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Spatio-temporal characteristics and predictions of the endangered leopard cat *Prionailirus bengalensis euptilura* road-kills in the Republic of Korea

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Abstract

Road-kills negatively impact wildlife populations, especially those that are threatened or small in size. The increase of linear structures such as roads or railways causes road-kills. Understanding and knowing where and when road-kill probability is high is important to prevent collisions. The leopard cat (*Prionailurus bengalensis euptilrura*) is listed on CITES Appendix Ⅱ and is considered as endangered in the Republic of Korea. We used 141 *P. b. euptilura* road-kill events occurring from 2006 to 2012 in the Republic of Korea with the same number of randomly generated points for spatial analyses. Further, 239 events were used for temporal analyses. Spatial analyses and graph modeling were conducted using geographic information system (GIS) and Graphab software. In landscape analyses, *P. b. euptilura* road-kills were concentrated around agricultural lands and forest, and less frequent near developed areas. The result of the traffic patterns analyses showed that traffic volume, the number of lanes, and distance from ramps were significantly different between the road-kill points and the random points. The road-kill frequency was significantly different by season, and there were two peaks in winter and fall reflecting the seasonal behavior of *P. b. euptilura*. Among the 14 candidate models, the best model with the lowest Akaike's Information Criterion (AIC) included five factors: traffic volume, distance from ramps, elevation, patch connectivity index, and distance from water. This study shows that *P. b. euptilura* road-kills are not randomly distributed, but rather are related to adjacent landscape, traffic patterns, and season. This study can contribute to minimizing future collisions and lead to conservation of the endangered populations through application to road-kill management policy.

Keywords: conservation, endangered species, *prionailurus bengalensis euptilura*, prediction modeling, road-kills, management policy.

Introduction

The extension of linear structures such as railroads and highways has resulted in habitat fragmentation and an increase in road-kills (Coulon, 2004; Coffin, 2007; Borda-de-Aqua, 2011; Clements et al., 2014) what is one of the most principal factors leading to population decline (Coffin, 2007, Jackson & Farhig, 2011).

In addition to species behavior and ecology (Forman et al., 2003), three other factors are important for road-kills: landscape, traffic and seasons. Road-kill locations and rates are influenced by landscape characteristics because wildlife is linked to specific habitats and land use types (Forman & Alexander, 1998; Clevenger et al., 2003). For example, road-kills of neotropical birds in Brazil were concentrated in rice fields and wetlands because these areas have high food availability and provide shelters (da Rosa & Badger, 2012). Habitat connectivity, defined as the functional response of wildlife movement to habitat patches and links between the patches (Taylor et al., 2006), best predicts the risk of road-kill among various predictive models for roe deer road-kills in France (Girardet et al., 2015). Moreover, habitat connectivity significantly influenced the road-kill frequency at different scales of dispersal ability in 18 forest mammal species (Kang et al., 2016) in the Republic of Korea. Other studies have implicated traffic related factors as correlates to mammal road-kills. Gunther et al. (1998) examined 939 road-kill of large mammals and concluded that speed of vehicles was the primary factor contributing road-kills. Also, in USA, deer road-kills increased with high traffic intensity (Hussain et al., 2007), whereas vertebrate road-kill hotspots had low traffic volume in the Republic of Korea (Seo et al., 2015). In addition, seasonal variation of animal behaviors according to ecological characteristics might be related to road-kill frequency across seasons (Main & Allen 2002). For instance, in South Africa, the number of serval road-kills was higher in dry season than wet season they enlarge home ranges when water is scarce (Williams *et al.*, 2019). Moreover, road-kill of raccoons peaked in fall which in line with their dispersal season (Conard & Gipson, 2006).

The effect of these factors to road-kills can be different by species and taxa (Forman et al., 2003) due to diversity of ecological patterns of each of them. Thus, it is crucial to examine factors which might influence road-kills for each species to reduce collisions, and consequently, to improve present road management policy for future biodiversity conservation. Our research takes an interest in an endangered species, the leopard cat (*Prionailurus bengalensis euptilura*). Historically, the Republic of Korea harbored three species of the Felidae family. However, *P. b. euptilrura* is the only remaining species. The populations have declined over the years due to anthropogenic disturbances, resulting in their 1988 “endangered” classification by the Ministry of Environment in the Republic of Korea and their listing on CITES Appendix II. *Prionailurus bengalensis euptilrura* is known as a habitat generalist inhabiting agricultural lands and forests (Choi et al., 2012). Their major diet is composed of rodents (Grassman, 2000; Rajaratnam et al., 2007) and their average home range size in the Republic of Korea is known as 3.69 ± 1.34 km^2 (Choi et al., 2012). They are seasonal in their behaviors; males enlarge their home range size during the mating season, which is winter to early spring in temperate areas (Maekawa, 1998; Ueno, 2004), to increase the possibility of finding mates (Izawa et al., 2009). Six or seven months after birth, juveniles start to disperse to find their own territories (Murayama, 2008).

Several studies showed that road-kill is one of the main reasons explaining the decline of *P. b. euptilura* in the Republic of Korea. A study on road-kills of mammals conducted on 119 km of roads found 103 killed *P. b. euptilura* between July 2004 and December 2006 (Choi, 2007). In addition, in four studies of 16 captured and released *P. b. euptilura* with GPS collars, 31.3 % of them died because of road-kills (Choi, 2007; Choi & Park, 2009; Park et al., 2012; Lee, 2017). Further, a study examining 78 individuals revealed that the recurrent “bottleneck effects”, defined as a drastic reduction in the size of a population, of *P. b. euptilura* populations resulted in significantly low genetic diversity compared to other endangered felid populations around the world and also pointed out that the local extinction risk of *P. b. euptilura* is substantial in the Republic of Korea (Ko et al., 2018).

Despite the important role of *P. b. euptilura* within their ecosystems, this species has only received minimal attention to reduce road-kills. Targeting the locations where *P. b. euptilura* road-kills are most likely to occur could be useful to set-up conservation actions in the Republic of Korea.

Prediction modeling on wildlife road-kills has already been conducted using various techniques (Seiler, 2005; Danks & Porter, 2010; Kang et al., 2016). However, they have focused on creating or improving models to predict road-kills, which have limited direct applications to management policy. The aim of this study is to understand spatio-temporal characteristics of *P. b. euptilura* road-kills, to predict locations with high road-kill probability, and to suggest a visualized road-kill prediction map to improve present road management policy for conservation of *P. b euptilura*.

Materials and Methods

Study area and data collection

There are 38 major highways in the Republic of Korea, approximately 4,717 km in total length. Although the proportion of the highways is about 4 % of the total roads in the Republic of Korea (Statistics Korea, 2017), they play an important role typically connecting major cities. Furthermore, highway have distinctive features compared to other types of road. The mean traffic volume in highways was 54,016 vehicles/day, whereas other roads, such as local roads, were 11,326 vehicles/day (calculated from data in Statistics Korea, 2017). Speed limit on highways is also higher than other roads. According to the Road Traffic Act 19, speed limit for highway is 100 to 120 km/h, whereas 60 to 90 km/h in other roads. Among the whole section of the highways, four lanes sections are predominant (3,567.5 km, e.g. 75 % of the network), followed by six lanes (608.5 km, e.g. 13 % of the network), eight lanes (494.8 km, e.g. 10 % of the network), and above ten lanes (44.4 km, e.g. 1 % of the network). The two lanes sections, which are the narrowest, are minor compared to the other ones, representing 2.2 km, occupying only 0.05 % of the total network (Statistics Korea, 2017).

The *P. b. euptilura* road-kill data originated from the Korea Expressway Corporation (http://www.ex.co.kr). Workers of the Korea Expressway Corporation check the road conditions of all major highways every day. They typically drive 80 km/h and report any irregularity including road-kills. A total of 255 *P. b. euptilura* road-kills were reported on 22 highways from February 2004 to February 2017 by the Korea Expressway Corporation. Observation date and location were included in every road-kill event. Out of 255 events, outliers involving overlapping road-kill events occurring in a single day were removed, resulting in 239 data points. Unlike we used all of 239 road-kills occurred from 2004 to 2017 for temporal analysis (seasonal pattern), we limited data occurred between 2006 and 2012 for spatial analyses (landscape characteristics and traffic patterns). This reduction was necessary because using too old or too recent data compared to the certain year of land cover map may cause problem while spatial analyses, as land covers change with time. Also, among the dataset from 2006 to 2012, some data were excluded due to difficulty of identifying exact locations, such as in tunnels. Consequently, 141 road-kill points were included in the spatial analyses.

Spatial data were obtained from the 2009 national land cover map with 30-m resolution provided by the Ministry of Environment (http://www.egis.me.go.kr). Land cover types were divided into seven categories: built-up area, agricultural land, forest, grassland, wetland, bare land, and water. Topographic data were derived from Digital Elevation Model (DEM) provided by USGS (2009) with 30-m resolution. Road data were obtained through Openstreetmap (2017). Data for annual average daily traffic and the number of lanes were obtained from the Traffic Monitoring System (http://www.road.re.kr) produced by the Ministry of Land, Infrastructure and Transport of Korea.

Landscape characteristics

To examine landscape characteristics of road-kills, variables were categorized into land cover types, topography, habitat suitability, and habitat connectivity (Table 1). For better understanding and comparisons with road-kill locations, we randomly generated points with the same number of road-kill points using Create Random Points tool provided by ArcMap (ver. 10.5; Redlands, California, USA). A randomly generated absence point was located at least 1 km away from a collision point (Fig. 1). This distance indeed corresponds to the daily movement of leopard cats (Rabinowitz, 1990; Grassman, 2000). This distance avoided overlaps with our road-kill presence points.

For land cover type analyses, we used two approaches: distance-based analysis (DA) and compositional analysis (CA). Conner et al. (2003) qualitatively compared the two methods and concluded that the DA approach could be more applicable to habitat analyses with Euclidean distance and randomly generated control sites, and less restrictive than the CA metric. However, the CA approach is one of the most widely used metrics for studies related to habitat analyses (Aebischer et al., 1993). Thus, in this study, both metrics were calculated for analyses of land cover covariates. We measured the Euclidean distance from each point to the seven land cover types. Then, a square-shaped buffer of 1-km^2 was generated for each point, and the proportion of each land cover type inside the buffer was computed. Lee and Song (2008) compared various types and sizes of buffers to evaluate habitat quality of the *P. b. euptilura* and showed that 1-km^2 square buffer is the most effective. For the topographical features, we used ArcMap 10.5 to derive elevation, slope, and aspects from the Digital Elevation Model (USGS) for each *P. b. euptilura* road-kill and random points.

Factors important for habitat suitability are different depending on species. Four factors including elevation, land cover type, distance from roads, and distance from water were used with the habitat suitability index model derived by Lee et al. (2012) to generate a habitat suitability map of *P. b. euptilura* in the Republic of Korea (Fig. 2). Then, we extracted the averaged habitat suitability index in the 1-km^2 buffer for each point.

We used a graph-based landscape modelling approach to quantify landscape connectivity (Galpern et al., 2011). A graph is composed of patches and links, representing respectively suitable habitats and species displacement (i.e., daily movement or dispersal distance of juveniles). In ecology, this approach can be applied to quantify the contribution of patches and link to connectivity, i.e. to measure the relative importance of each landscape feature for an area connectivity (Serret et al., 2014; Minor & Urban, 2008). The set of patches was developed using the habitat suitability map (Fig. 2). In this map, the habitat suitability index was scored from 0 to 10 and categorized into five categories hierarchically with the same interval. We considered the two highest categories as “habitat patches”. Links between patches were generated using the least-cost path geometry, which represent the displacement resistance from a patch to another according to the landscape features. We used Graphab 2.2.1 (Foltête et al., 2012) to generate the graph and calculate habitat connectivity metrics of each patch and link. The minimum patch area was set as 1 ha with a 12-km threshold distance as described by Kang et al. (2016). Then, the Flux (Urban & Keitt, 2001) metric was applied to measure habitat connectivity of patches, and Betweenness Centrality (BC) (Foltête et al., 2012) to quantify habitat connectivity of links between pairs of patches. The Flux (F) sums the capacities of non-focal patches and is weighted according to their minimum distance to the focal patch *i* through the graph. It is an indicator of the potential dispersion from the focal patch or to the focal patch.

The F of patch *i* is given by:

$$F_i = \sum a_j \, e^{-ad_{ij}} \qquad j \neq i$$

Where $e^{-ad_{ij}}$ is the probability of movement between patches *i* and *j*.

BC sums the shortest path to a focal patch given all possible paths in the graph. The index is weighted by the capacities and their interaction probability P_{jk} of the two connected patches *j* and *k*.

The BC of a link *i* is given by:

$$BC_i = \sum j \sum k \; a_j a_k P_{jk} \qquad j, k \in \{1..n\}, k < j, i \in L_{jk}$$

Where L_{jk} is the set of links crossing by the least-cost path between pair of connected patches *j* and *k*.

After computation of habitat connectivity for both patches and links, we generated an index *I* by dividing by Euclidean distance to the patch or link from each point to take into account of distance as well.

The *I* of both patches and links is given by:

$$I = \frac{Connectivity\ value\ of\ the\ closest\ link\ or\ patch}{Distance\ from\ the\ closest\ link\ or\ patch}$$

After these measurements were calculated, variables were compared using RStudio v. 1.1.383 (RStudio team, 2017) and SPSS (SPSS Inc., 2016) at each pair of road-kill and random points.

Traffic patterns

Traffic-related variables are among the most influencing factors for occurrence of road kills in previous studies (Gunther et al., 1998; Hussain et al., 2007). We collected data for annual average daily traffic volume (vehicles/day), number of lanes, and distance from ramps (Table 1). Distance from ramps has not been considered commonly in other studies; however, ramps make changes of vehicular movement rapidly to overall condition of the roads in terms of traffic volume, road width, and speed.

Seasonal pattern

We investigated the pattern of *P. b. euptilura* road-kills across seasons. Season was categorized into spring (Mar – May), summer (Jun – Aug), autumn (Sep – Nov), and winter (Dec – Feb) based on average monthly temperature (Korea Meteorological Administration; http://www.kma.go.kr/). Then, the number of *P. b. euptilura* road-kill events for each season was compared using ANOVA.

Prediction modeling and mapping

To identify a best fit model predicting *P. b. euptilura* road-kill risk, we performed logistic regression using a stepwise approach (Hosmer and Lemeshow, 1989) with landscape and traffic variables. To meet the linearity assumption of logistic regression, covariates for distance analysis of the landscape characteristics were transformed into log(10) and the compositional data were transformed into square-root format as the range of most the data was between 0 to 20 percentages (Ahrens et al., 1990). Before modeling, we tested multicollinearity using spearman's rho and VIF (Variance Inflation Factor). Covariates which closely correlated ($r > |0.75|$ and $VIF > 10$) were targeted and one of the correlated variables in each pair of covariates which minimized the Akaike's Information Criteria (AIC) were included in the final covariate list for the modeling. Then candidate models were compared by AIC and weights (w_i) to determine the best predictive model. Model fit was tested using area under the curve (AUC) and McFadden's pseudo R^2.

Based on the model generated, a *P. b. euptilura* road-kill prediction map was created to show the result more effectively and thus to be applied to highway management conveniently. The formula to predict the probability of presence of the *P. b. euptilura* road-kills (P) using logistic regression is given by:

$$P = \frac{e^{(\alpha+\beta_1 X_1+\cdots+\beta_n X_n)}}{1+e^{(\alpha+\beta_1 X_1+\cdots+\beta_n X_n)}}$$

Where α and β represent intercept of the model and estimates of each parameter X respectively. The predicted probability of *P. b. euptilura* road-kills for each highway was computed and visualized using Raster Calculator in ArcMap 10.5.

Results

Landscape characteristics

Of the 20 variables for landscape characteristics, only three were significantly different between the road-kill and random points (Table 2): distance from agricultural lands (P = 0.018) and forest (P = 0.006) to the points, and proportion of built-up areas in buffers (P = 0.013). Mean distance from agricultural lands and forest to the road-kills were approximately 1.7 and 1.5 time closer to road-kill points than the random points (Fig. 3-A,B). Proportion of built-up areas was 2.3 times lower in the road-kill compared to the random points (Fig. 3-C). There were no significant variables which distinguished the road-kills from random points in topographic features, habitat suitability and habitat connectivity. The results showed that the locations of *P. b. euptilura* road-kills are related to distance to their habitats and proportion of the area with high human disturbance.

Traffic patterns

All three variables tested for traffic pattern analyses were significantly different between the road-kill and the random points (Table 3). Traffic volume was significantly different between road-kills and random points (P < 0.001) and averaged 2.7 times lower at the road-kill points than at random points (Fig.2-D). The frequency of road-kills peaked at 10,000 – 25,000 vehicles/day, and nearly 62% of the collisions were concentrated at this range. Distance from ramps was more than 1.7 times further to the road-kill points compared to the random points (Fig. 2-E), and the difference was significant ($P < 0.001$). In general, 92.2% of road-kills were occurred on four- lanes highways, whereas only 67.4% of random points were found on the same road width. Four-lane roads are representing 75 % of the highway network, what make the road-kill occurrences on this types of roads higher than expected. Moreover, no road-kill points were found on roads with eight lanes or more (Fig. 2-F). The number of lanes was lower at the road-kill points than at the random points ($\chi^2 = 50$, df = 4, $P < 0.001$) indicating that the roads with *P. b. euptilura* road-kills were narrower.

Seasonal pattern

Overall seasonal pattern showed that the *P. b. euptilura* road-kill frequency increased from fall to winter and decreased from winter to spring. The number of road-kills was significantly different across seasons ($F_{3,151} = 6.02$, $P = 0.001$; $n = 239$). The result of post-hoc comparisons showed the mean of road-kill frequency in summer (Mean = 0.68, SD = 0.96) was significantly lower compared to other seasons.

Prediction modeling and mapping

Road-kill probability was determined through logistic regression modeling using a stepwise approach. Five variables (DB, DA, DBL, PA and PW) were removed before performing logistic regression due to high multicollinearity. Among 14 candidate models (see supporting information), the best model included traffic volume, patch connectivity index, distance from ramps, elevation, and distance from water (Table 4). Predicted probability of *P. b. euptilura* road-kills was negatively correlated with traffic volume, patch connectivity index, elevation, and distance from water. Among the parameters which negatively associated with the predicted probability, patch connectivity index can be defined by the combination of patch connectivity itself and the distance to patches from road-kill locations. Thus, we examined the patch connectivity and distance between patch and each point using independent *t*-test to identify the effect of each parameter on patch connectivity index. The result showed that the distance between patch and point was significantly lower ($p = 0.024$) in road-kill points compared to random points. However, patch connectivity was not significantly different between the road-kill and random points ($p = 0.837$). The only parameter that positively correlated with *P. b. euptilura* road-kills was distance from ramps. The best model was better supported than the full model (ΔAIC = 23.08). The final model exhibited high predictive power (AUC = 0.845) with excellent model fit (McFadden's Pseudo $R^2 = 0.308$; McFadden, 1977).

The *P. b. euptilura* road-kill prediction map was generated based on the best predictive model (Fig. 4). The range of the predicted probability showed values between 0 and 0.954. The mean of predicted probability of *P. b. euptilura* road-kills was 0.67, and 0.44 at the random points.

Discussion

Findings of this study confirm that *P. b. euptilura* road-kills are highly influenced by surrounding landscape, traffic, and seasonality. The results of landscape characteristics are consistent with other studies. Choi (2007) investigated 103 *P. b. euptilura* road-kills on various types of roads and showed that only a few road-kills were located around human residential areas. Thus, the risk of *P. b. euptilura* road-kills is high around their typical habitats. Moreover, *P. b. euptilura* are commonly considered an edge species (Azlan & Sharma, 2006; McCarthy et al., 2015), utilizing various environmental elements for foraging, resting, and sheltering sites. We suspect that this ecological pattern could increase the probability of road-kills while moving across habitats, and thus distance from habitats is important.

For traffic patterns, traffic volume was lower at road-kill points than random points. In a previous study, low traffic volume increased the risk of mammalian road-kills in various types of roads in Korea (Seo et al., 2015). In case of moose (*Alces alces*), the road-kill frequency peaked at low-intermediate traffic volume (Danks & Porter 2010). Road section with high traffic volume in high speed highways may present as a great hurdle and thus leopard cats would not attempt to cross. Compared to random points, *P. b. euptilura* road-kill points are likely to occur on narrow roads, especially on the four lanes. As described before, highways with two lanes are the narrowest, but the proportion of them is very low (below 0.05 % of the total length). Thus we conclude that the high proportion of collisions on four-lanes roads (92.2% of road-kills occurred on four-lanes roads, which occupies 75% of the highway network) compared to random points (67.4%) can be interpreted as a higher probability of leopard cat road-kills on narrow highways. This is in line with the study of Smith-Patten and Patten (2008), which showed that narrow roads have high risk of mammal road-kills due to higher connectivity compared to large roads. Among the parameters which negatively associated and narrow road width around road-kill locations may indicate relatively small scales of highways and regional characteristics such as rural or suburban areas. As shown in the landscape analyses, the proportion of developed areas was very low (Table 2) around *P. b. euptilura* road-kill locations. In a previous study, a large percentage of road-kills occurred on small scaled rural roads compared to urban roads, and an averaged percentage of road-kill rates in rural areas were up to 12 times higher than on the urban roads (Hughes et al., 1996). Thus, the results of this study concur with the general pattern of mammalian road-kills.

Highway ramps also played a role in predicting *P. b. euptilura* road-kills. Our findings suggest that *P. b. euptilura* road-kills tend to occur when ramps are farther away where conditions are relatively stable on highways. However, Byeon (2013) examined a 60-km section of the Jungbu highway, concluding that the road-kill frequency of *P. b. euptilura* within 500 meters of ramps was higher compared to other species. We assumed this difference in two studies may arise because of the scale of ramp areas and the analytical methods used between two studies. In the previous study, road-kill events 500-m before and after ramps were considered, whereas we measured and compared the distance from points to the closest ramp. Additionally, there are many uncontrolled factors affecting the existence of ramps. For instance, presence or absence of mitigation fences around ramps could be an important factor explaining road-kills (Clevenger et al., 2001). Thus, future studies are needed to investigate the effect of ramps more concretely.

The resulting seasonal pattern showed that *P. b. euptilura* road-kills are highly influenced by their seasonal behaviors. Road-kills of *P. b. euptilura* were most frequent in winter, which is the mating season of the *P. b. euptilura*. Males increase home ranges during the mating season (Maekawa, 1998; Ueno, 2004), to increase the possibility of finding mates (Izawa et al., 2009), likely to cross roads in fragmented habitats. It is predicted that road-kills were male-biased in our dataset. Unfortunately, this prediction could not be tested because the road-kills were not sexed at the time of retrieval in our study. The second peak of *P. b. euptilura* road-kills was in fall, the dispersal season of juveniles. Dispersal paths to new territories by inexperienced individuals may intersect frequently with roads, leading to road-kills (Bonnet et al., 1999). This result matches with the finding by the Chungnam Wildlife Rescue Center in Korea. In South Chungcheong province, 64% of *P. b. euptilura* road-kill victims were identified as juveniles (age under 1 yr) among 29 individuals collected during 2004 to 2017.

The road-kill prediction map shows clear patterns of low probability of *P. b. euptilura* road-kills in the major cities (Seoul, Daejeon, Daegu, Gwangju, and Busan) and high probability around large plains in the western part of the Republic of Korea. Highways located close to big cities are usually expected to have higher traffic volume, contain less suitable habitats for *P. b. euptilura*, and are larger in dimension compared to highways in rural areas. This pattern may indicate the low population density of *P. b. euptilura* in urban areas due to high habitat fragmentation and modification. Moreover, high risks of *P. b. euptilura* road-kills around areas where large plains are located may also represent their typical habitat. Plains such as rice paddies and fields play an important role as foraging sites of *P. b. euptilura* (Choi et al., 2012). Therefore, we tentatively conclude that *P. b. euptilura* road-kill probability is linked with their population density, and the map in this study might be used as an indicator estimating the population density of *P. b. euptilura* inhabiting nearby highways. The road-kill prediction map generated with the five predictive parameters can be applied to management planning of road-kills of *P. b. euptilura* on highways. Moreover, the map and the model will also be helpful when planning construction of future roads to prevent collisions on the new ones.

The present study highlights that integrated road-kill management is necessary. It is important to take into account environmental features surrounding highways to reduce *P. b. euptilura* road-kills. Management planning must include land cover types adjacent to highways, traffic patterns, and season. Areas close to *P. b. euptilura* habitats and less composed by human structures within 1-km^2, particularly nearby small scaled highways should be identified as places having high possibility of *P. b. euptilura* road-kills, especially during fall and winter.

In the Republic of Korea, road-kills continue to occur consistently despite efforts by the Korean government such as installing wildlife crossing structures to prevent collisions (Korea Expressway Corporation, 2013). For small- to medium-sized mammals, it has been recommended to install passages with an interval of 150 to 300 m to improve the permeability of roads (Clevenger et al., 2001). Currently, there is one structure which can be used as wildlife crossing structures in every 133 m in highways in the Republic of Korea (Choi, 2007, quoted from Korea Expressway Corporation, unpublished data), which is greater than the number of passages suggested by the previous study. This is beneficial to *P. b. euptilura* which is described as a species that frequently uses wildlife passages (Choi, 2007). Therefore, consistently observed *P. b. euptilura* road-kills may not result from lack of wildlife passages. We recommend increasing efficiency of the passages and inducing the animals to the passages by fencing where road-kill probability is high based on the results of this study. Additionally, it is also recommended to establish the management policy accounting for seasonality of *P. b. euptilura* behaviors.

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Tables

Table 1. Abbreviations and descriptions for the variables used to spatial analyses (landscape characteristics and traffic patterns).

Category Ⅰ	Category Ⅱ	Abbreviation	Description
Landscape characteristics	Land cover	DB	Distance from built-up areas
		DA	Distance from agricultural lands
		DF	Distance from forest
		DG	Distance from grasslands
		DWL	Distance from wetlands
		DBL	Distance from bare lands
		DW	Distance from water
		PB	Proportion of built-up areas
		PA	Proportion of agricultural lands
		PF	Proportion of forest
		PG	Proportion of grasslands
		PWL	Proportion of wetlands
		PBL	Proportion of bare lands
		PW	Proportion of water
	Topography	EL	Elevation
		SL	Slope
		AS	Aspects (categorical)
	Suitability	HSI	Habitat suitability index
	Connectivity	PI	Patch connectivity index
		LI	Link connectivity index
Traffic patterns		TV	Traffic Volume
		DR	Distance from ramps
		LA	Number of lanes (categorical)

534 Table 2. Results of descriptive statistics of spatial analyses (landscape characteristics and traffic 535 patterns). Independent *t*-test and chi-square test were tested for continuous and categorical variables 536 respectively.

Independent *t*-test

Category	Variables	Road-kill points Mean	Road-kill points SD	Random points Mean	Random points SD	*t*	*P*
Land cover	DB	446.07	526.71	385.69	471.80	-1.01	0.311
	DA	50.65	59.18	85.70	163.27	2.40	0.018
	DF	54.43	57.67	82.02	103.08	2.77	0.006
	DG	147.19	274.79	204.31	502.36	1.19	0.237
	DWL	3912.29	4263.28	4829.62	7064.95	1.32	0.188
	DBL	779.95	1234.65	861.22	3113.60	0.29	0.773
	DW	1093.38	1075.28	1367.48	2756.10	1.10	0.272
	PB	1.35	2.20	3.16	8.23	2.53	0.013
	PA	39.49	24.42	39.33	26.83	-0.54	0.957
	PF	52.67	27.01	48.99	30.20	-1.08	0.281
	PG	3.79	3.94	4.00	4.38	0.42	0.673
	PWL	0.08	0.33	0.82	6.37	1.37	0.171
	PBL	1.60	2.78	2.05	4.12	1.08	0.280
	PW	1.02	3.97	1.66	6.90	0.95	0.344
Topography	EL	125.93	123.90	148.93	130.83	1.52	0.131
	SL	2.13	1.79	2.12	1.84	-0.05	0.964
Connectivity	PI	3.64.E+06	3.75.E+06	4.67.E+06	7.82.E+06	1.41	0.161
	LI	1.05.E+14	6.10.E+14	1.16.E+14	5.40.E+14	0.16	0.871
Suitability	HSI	3.31	1.30	3.18	1.25	-0.85	0.394
Traffic	DR	3671.09	3988.47	2110.50	3831.58	-3.35	<0.001
	TV	21762.55	12241.65	58668.28	49522.38	8.59	<0.001

Chi-square test

Category	Variables	χ^2	*df*	*P*
Topography	AS	8.63	7	0.28
Traffic	LA	50	4	<0.001

537

Table 3. Parameters included in the best predicting model selected using logistic regression with stepwise approach. Best model included traffic volume, patch connectivity index, distance from ramps, elevation, and distance from water.

Parameter	**Estimate**	**SE**	**Wald**	***P***	**Odds ratio**	**95% CI**
Intercept	4.652	1.0660	19.029	<0.001		
TV	-0.0000788	0.0000	39.739	<0.001	1.000	1.000, 1.000
PI	-0.0000001	0.0000	8.818	0.003	1.000	1.000, 1.000
DR	0.0000613	0.0000	2.245	0.134	1.000	1.000, 1.000
EL	-0.002178	0.0011	3.813	0.051	0.998	0.996, 1.000
DW	-0.5837	0.3062	3.635	0.057	0.558	0.306, 1.017

Figures

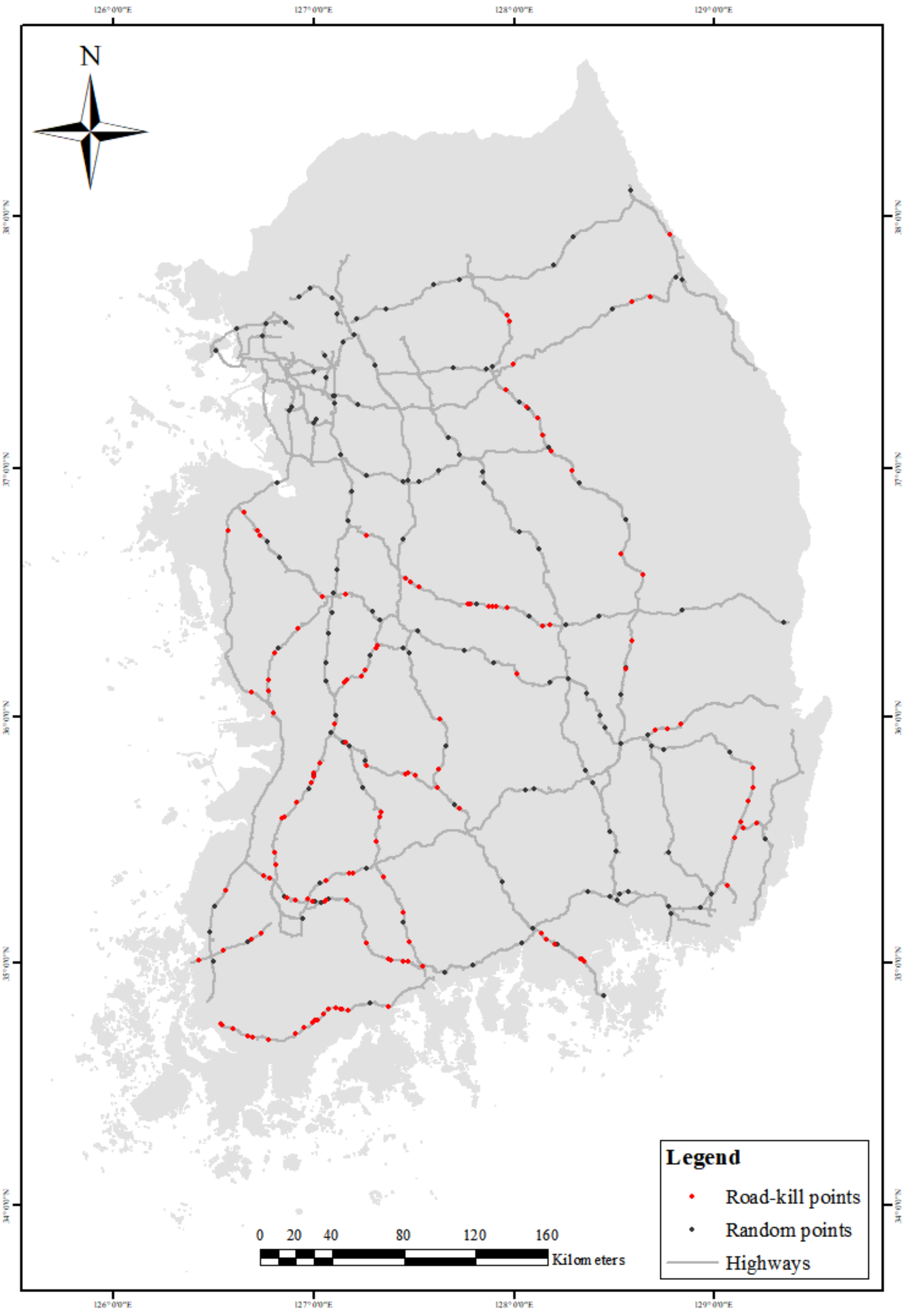

Fig. 1. Map of the study area with *P. b. euptilura* road-kill points and the random points located on highways.

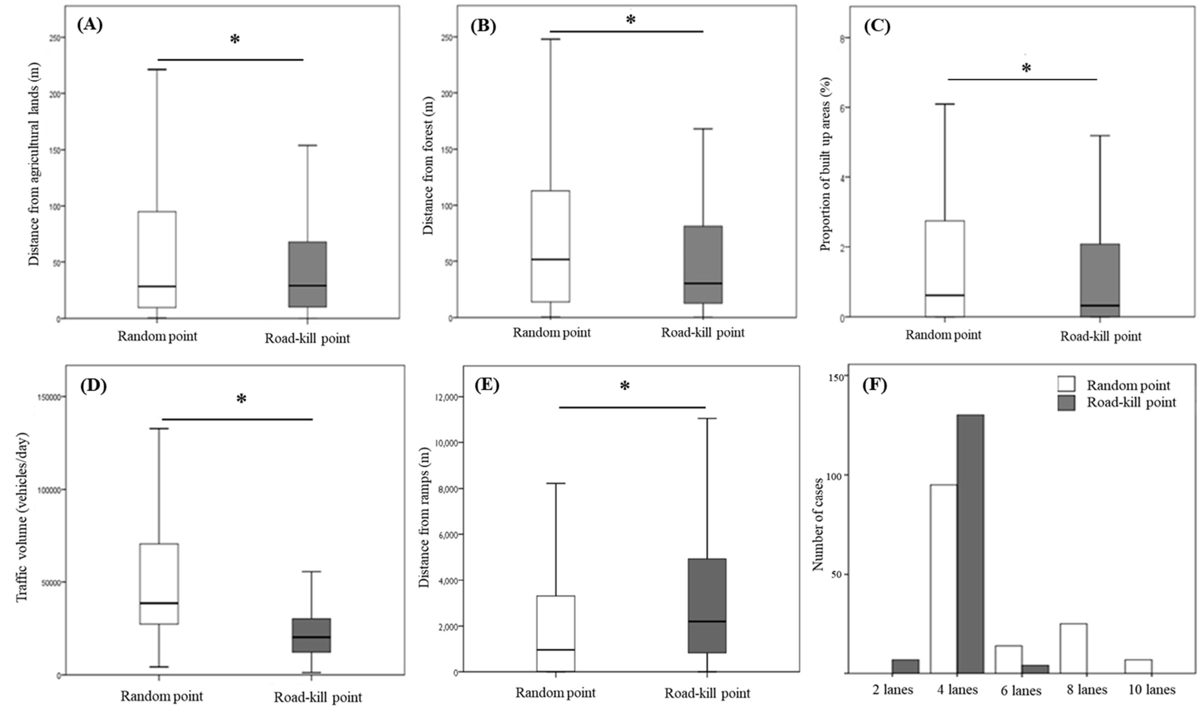

Fig. 2. Result graphs of the landscape characteristics and traffic patterns analyses. (A) distance from agricultural lands, (B) distance from forests, (C) proportion of built up areas, (D) traffic volume, (E) distance from ramps and (F) the number of lanes. In each graph, variables were compared in road-kill (white) and random points (grey).

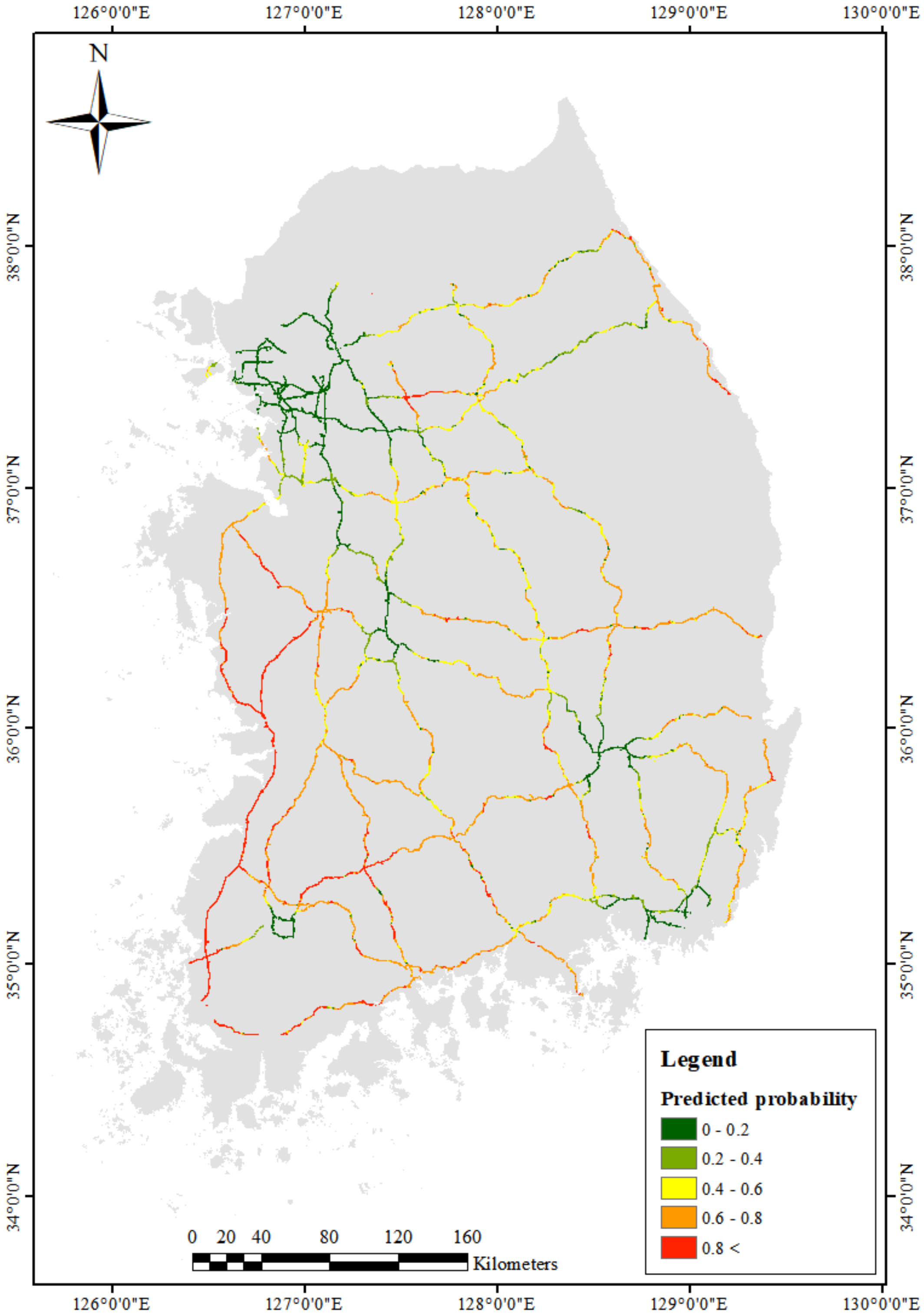

Fig. 3. Prediction map of *P. b. euptilura* road-kills on highways in the Republic of Korea. Green and red sections indicate respectively low and high predicted probability of *P. b. euptilura* road-kills.

Supplementary table

Model-fitting results from logistic regressions to predict *P. b. euptilura* road-kills in highways. Candidate models are ranked using change in Akaike's Information Creterion (ΔAIC). Fit statistics include the Akaike weight (w_i) and the area under curve (AUC). For each model, n = 282.

Covariates	***K***	***D***	**AIC**	**ΔAIC**	w_i	**AUC**
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG+LA+PBL+SL + HSI+AS	30	257.478	305.45	23.08	0.000	0.864
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG+LA+PBL+ SL +HSI	22	259.012	298.25	15.88	0.000	0.863
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG+LA+PBL+SL	21	259.013	296.25	13.88	0.000	0.864
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG+LA+PBL	20	259.058	294.31	11.94	0.001	0.863
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG+LA	19	259.426	292.59	10.22	0.002	0.863
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG+DG	14	262.951	291.28	8.91	0.004	0.857
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI+PG	13	263.445	289.77	7.4	0.009	0.857
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF+LI	12	263.594	287.97	5.6	0.022	0.855
DW+TV+DR+EL+PI+PB+PWL+DWL +DF+PF	11	264.464	286.77	4.4	0.039	0.854
DW+TV+DR+EL+PI+PB+PWL+DWL +DF	10	265.185	285.55	3.18	0.073	0.854
DW+TV+DR+EL+PI+PB+PWL+DWL	9	266.373	284.81	2.44	0.105	0.853
DW+TV+DR+EL+PI+PB+PWL	8	268.333	284.33	1.96	0.133	0.851
DW+TV+DR+EL+PI+PB	7	269.027	283.03	0.66	0.265	0.850
DW+TV+DR+EL+PI	6	270.371	282.37	0	0.356	0.845