persistence, which is defined as the time each road-killed animal remains on the road, can induce bias in road mortality estimates (e.g., Santos et al. 2011). Large animals are assumed to have longer carcass persistence than small ones. This indicates that the frequency of a roadkill survey contributes to the reliability of carcass reports (Santos et al. 2011). As a caveat, the count survey used in the study was conducted at least once a week from a car driving at low speed. Some studies recommend alternative methods, such as a count survey by foot on a daily basis despite the difficulty of time and manpower (e.g., Enge and Wood 2002; Santos et al. 2011; Slater 2002).

Roads are indeed barriers for many specialized forest species as well as others that are attracted to the roads (Fahrig and Rytwinski 2009; Forman and Alexander 1998). It is evident from this study that roads passing through areas with high existing or potential habitat connectivity have the highest roadkill frequency. Roadkill monitoring may identify such areas, but an easier approach may be to use connectivity modeling. By establishing the relationship between roadkill patterns and connectivity at multiple scales and then by identifying areas of high roadkill risk, plausible recommendations for roadkill mitigation can be made as follows: (1) to construct fences on roads and wildlife crossing structures based on species- or group-specific preferences, such as overpasses and underpasses, (2) to notify vehicle drivers with wildlife warning signs to draw attention in high-occurrence zones, and (3) to use speed limit signs, speed bumps, or speed traps to reduce vehicle speeds.

Because the occurrence of roadkills may spatially and temporally differ depending on local environmental conditions and landscape context, more detailed research is necessary to verify the relationship between roadkill levels and connectivity. Further research is also required to identify high-risk road sections and select suitable locations for multispecies crossing structures. The rapid development of roads and subsequent continuous decrease in connectivity will be a consistent major threat to long-term survival of mammal populations.

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