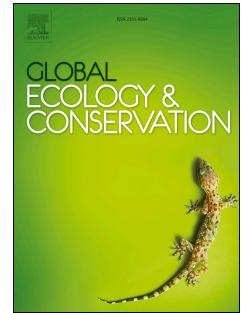


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Prionailurus bengalensis euptilura road-kills in the Republic of Korea

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1 **Spatio-temporal characteristics and predictions of the endangered leopard cat**

2 ***Prionailurus bengalensis euptilura* road-kills in the Republic of Korea**

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20 Abstract

21 Road-kills negatively impact wildlife populations, especially those that are threatened or small in size.
22 The increase of linear structures such as roads or railways causes road-kills. Understanding and
23 knowing where and when road-kill probability is high is important to prevent collisions. The leopard
24 cat (*Prionailurus bengalensis euptilura*) is listed on CITES Appendix II and is considered as
25 endangered in the Republic of Korea. We used 141 *P. b. euptilura* road-kill events occurring from
26 2006 to 2012 in the Republic of Korea with the same number of randomly generated points for spatial
27 analyses. Further, 239 events were used for temporal analyses. Spatial analyses and graph modeling
28 were conducted using geographic information system (GIS) and Graphab software. In landscape
29 analyses, *P. b. euptilura* road-kills were concentrated around agricultural lands and forest, and less
30 frequent near developed areas. The result of the traffic patterns analyses showed that traffic volume,
31 the number of lanes, and distance from ramps were significantly different between the road-kill points
32 and the random points. The road-kill frequency was significantly different by season, and there were
33 two peaks in winter and fall reflecting the seasonal behavior of *P. b. euptilura*. Among the 14
34 candidate models, the best model with the lowest Akaike's Information Criterion (AIC) included five
35 factors: traffic volume, distance from ramps, elevation, patch connectivity index, and distance from
36 water. This study shows that *P. b. euptilura* road-kills are not randomly distributed, but rather are
37 related to adjacent landscape, traffic patterns, and season. This study can contribute to minimizing
38 future collisions and lead to conservation of the endangered populations through application to road-
39 kill management policy.

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

42 Introduction

43 The extension of linear structures such as railroads and highways has resulted in habitat
44 fragmentation and an increase in road-kills (Coulon, 2004; Coffin, 2007; Borda-de-Aqua, 2011;
45 Clements et al., 2014) what is one of the most principal factors leading to population decline (Coffin,
46 2007, Jackson & Farhig, 2011).

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

66 The effect of these factors to road-kills can be different by species and taxa (Forman et al.,
67 2003) due to diversity of ecological patterns of each of them. Thus, it is crucial to examine factors

68 which might influence road-kills for each species to reduce collisions, and consequently, to improve
69 present road management policy for future biodiversity conservation. Our research takes an interest in
70 an endangered species, the leopard cat (*Prionailurus bengalensis euptilura*). Historically, the Republic
71 of Korea harbored three species of the Felidae family. However, *P. b. euptilura* is the only remaining
72 species. The populations have declined over the years due to anthropogenic disturbances, resulting in
73 their 1988 “endangered” classification by the Ministry of Environment in the Republic of Korea and
74 their listing on CITES Appendix II. *Prionailurus bengalensis euptilura* is known as a habitat
75 generalist inhabiting agricultural lands and forests (Choi et al., 2012). Their major diet is composed of
76 rodents (Grassman, 2000; Rajaratnam et al., 2007) and their average home range size in the Republic
77 of Korea is known as $3.69 \pm 1.34 \text{ km}^2$ (Choi et al., 2012). They are seasonal in their behaviors; males
78 enlarge their home range size during the mating season, which is winter to early spring in temperate
79 areas (Maekawa, 1998; Ueno, 2004), to increase the possibility of finding mates (Izawa et al., 2009).
80 Six or seven months after birth, juveniles start to disperse to find their own territories (Murayama,
81 2008).

82 Several studies showed that road-kill is one of the main reasons explaining the decline of *P. b.*
83 *euptilura* in the Republic of Korea. A study on road-kills of mammals conducted on 119 km of roads
84 found 103 killed *P. b. euptilura* between July 2004 and December 2006 (Choi, 2007). In addition, in
85 four studies of 16 captured and released *P. b. euptilura* with GPS collars, 31.3 % of them died because
86 of road-kills (Choi, 2007; Choi & Park, 2009; Park et al., 2012; Lee, 2017). Further, a study
87 examining 78 individuals revealed that the recurrent “bottleneck effects”, defined as a drastic
88 reduction in the size of a population, of *P. b. euptilura* populations resulted in significantly low
89 genetic diversity compared to other endangered felid populations around the world and also pointed
90 out that the local extinction risk of *P. b. euptilura* is substantial in the Republic of Korea (Ko et al.,
91 2018).

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

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

101

102 **Materials and Methods**

103 **Study area and data collection**

104 There are 38 major highways in the Republic of Korea, approximately 4,717 km in total
105 length. Although the proportion of the highways is about 4 % of the total roads in the Republic of
106 Korea (Statistics Korea, 2017), they play an important role typically connecting major cities.
107 Furthermore, highway have distinctive features compared to other types of road. The mean traffic
108 volume in highways was 54,016 vehicles/day, whereas other roads, such as local roads, were 11,326
109 vehicles/day (calculated from data in Statistics Korea, 2017). Speed limit on highways is also higher
110 than other roads. According to the Road Traffic Act 19, speed limit for highway is 100 to 120 km/h,
111 whereas 60 to 90 km/h in other roads. Among the whole section of the highways, four lanes sections
112 are predominant (3,567.5 km, e.g. 75 % of the network), followed by six lanes (608.5 km, e.g. 13 %
113 of the network), eight lanes (494.8 km, e.g. 10 % of the network), and above ten lanes (44.4 km, e.g.
114 1 % of the network). The two lanes sections, which are the narrowest, are minor compared to the other
115 ones, representing 2.2 km, occupying only 0.05 % of the total network (Statistics Korea, 2017).

116 The *P. b. euphilura* road-kill data originated from the Korea Expressway Corporation
117 (<http://www.ex.co.kr>). Workers of the Korea Expressway Corporation check the road conditions of all
118 major highways every day. They typically drive 80 km/h and report any irregularity including road-
119 kills. A total of 255 *P. b. euphilura* road-kills were reported on 22 highways from February 2004 to
120 February 2017 by the Korea Expressway Corporation. Observation date and location were included in

121 every road-kill event. Out of 255 events, outliers involving overlapping road-kill events occurring in a
122 single day were removed, resulting in 239 data points. Unlike we used all of 239 road-kills occurred
123 from 2004 to 2017 for temporal analysis (seasonal pattern), we limited data occurred between 2006
124 and 2012 for spatial analyses (landscape characteristics and traffic patterns). This reduction was
125 necessary because using too old or too recent data compared to the certain year of land cover map
126 may cause problem while spatial analyses, as land covers change with time. Also, among the dataset
127 from 2006 to 2012, some data were excluded due to difficulty of identifying exact locations, such as
128 in tunnels. Consequently, 141 road-kill points were included in the spatial analyses.

129 Spatial data were obtained from the 2009 national land cover map with 30-m resolution
130 provided by the Ministry of Environment (<http://www.egis.me.go.kr>). Land cover types were divided
131 into seven categories: built-up area, agricultural land, forest, grassland, wetland, bare land, and water.
132 Topographic data were derived from Digital Elevation Model (DEM) provided by USGS (2009) with
133 30-m resolution. Road data were obtained through Openstreetmap (2017). Data for annual average
134 daily traffic and the number of lanes were obtained from the Traffic Monitoring System
135 (<http://www.road.re.kr>) produced by the Ministry of Land, Infrastructure and Transport of Korea.

136

137 **Landscape characteristics**

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

146 For land cover type analyses, we used two approaches: distance-based analysis (DA) and

147 compositional analysis (CA). Conner et al. (2003) qualitatively compared the two methods and
148 concluded that the DA approach could be more applicable to habitat analyses with Euclidean distance
149 and randomly generated control sites, and less restrictive than the CA metric. However, the CA
150 approach is one of the most widely used metrics for studies related to habitat analyses (Aebischer et
151 al., 1993). Thus, in this study, both metrics were calculated for analyses of land cover covariates. We
152 measured the Euclidean distance from each point to the seven land cover types. Then, a square-shaped
153 buffer of 1-km² was generated for each point, and the proportion of each land cover type inside the
154 buffer was computed. Lee and Song (2008) compared various types and sizes of buffers to evaluate
155 habitat quality of the *P. b. euptilura* and showed that 1-km² square buffer is the most effective. For the
156 topographical features, we used ArcMap 10.5 to derive elevation, slope, and aspects from the Digital
157 Elevation Model (USGS) for each *P. b. euptilura* road-kill and random points.

158 Factors important for habitat suitability are different depending on species. Four factors
159 including elevation, land cover type, distance from roads, and distance from water were used with the
160 habitat suitability index model derived by Lee et al. (2012) to generate a habitat suitability map of *P. b.*
161 *euptilura* in the Republic of Korea (Fig. 2). Then, we extracted the averaged habitat suitability index
162 in the 1-km² buffer for each point.

163 We used a graph-based landscape modelling approach to quantify landscape connectivity
164 (Galpern et al., 2011). A graph is composed of patches and links, representing respectively suitable
165 habitats and species displacement (i.e., daily movement or dispersal distance of juveniles). In ecology,
166 this approach can be applied to quantify the contribution of patches and link to connectivity, i.e. to
167 measure the relative importance of each landscape feature for an area connectivity (Serret et al., 2014;
168 Minor & Urban, 2008). The set of patches was developed using the habitat suitability map (Fig. 2). In
169 this map, the habitat suitability index was scored from 0 to 10 and categorized into five categories
170 hierarchically with the same interval. We considered the two highest categories as “habitat patches”.
171 Links between patches were generated using the least-cost path geometry, which represent the
172 displacement resistance from a patch to another according to the landscape features. We used Graphab
173 2.2.1 (Foltête et al., 2012) to generate the graph and calculate habitat connectivity metrics of each

174 patch and link. The minimum patch area was set as 1 ha with a 12-km threshold distance as described
 175 by Kang et al. (2016). Then, the Flux (Urban & Keitt, 2001) metric was applied to measure habitat
 176 connectivity of patches, and Betweenness Centrality (BC) (Foltête et al., 2012) to quantify habitat
 177 connectivity of links between pairs of patches. The Flux (F) sums the capacities of non-focal patches
 178 and is weighted according to their minimum distance to the focal patch i through the graph. It is an
 179 indicator of the potential dispersion from the focal patch or to the focal patch.

180 The F of patch i is given by:

$$F_i = \sum_j a_j e^{-ad_{ij}} \quad j \neq i$$

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

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

184 The BC of a link i is given by:

$$BC_i = \sum_j \sum_k a_j a_k P_{jk} \quad j, k \in \{1..n\}, k < j, i \in L_{jk}$$

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

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

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

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

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

192

193 **Traffic patterns**

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

200

201 **Seasonal pattern**

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

207

208 **Prediction modeling and mapping**

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

219 tested using area under the curve (AUC) and McFadden's pseudo R^2 .

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

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

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

227

228 **Results**

229 **Landscape characteristics**

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

239

240 **Traffic patterns**

241 All three variables tested for traffic pattern analyses were significantly different between the
 242 road-kill and the random points (Table 3). Traffic volume was significantly different between road-
 243 kills and random points ($P < 0.001$) and averaged 2.7 times lower at the road-kill points than at

244 random points (Fig.2-D). The frequency of road-kills peaked at 10,000 – 25,000 vehicles/day, and
245 nearly 62% of the collisions were concentrated at this range. Distance from ramps was more than 1.7
246 times further to the road-kill points compared to the random points (Fig. 2-E), and the difference was
247 significant ($P < 0.001$). In general, 92.2% of road-kills were occurred on four- lanes highways,
248 whereas only 67.4% of random points were found on the same road width. Four-lane roads are
249 representing 75 % of the highway network, what make the road-kill occurrences on this types of roads
250 higher than expected. Moreover, no road-kill points were found on roads with eight lanes or more (Fig.
251 2-F). The number of lanes was lower at the road-kill points than at the random points ($\chi^2 = 50$, $df = 4$,
252 $P < 0.001$) indicating that the roads with *P. b. euptilura* road-kills were narrower.

253

254 **Seasonal pattern**

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

260

261 **Prediction modeling and mapping**

262 Road-kill probability was determined through logistic regression modeling using a stepwise
263 approach. Five variables (DB, DA, DBL, PA and PW) were removed before performing logistic
264 regression due to high multicollinearity. Among 14 candidate models (see supporting information),
265 the best model included traffic volume, patch connectivity index, distance from ramps, elevation, and
266 distance from water (Table 4). Predicted probability of *P. b. euptilura* road-kills was negatively
267 correlated with traffic volume, patch connectivity index, elevation, and distance from water. Among
268 the parameters which negatively associated with the predicted probability, patch connectivity index
269 can be defined by the combination of patch connectivity itself and the distance to patches from road-

270 kill locations. Thus, we examined the patch connectivity and distance between patch and each point
271 using independent *t*-test to identify the effect of each parameter on patch connectivity index. The
272 result showed that the distance between patch and point was significantly lower ($p = 0.024$) in road-
273 kill points compared to random points. However, patch connectivity was not significantly different
274 between the road-kill and random points ($p = 0.837$). The only parameter that positively correlated
275 with *P. b. euptilura* road-kills was distance from ramps. The best model was better supported than the
276 full model ($\Delta AIC = 23.08$). The final model exhibited high predictive power ($AUC = 0.845$) with
277 excellent model fit (McFadden's Pseudo $R^2 = 0.308$; McFadden, 1977).

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

281

282 Discussion

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

292 For traffic patterns, traffic volume was lower at road-kill points than random points. In a
293 previous study, low traffic volume increased the risk of mammalian road-kills in various types of
294 roads in Korea (Seo et al., 2015). In case of moose (*Alces alces*), the road-kill frequency peaked at
295 low-intermediate traffic volume (Danks & Porter 2010). Road section with high traffic volume in high

296 speed highways may present as a great hurdle and thus leopard cats would not attempt to cross.
297 Compared to random points, *P. b. euphilura* road-kill points are likely to occur on narrow roads,
298 especially on the four lanes. As described before, highways with two lanes are the narrowest, but the
299 proportion of them is very low (below 0.05 % of the total length). Thus we conclude that the high
300 proportion of collisions on four-lanes roads (92.2% of road-kills occurred on four-lanes roads, which
301 occupies 75% of the highway network) compared to random points (67.4%) can be interpreted as a
302 higher probability of leopard cat road-kills on narrow highways. This is in line with the study of
303 Smith-Patten and Patten (2008), which showed that narrow roads have high risk of mammal road-kills
304 due to higher connectivity compared to large roads. Among the parameters which negatively
305 associated and narrow road width around road-kill locations may indicate relatively small scales of
306 highways and regional characteristics such as rural or suburban areas. As shown in the landscape
307 analyses, the proportion of developed areas was very low (Table 2) around *P. b. euphilura* road-kill
308 locations. In a previous study, a large percentage of road-kills occurred on small scaled rural roads
309 compared to urban roads, and an averaged percentage of road-kill rates in rural areas were up to 12
310 times higher than on the urban roads (Hughes et al., 1996). Thus, the results of this study concur with
311 the general pattern of mammalian road-kills.

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

323 The resulting seasonal pattern showed that *P. b. euptilura* road-kills are highly influenced by
324 their seasonal behaviors. Road-kills of *P. b. euptilura* were most frequent in winter, which is the
325 mating season of the *P. b. euptilura*. Males increase home ranges during the mating season (Maekawa,
326 1998; Ueno, 2004), to increase the possibility of finding mates (Izawa et al., 2009), likely to cross
327 roads in fragmented habitats. It is predicted that road-kills were male-biased in our dataset.
328 Unfortunately, this prediction could not be tested because the road-kills were not sexed at the time of
329 retrieval in our study. The second peak of *P. b. euptilura* road-kills was in fall, the dispersal season of
330 juveniles. Dispersal paths to new territories by inexperienced individuals may intersect frequently
331 with roads, leading to road-kills (Bonnet et al., 1999). This result matches with the finding by the
332 Chungnam Wildlife Rescue Center in Korea. In South Chungcheong province, 64% of *P. b. euptilura*
333 road-kill victims were identified as juveniles (age under 1 yr) among 29 individuals collected during
334 2004 to 2017.

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

349 The present study highlights that integrated road-kill management is necessary. It is

350 important to take into account environmental features surrounding highways to reduce *P. b. euptilura*
351 road-kills. Management planning must include land cover types adjacent to highways, traffic patterns,
352 and season. Areas close to *P. b. euptilura* habitats and less composed by human structures within 1-
353 km², particularly nearby small scaled highways should be identified as places having high possibility
354 of *P. b. euptilura* road-kills, especially during fall and winter.

355 In the Republic of Korea, road-kills continue to occur consistently despite efforts by the
356 Korean government such as installing wildlife crossing structures to prevent collisions (Korea
357 Expressway Corporation, 2013). For small- to medium-sized mammals, it has been recommended to
358 install passages with an interval of 150 to 300 m to improve the permeability of roads (Clevenger et
359 al., 2001). Currently, there is one structure which can be used as wildlife crossing structures in every
360 133 m in highways in the Republic of Korea (Choi, 2007, quoted from Korea Expressway
361 Corporation, unpublished data), which is greater than the number of passages suggested by the
362 previous study. This is beneficial to *P. b. euptilura* which is described as a species that frequently uses
363 wildlife passages (Choi, 2007). Therefore, consistently observed *P. b. euptilura* road-kills may not
364 result from lack of wildlife passages. We recommend increasing efficiency of the passages and
365 inducing the animals to the passages by fencing where road-kill probability is high based on the
366 results of this study. Additionally, it is also recommended to establish the management policy
367 accounting for seasonality of *P. b. euptilura* behaviors.

368

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375

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530

Tables

531 Table 1. Abbreviations and descriptions for the variables used to spatial analyses (landscape
532 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	
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)

533

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.

		Road-kill points		Random points			
Independent <i>t</i>-test							
Category	Variables	Mean	SD	Mean	SD	<i>t</i>	<i>P</i>
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	<i>df</i>	<i>P</i>			
Topography	AS	8.63	7	0.28			
Traffic	LA	50	4	<0.001			

537

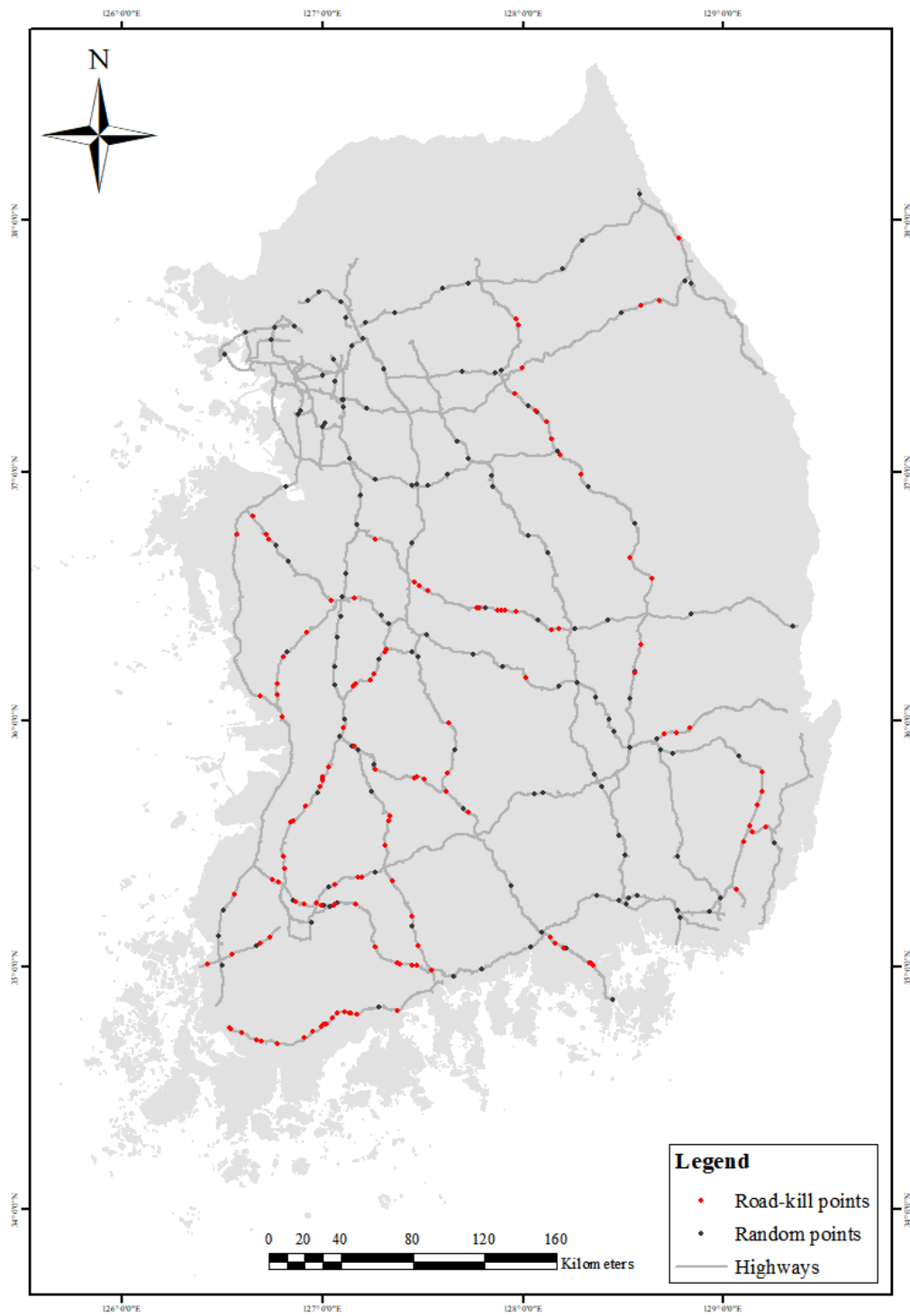
538 Table 3. Parameters included in the best predicting model selected using logistic regression with
 539 stepwise approach. Best model included traffic volume, patch connectivity index, distance from ramps,
 540 elevation, and distance from water.

Parameter	Estimate	SE	Wald	<i>P</i>	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

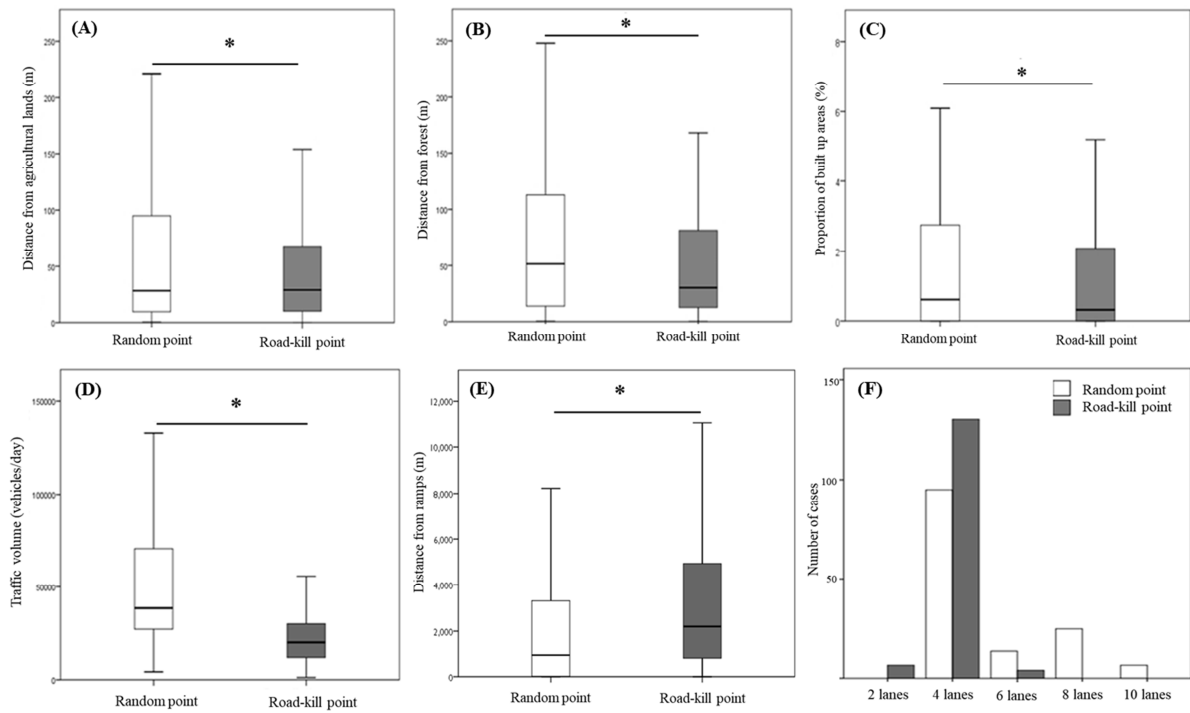
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Figures

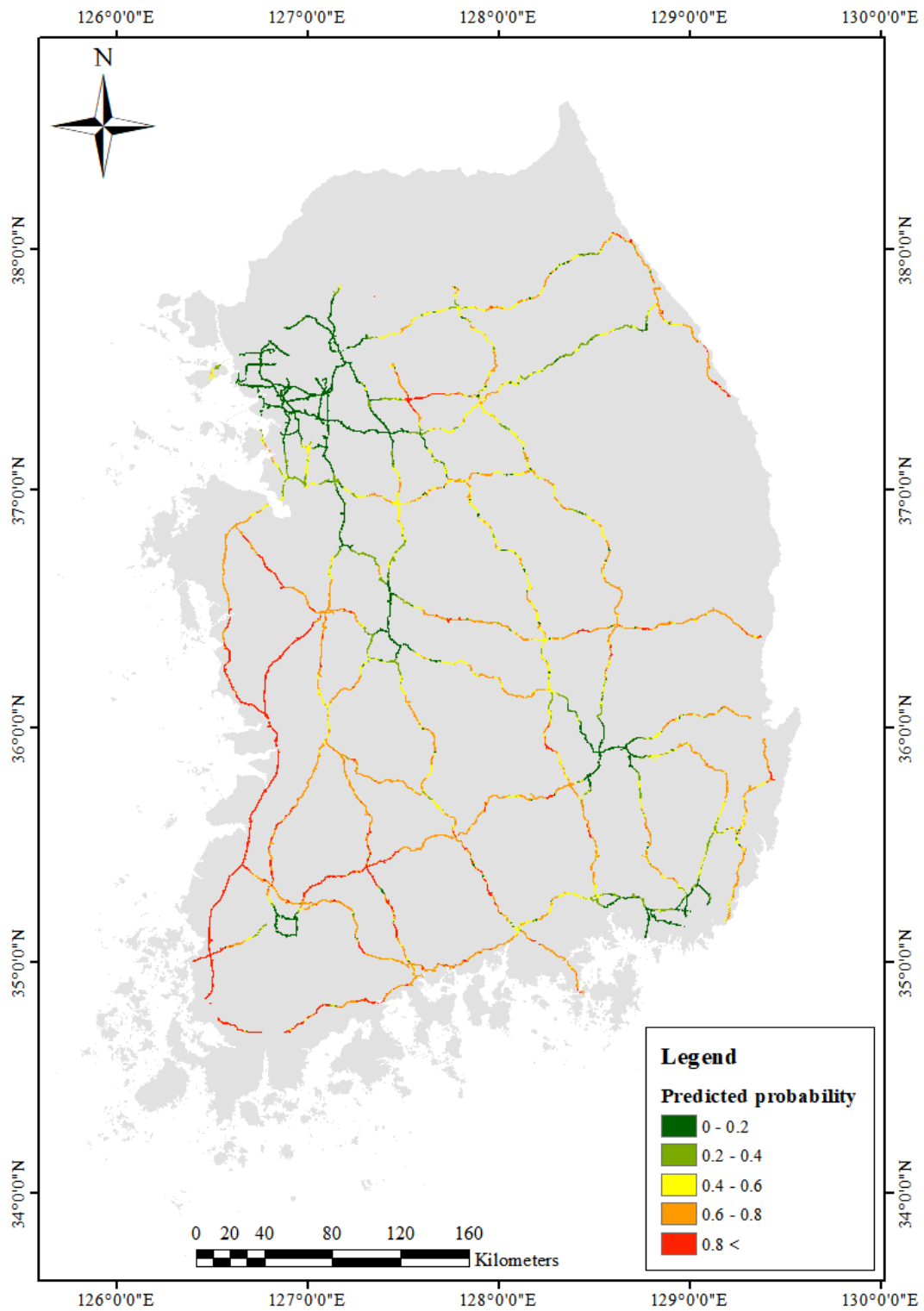


543 Fig. 1. Map of the study area with *P. b. euptilura* road-kill points and the random points located on
544 highways.



545

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



550

551 Fig. 3. Prediction map of *P. b. euphilura* road-kills on highways in the Republic of Korea. Green and552 red sections indicate respectively low and high predicted probability of *P. b. euphilura* road-kills.

553

554 **Supplementary table**

555

556 Model-fitting results from logistic regressions to predict *P. b. euptilura* road-kills in highways.557 Candidate models are ranked using change in Akaike's Information Criterion (ΔAIC). Fit statistics558 include the Akaike weight (w_i) and the area under curve (AUC). For each model, $n = 282$.

Covariates	<i>K</i>	<i>D</i>	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

559