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Predictive modeling of animal-vehicle collisions involving the threatened leopard cat (*Prionailurus bengalensis*) and Eurasian otter (*Lutra lutra*), in the Republic of Korea

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ABSTRACT

Animal-vehicle collisions (AVCs) substantially contribute to wildlife population decline and adversely impact threatened species with already limited numbers. In this study, we aimed to investigate the factors contributing to AVCs involving two threatened species in the Republic of Korea: the leopard cat (*Prionailurus bengalensis*) and Eurasian otter (*Lutra lutra*). These two species are the most frequently affected by AVCs among threatened mammals in Korea. To achieve this, we used data from the Korea Roadkill Observation System (KROS), a government-sponsored web-based AVC monitoring system. Our analysis focused on 17 variables, categorized into bioclimatic, landscape, and traffic factors, using machine-learning-based predictive modeling. From 2019 to 2021, 589 AVC incidents of *P. bengalensis* and 228 AVC incidents of *L. lutra* were recorded in KROS. Our findings indicate that AVC frequencies peaked during the most active seasons of the year, corresponding to the mating or dispersal periods, with *P. bengalensis* showing the highest AVC frequency in fall and *L. lutra* peaking in summer. For *P. bengalensis*, habitat suitability consistently exerted a strong influence on AVC risk across all seasons, whereas for *L. lutra*, the key factors affecting AVC risk highly varied seasonally. These results underscore the importance of seasonal and species-specific approaches for AVC mitigation. Targeted strategies, including wildlife corridors, underpasses, and speed reduction zones in high-risk areas, are recommended to mitigate AVC risks. By identifying the key factors and their seasonal dynamics, this study provides critical insights for conserving threatened wildlife and effectively reducing AVC incidents.

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Animal-vehicle collision; habitat fragmentation; seasonal behavior; spatial modeling; MaxEnt

Introduction

Animal-vehicle collisions (AVCs) often result in wildlife mortality, thereby contributing to population declines and biodiversity loss (Coffin 2007). The impact of AVCs on threatened or rare wildlife species is more severe than that on more prevalent species because of their small population sizes (Grilo et al. 2021; Jones 2000; Rocus and Mazzotti 1996). For example, in Australia, both the Eastern quoll (*Dasyurus viverrinus*) and the Tasmanian devil (Sarcophilus laniarius), which are both classified as endangered species, have experienced significant population declines due to AVCs (Jones 2000). Similarly, in Florida, USA, AVC constituted the predominant cause of mortality for four endangered species: the Key deer (*Odocoileus virginianus*), American crocodile (*Crocodylus acutus*), Florida panther (*Puma concolor coryi*), and bald eagle (*Haliaeetus leucocephalus*) (Rocus and Mazzotti 1996). Consequently, addressing the impact of AVCs on threatened species is imperative to ensure effective biodiversity conservation.

In the Republic of Korea, two threatened mammalian species, specifically the leopard cat (*Prionailurus bengalensis*) and Eurasian otter (*Lutra lutra*), are widely distributed across the country (Jo et al. 2020; Kim et al. 2021). These species play crucial roles as apex predators within terrestrial and aquatic habitats, respectively (Lee 2012; Lee et al. 2015). Unfortunately, their populations have declined due to anthropogenic

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disturbances, including habitat loss and illegal hunting (Won and Smith 1999; Choi 2007). These declines are further exacerbated by ongoing human-induced environmental modifications that alter the ecological balance within the Republic of Korea (Andersen et al. 2025). In addition, both species are highly susceptible to AVCs because of their extensive movement patterns and frequent use of habitats that are fragmented by road networks, thereby increasing their likelihood of encountering vehicles (Hauer et al. 2002a; Murayama 2008; Kim et al. 2019a; Fabrizio et al. 2019). Given this susceptibility, *P. bengalensis* and *L. lutra* emerged as the most frequently reported victims of AVCs among threatened mammalian species in the Republic of Korea, accounting for 66.8% and 26.4% of all such incidents reported in 2022, respectively (National Institute of Ecology 2022). Furthermore, AVC constitutes a critical factor contributing to the population decline of *P. bengalensis* in the Republic of Korea (Jo et al. 2018). In a comprehensive investigation comprising four studies involving 16 *P. bengalensis* individuals equipped with GPS collars, over 30% succumbed to AVCs (Choi 2007; Choi and Park 2009; Park et al. 2012; Lee 2017). Therefore, addressing the unique vulnerabilities of these species to AVCs, particularly in relation to their respective habitats and behaviors, is crucial.

The leopard cat is listed in CITES Appendix II and designated as an endangered species of category II under Korean law. This species occupies various habitats (from agricultural lands to forests) and is considered an edge species that primarily preys on rodents (Grassman 2000; Azlan and Sharma 2006; Rajaratnam et al. 2007; Choi et al. 2012; McCarthy et al. 2015). Edge species thrive in habitats situated at the boundaries of different ecosystems, such as forests and agricultural lands. These areas frequently intersect with road networks, thereby increasing the likelihood of vehicle encounters. Their dispersal ability extends up to 12 km (Kang et al. 2016), and their average home range is 2–3 km^2 (Jo et al. 2018). The considerable mobility of these species makes them particularly susceptible to AVCs in fragmented landscapes, particularly in road-induced habitats.

The Eurasian otter is listed as Near Threatened on the IUCN Red List, included in CITES Appendix I, and designated an endangered species in Category I and a natural monument by the Korean government. *L. Lutra* primarily inhabits semi-aquatic environments, including riverine and littoral zones, where it predominantly preys on fish; however, it is also observed in mountainous regions (Hung and Law 2016; Jo et al. 2018). This species can disperse up to 21 km (Quaglietta et al. 2013) and maintains a linear territory along aquatic systems, with an average length of 18 km (Jo et al. 2018). Roads often intersect with aquatic systems, particularly at bridges and culverts, forcing *L. lutra* into close proximity to vehicles and significantly increasing the risk of AVCs.

Numerous mammalian species demonstrate seasonal movement patterns that may correlate with fluctuations in AVC rates. Two key behaviors directly linked to mammalian AVCs are mating and dispersal. During the mating season, mammals often expand or move beyond their established home ranges in pursuit of potential mates (Schmidt et al. 2003; Cooper and Randall 2007; Lesmeister et al. 2009). Similarly, during the dispersal season, juveniles leave their natal habitats to search for new territories. Males of *P. bengalensis* expand their home ranges to enhance their opportunities for mating during the winter breeding season (Ueno 2004; Izawa et al. 2009). The following spring, juvenile individuals typically disperse from their natal habitats in fall (Maekawa 1998; Ueno 2004; Murayama 2008; Izawa et al. 2009). Similarly, *L. lutra* breeds from late summer to late fall (Hauer et al. 2002b), with juveniles reaching independence between 9 and 12 months of age, typically during the summer-to-fall period (Heggberget and Christensen 1994). These increased movements during mating or dispersal periods elevate the risk of AVC (Garriga et al. 2017; Kreling et al. 2019). For instance, AVC frequencies increase during the dispersal season of *Hydropotes inermis* and the mating season of *P. bengalensis* in the Republic of Korea (Kim et al. 2019a; Kim et al. 2021; Kim et al. 2023). Moreover, other species, including the black-tailed deer (*Odocoileus hemionus*) and raccoon (*Procyon lotor*), also exhibited notable peaks in AVCs during their respective mating and dispersal seasons (Kreling et al. 2019).

Bioclimatic variables, such as temperature and precipitation, substantially influence AVC occurrences (Carvalho et al. 2017; Raymond et al. 2021). Temperature influences the behavior of homeothermic mammals, including activity levels, which may vary with thermal conditions (Eom et al. 2023; Rafiq et al. 2023). Because of the relationship between animal activity and AVC risk, temperature is a key factor influencing the likelihood of mammalian AVC events (Garriga et al. 2017). Moreover, bioclimatic factors strongly influence AVCs by shaping wildlife habitats and movement patterns. For instance, research has shown that the incidence of AVCs involving *L. lutra* exhibits a significant positive correlation with rainfall; increased precipitation results in elevated water levels, compelling animals to traverse roads rather than use the underlying channels in the UK (Philcox et al. 1999).

The characteristics of surrounding landscapes strongly influence the distribution of AVCs. This phenomenon is attributable to the close association between wildlife and specific habitats and land-use types (Forman and Alexander 1998; Clevenger et al. 2003). Animal populations frequently display clumped distributions that are influenced by resource availability and dictated by landscape characteristics. Consequently, AVC locations are commonly concentrated in high-quality habitats that offer abundant food and shelter (Rosa and Badger 2012). For instance, the incidence of AVCs in the serval (*Leptailurus serval*) is influenced by the proportion of wetlands and vegetation indices, which are associated with the species' habitat preferences (Williams et al. 2019). Furthermore, AVCs involving three carnivores, the maned wolf (*Chrysocyon brachyurus*), the ocelot (*Leopardus pardalis*), and the Jaguarundi (*Herpailurus yagouaroundi*), tend to cluster in proximity to herbaceous vegetation. In contrast, urban areas are typically avoided, indicating that habitat preferences directly shape AVC risks (Costa et al. 2022). Landscape features, such as roads near forests, open areas, and water bodies, increase AVC risk by intersecting wildlife pathways (Pagany 2020). Global landscape fragmentation induced by roads disrupts wildlife connectivity and increases mortality rates, particularly for species with specific habitat requirements (Grilo et al. 2021). Dense vegetation along roads is a key factor influencing wildlife crossing patterns and AVC hotspots (Pagany 2020; Grilo et al. 2021). These findings highlight the need to integrate spatial data with ecological models to help understand how specific landscape characteristics contribute to AVC risks and to inform mitigation strategies, including wildlife corridors and underpasses.

Traffic factors are crucial for determining the incidence of AVCs (Colino-Rabanal et al. 2011; Seo et al. 2015; Fabrizio et al. 2019). The likelihood of animals successfully crossing roads depends on specific road conditions. For example, the probability of AVCs involving mammals decreases with high traffic volumes because animals are less inclined to cross heavily trafficked roads (Seo et al. 2015). In contrast, in the United States, deer-vehicle collisions are more prevalent in regions with elevated traffic volume, likely because of the intersection of high-speed roads with deer-feeding habitats, thereby increasing the collision risk (Hussain et al. 2007). Additionally, narrow roads pose a greater risk to mammalian AVCs than wide roads because the limited connectivity of wide roads acts as a substantial barrier, thereby decreasing the frequency of crossing attempts (Smith-Patten and Patten 2008).

In this study, we aimed to examine the factors contributing to AVCs associated with two threatened species, *P. bengalensis* and *L. lutra*, in the Republic of Korea. AVC data were extracted from the Korea Roadkill Observation System (KROS), which was established to collect AVC data nationwide (Kim et al. 2019b). While previous studies have explored general AVC patterns, this study focused on the specific bioclimate, landscape, and traffic factors that influence the collision risks of these species across different seasons. By investigating the spatial and temporal patterns of AVCs in relation to species habitat preferences and temporal movement behaviors, we sought to provide critical insights for developing targeted mitigation strategies. These strategies may mitigate AVCs and support the conservation of threatened species, thereby enhancing the body of knowledge relevant to wildlife management practices in similar global contexts.

Materials and methods

Study area

The study area encompasses the entire Republic of Korea, covering approximately 100,339 km^2. It is characterized by diverse topography, with approximately 70% of the land consisting of mountainous terrain interspersed with plains and river basins. These complex mountain systems, such as those extending across the region, serve as critical habitats and evolutionary refugia for various endemic and threatened taxa, influencing their movement patterns and distributions (Borzée et al. 2025). The elevation ranges from sea level along coastlines to peaks exceeding 1000 m in mountainous regions. There are four distinct seasons in the Republic of Korea: a warm, humid summer, typically between June and August; a cold, dry winter, typically between December and February; a relatively mild spring, typically between March and May; and a fall, typically between September and November. The annual average temperature ranges from 10°C to 16°C, with summer temperatures averaging 25°C to 30°C and winter temperatures averaging −10°C to 5°C. Annual precipitation ranges from 1200 to 1500 mm, with a substantial portion falling in summer due to seasonal rainfall patterns.

As of 2021, the Republic of Korea had 113,405 km of roads (Korean Statistical Information Service 2021), resulting in a road density of 1.13 km/km^2 nationwide (Andersen and Jang 2021) (Figure 1). However, this density was unevenly distributed; urban areas and lowland regions exhibit higher road densities because

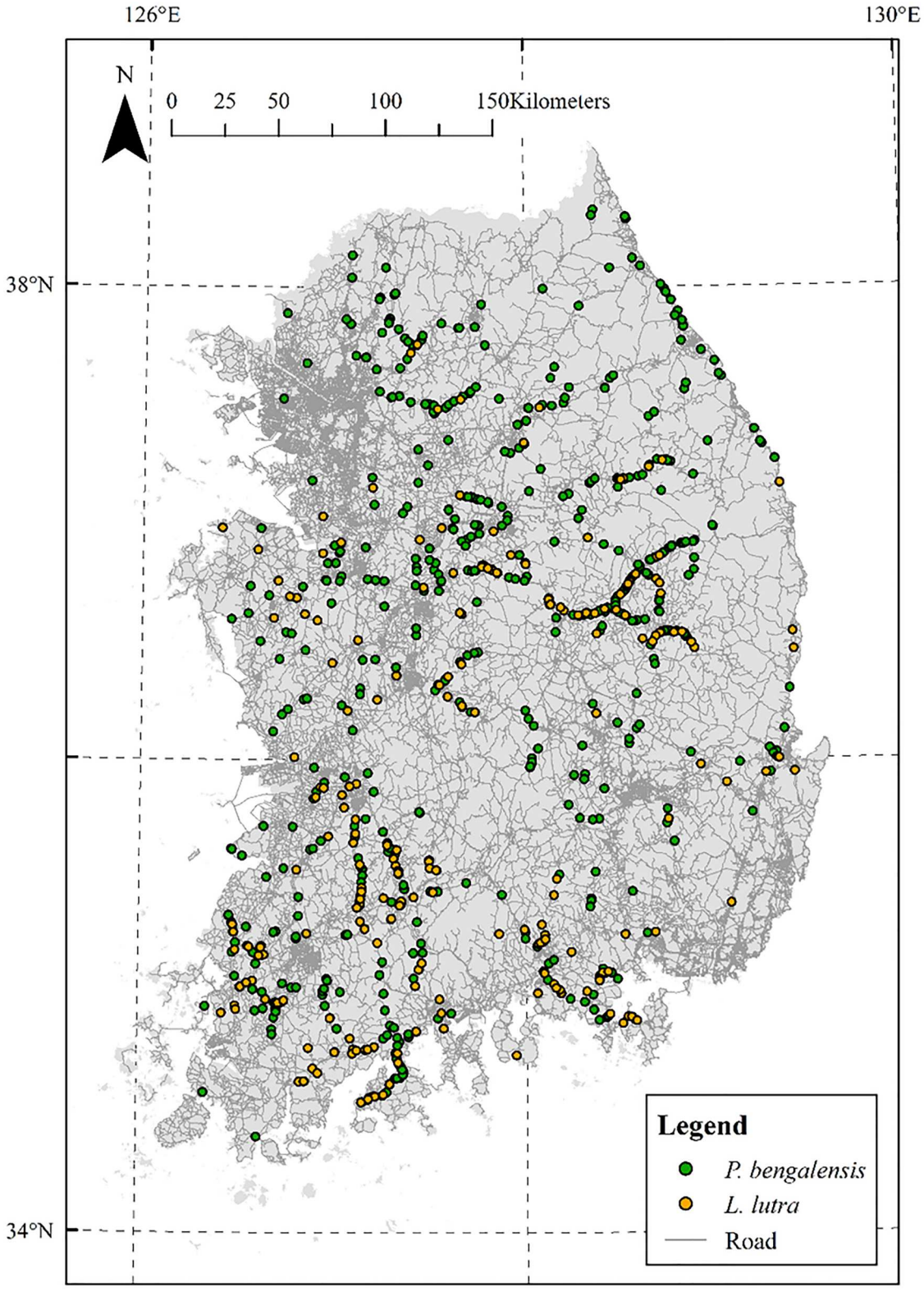


Figure 1. Road network in the Republic of Korea, encompassing all seven types of roads, with clusters of roads typically indicating large cities, marked by gray areas. The animal-vehicle collision (AVC) locations involving *P. bengalensis* and *L. lutra* between 2019 and 2021 are represented by green and orange dots, respectively.

of concentrated human activities, whereas mountainous and rural areas, frequently coinciding with wildlife habitats, demonstrate relatively lower densities. The country officially classifies roads into seven categories: expressways, national highways, metropolitan roads, provincial roads, municipal roads, county roads, and district roads. Expressways and national highways function as interprovincial roads, whereas other road types operate within their respective administrative boundaries. Expressways are toll roads with speed limits exceeding 100 km/h and managed by the Korea Expressway Corporation (ex.co.kr). National highways connect major cities and have speed limits of up to 80 km/h, and are maintained by the Ministry of Land, Infrastructure, and Transport of the Korean government. Metropolitan roads are located in urban cities, whereas provincial roads serve as arterial roads within provinces. Municipal, county, and district roads are generally smaller in scale, have lower speed limits, and are situated within municipalities, counties, and districts, respectively.

Data collection

The AVC data for *P. bengalensis* and *L. lutra* used in this study were extracted from the KROS database covering the years 2019–2021 (Figure 1). The KROS mobile application was exclusively distributed to more than 5000 road workers and associated managers responsible for removing animal carcasses across various road types in the region. Upon encountering an animal carcass during routine road patrols or in response to civil complaints regarding AVC incidents, road workers promptly documented the findings by capturing photographs. These images, accompanied by the precise location and timestamp data, were swiftly transmitted to the KROS platform. Subsequently, wildlife experts meticulously analyzed the photos to ascertain species identity and accurately pinpoint the geographic location of each data point, thereby ensuring the accuracy of the AVC data. All AVC data were analyzed without distinction by age or sex. In addition to leveraging the KROS dataset, essential road-related spatial data required for comprehensive spatial analyses were obtained from the National Transport Information Center (www.its.go.kr/).

AVC modeling

To map the probability of AVCs for the two threatened mammalian species in the Republic of Korea, we developed distinct MaxEnt models for each species by season (spring: March – May; summer: June – August; fall: September – November; and winter: December – February). The environmental variables for AVC modeling included bioclimatic, landscape, and traffic variables. Specifically, the bioclimatic variables incorporated in the AVC modeling were annual mean temperature and precipitation. Although we developed AVC predictive models by season, bioclimatic variables were included to account for regional climatic differences and provide a broader climatic context. These variables complement seasonal data by capturing the environmental conditions that affect habitat suitability and wildlife movement across regions with distinct climatic characteristics.

Before constructing the AVC probability models, we developed habitat suitability maps for *P. bengalensis* and *L. lutra* to incorporate species-specific habitat preferences into the modeling framework. Habitat suitability models (HSMs) were generated using MaxEnt, informed by presence-only occurrence records sourced from the Global Biodiversity Information Facility (GBIF; GBIF.org 2022a, 2022b). Given the limited representation of threatened species in public databases, additional occurrence points from Lee et al. (2017) and Jo et al. (2020) were included in the analyses for *P. bengalensis* and *L. lutra*, respectively. Environmental variables, including bioclimatic and landscape factors (Tables 1 and 2), were used to train the habitat suitability models. The final suitability layers were generated after removing spatially imprecise records that exceeded the resolution of the environmental layers (100 m). The resulting habitat suitability maps derived from the HSMs were used as explanatory covariates in the AVC models to account for spatial variations in collision risk associated with habitat quality. In this context, habitat suitability represents a derived predictor variable generated from the MaxEnt-based HSMs, rather than an input variable used for model construction. Habitat suitability values derived from the HSMs were extracted along road segments and included as continuous covariates in the AVC models to ensure that only areas adjacent to roads were included in the AVC risk prediction.

Table 1. Environmental variables used for habitat suitability models (HSM) and AVC probability of the two threatened species in the Republic of Korea.

Category	Variable	Model used	Explanation
Bioclimatic	Annual mean temperature	HSM, AVC	–
	Mean diurnal range	HSM	Mean of monthly (max temp – min temp)
	Isothermality	HSM	Mean diurnal range/Temperature annual range × 100
	Temperature seasonality	HSM	Standard deviation * 100
	Maximum temperature of warmest month	HSM	–
	Minimum temperature of coldest month	HSM	–
	Temperature annual range	HSM	Maximum temperature of warmest month – Minimum temperature of coldest month
	Mean temperature of wettest quarter	HSM	–
	Mean temperature of driest quarter	HSM	–
	Mean temperature of warmest quarter	HSM	–
	Mean temperature of coldest quarter	HSM	–
	Annual precipitation	HSM, AVC	–
	Precipitation of wettest month	HSM	–
	Precipitation of driest month	HSM	–
	Precipitation seasonality	HSM	Coefficient of variation
	Precipitation of wettest quarter	HSM	–
	Precipitation of driest quarter	HSM	–
	Precipitation of warmest quarter	HSM	–
	Precipitation of coldest quarter	HSM	–
Landscape	Elevation	HSM, AVC	Digital Elevation Model (DEM; GMTED provided by USGS) smoothed using focal statistics
	Slope	HSM, AVC	Derived from DEM using Slope tool in ArcMap
	Ruggedness	HSM, AVC	Derived from DEM – standard deviation of slope using focal statistics
	Landcover	HSM, AVC	Extracted from World Land Cover 30 m BaseVue 2013, Source: MDAUS
	Forest distance	HSM, AVC	Euclidean distance to forest land cover class (BaseVue 2013)
	Urban distance	HSM, AVC	Euclidean distance to urban land cover class (BaseVue 2013)
	Water distance	HSM, AVC	Euclidean distance to water cover class (BaseVue 2013)
	River distance	HSM, AVC	Euclidean distance to streams/rivers
	River-coast distance	HSM, AVC	Euclidean distance to streams/rivers or coast
	Greenness	HSM, AVC	Vegetation index, derived using Tasselled Cap transformation of corrected Landsat reflectance imagery
	Wetness	HSM, AVC	Surface and canopy moisture, derived using Tasselled Cap transformation of corrected Landsat reflectance imagery
Traffic	Lanes	AVC	Number of lanes per road (two-way)
	Max speed	AVC	Maximum road speed
	Corridor distance	AVC	Euclidean distance to wildlife crossings

Although the landscape variables aligned with those used in the HSMs, we also incorporated the HSM outputs as covariates in the AVC model to assess the influence of suitable habitats on AVC likelihood. The traffic variables included the number of lanes, maximum speed, and distance to the corridor (i.e. wildlife crossing). Environmental layers were extracted exclusively along roads because AVCs occurred only on roads. This approach ensured that background points beyond roads were not misinterpreted as areas

Table 2. Categories of the landcover variable used for habitat suitability and AVC probability modelling (BaseVue 2013).

Category	Explanation
1	Deciduous forest
2	Evergreen forest
3	Shrub/Scrub
4	Grassland
5	Barren or minimal vegetation
7	Agriculture, general (cultivated crop lands)
8	Agriculture, paddy (crop lands characterized by inundation)
9	Wetland
11	Water
20	High density urban (over 70% constructed materials)
21	Medium-low density urban (30 - 70% constructed materials)

devoid of AVCs. Similar to the HSMs, the AVC probability models were developed using five replicates with a cross-validated run type, and the results were averaged to produce the final AVC probability maps. In contrast to the HSMs, duplicate presence points were not removed from the AVC models, as each AVC occurrence was treated as an independent event rather than multiple counts for the same individual. We set the default prevalence as the AVC percentage for each group (species by season). Multicollinearity among all predictors was evaluated by computing the variance inflation factors (VIFs) from the pixel values extracted across all raster layers. The final models were evaluated using the area under the receiver operating curve (AUC) and accurate scale statistics (TSS). Spatial analysis was performed using ArcGIS Desktop 10.8.1 and ArcGIS Pro 2.8.0.

Results

Data descriptions

From 2019 to 2021, 589 AVC incidents involving *P. bengalensis* and 228 incidents involving *L. lutra* were georeferenced and collected using KROS. The AVC frequency for *P. bengalensis* was the highest in fall, coinciding with its dispersal season, and was 6.9 times higher than that in summer (Figure 2). The second-highest AVC frequency for *P. bengalensis* occurred in winter, aligning with the breeding season. For *L. lutra*, the AVC frequencies peaked in summer and were closely followed by those in fall. These seasons correspond to the species dispersal and breeding seasons. Specifically, the AVC frequency of *L. lutra* was 3.4 times higher in summer than in winter. In summary, the highest AVC frequencies in both species occurred during their most active seasons.

Habitat suitability models

The habitat suitability model for *P. bengalensis* had an average AUC value of 0.668 ± 0.019, indicating marginally inadequate explanatory power. The key variables retained in the model included the annual temperature range, annual precipitation, precipitation of the wettest month, precipitation of the warmest quarter, elevation, greenness, land cover, and slope. Among these, greenness had the highest contribution, followed by the annual temperature range and land cover. In terms of permutation importance, annual temperature

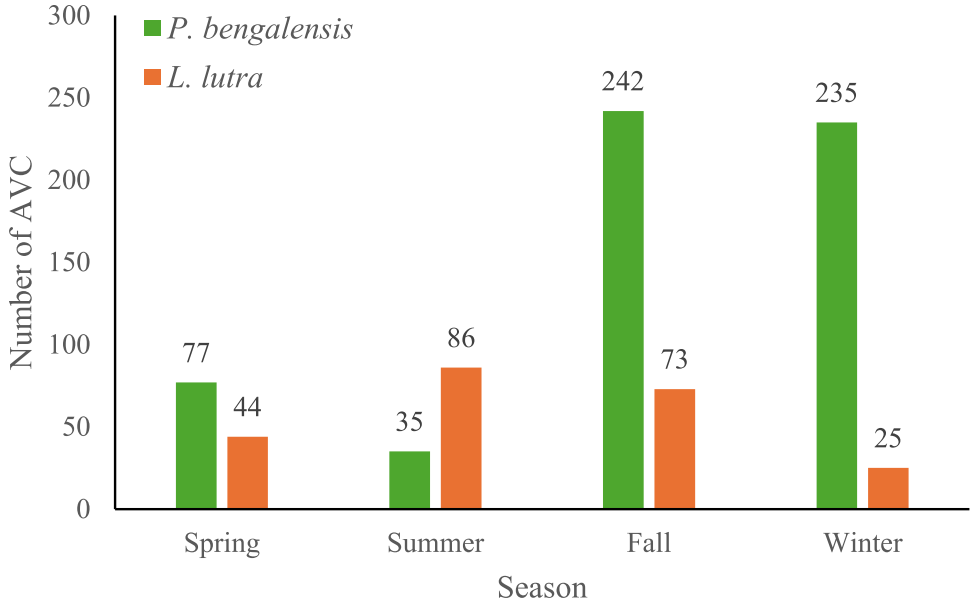


Figure 2. Number of georeferenced animal-vehicle collision (AVC) events for *P. bengalensis* (yellow) and *L. lutra* (orange) by season between 2019 and 2021 in the Republic of Korea. AVC data were collected from the KROS. Spring: March – May; Summer: June – August; Fall: September – November; Winter: December – February.

range was the most significant, followed by annual precipitation and greenness. These variables effectively represented the habitat conditions of *P. bengalensis*.

For *L. lutra*, the habitat suitability model was more robust, with an AUC of 0.769 ± 0.013. The key retained variables included temperature seasonality, precipitation during the wettest month, and river-coast distance. River-coast distance contributed the most, followed by temperature seasonality and precipitation during the wettest month. Similarly, river-coast distance was the most critical factor in permutation importance, followed by precipitation during the wettest month and temperature seasonality. These variables accurately reflect the distribution of *L. lutra* in water bodies. Overall, the environmental variables retained in the models mirrored the general habitat conditions of the two threatened species.

AVC models of P. bengalensis

We included all predictors in the final models, as their VIF values were below 5, indicating that multicollinearity was not a concern. The predictive power of the AVC probability models for *P. bengalensis* was considered acceptable (AUC > 0.7; TSS > 0.4) across seasons (Table 3). The models indicated particularly high AVC probabilities in the mid-eastern areas of the country, including national parks (Figure 3). Habitat suitability and traffic-related variables were critical predictors across seasons (Table 4). Habitat suitability exhibited the highest permutation importance in spring, fall, and winter, whereas urban distance was the most crucial factor in summer (Table 4). Given that most AVC events occurred in fall and winter, habitat suitability emerged as the best predictor of AVC in P. bengalensis, with traffic-related variables ranking second across seasons.

The likelihood of AVC increased monotonically with habitat suitability (Figure 4), indicating that AVC was most likely to occur in suitable habitats. The AVC probability was high near forests up to approximately 100 m from the edge. The AVC probability also peaked at speeds between 40 and 50 km/h and at speeds above 100 km/h, indicating that small and large roads, such as expressways, were dangerous for *P. bengalensis*. The probability was high near urban areas and decreased with increasing distance from them. The AVC probability peaked on roads with three to four lanes, indicating that relatively wide roads, including expressways and national highways, pose considerable risk. Therefore, in *P. bangalensis* AVC predictive models, both habitat – and traffic-related variables played consistently important roles across all seasons.

AVC models of L. lutra

All predictors had VIF values below 5, indicating that multicollinearity was not a concern. The predictive models for the probability of AVC in *L. lutra* were considered acceptable across all seasons (Table 3). High AVC probabilities were observed in the southern part of the country, particularly along coastlines (Figure 5). The critical variables influencing AVC probability varied by season (Table 5). Considering that most AVC events occur in summer and fall, the critical variables in these seasons carry more weight than those in the other seasons. In summer and fall, habitat suitability emerged as the most crucial variable for AVC probability. During summer, land cover and river-coast distance were also significant predictors, highlighting the importance of habitat-related variables for *L. lutra* during this season. In the fall, elevation, wetness, and the number of lanes were key factors that differed considerably from those in summer. There was no single dominant variable for AVC probability across seasons; however, habitat-related factors consistently played a crucial role in seasons with high AVC occurrence.

Table 3. Area under the receiver operating curve (AUC) and true scale statistics (TSS) of eight AVC probability models between 2019 and 2021 in the Republic of Korea.

	Spring	Summer	Fall	Winter
P. bengalensis				
AUC	0.809 ± 0.056	0.765 ± 0.105	0.852 ± 0.026	0.844 ± 0.030
TSS	0.492 ± 0.089	0.433 ± 0.065	0.510 ± 0.034	0.521 ± 0.053
L. lutra				
AUC	0.731 ± 0.089	0.830 ± 0.047	0.872 ± 0.044	0.762 ± 0.089
TSS	0.333 ± 0.096	0.487 ± 0.102	0.606 ± 0.092	0.300 ± 0.157

Note: Values (mean ± standard error) for spring, summer, fall, and winter AVC in each species.

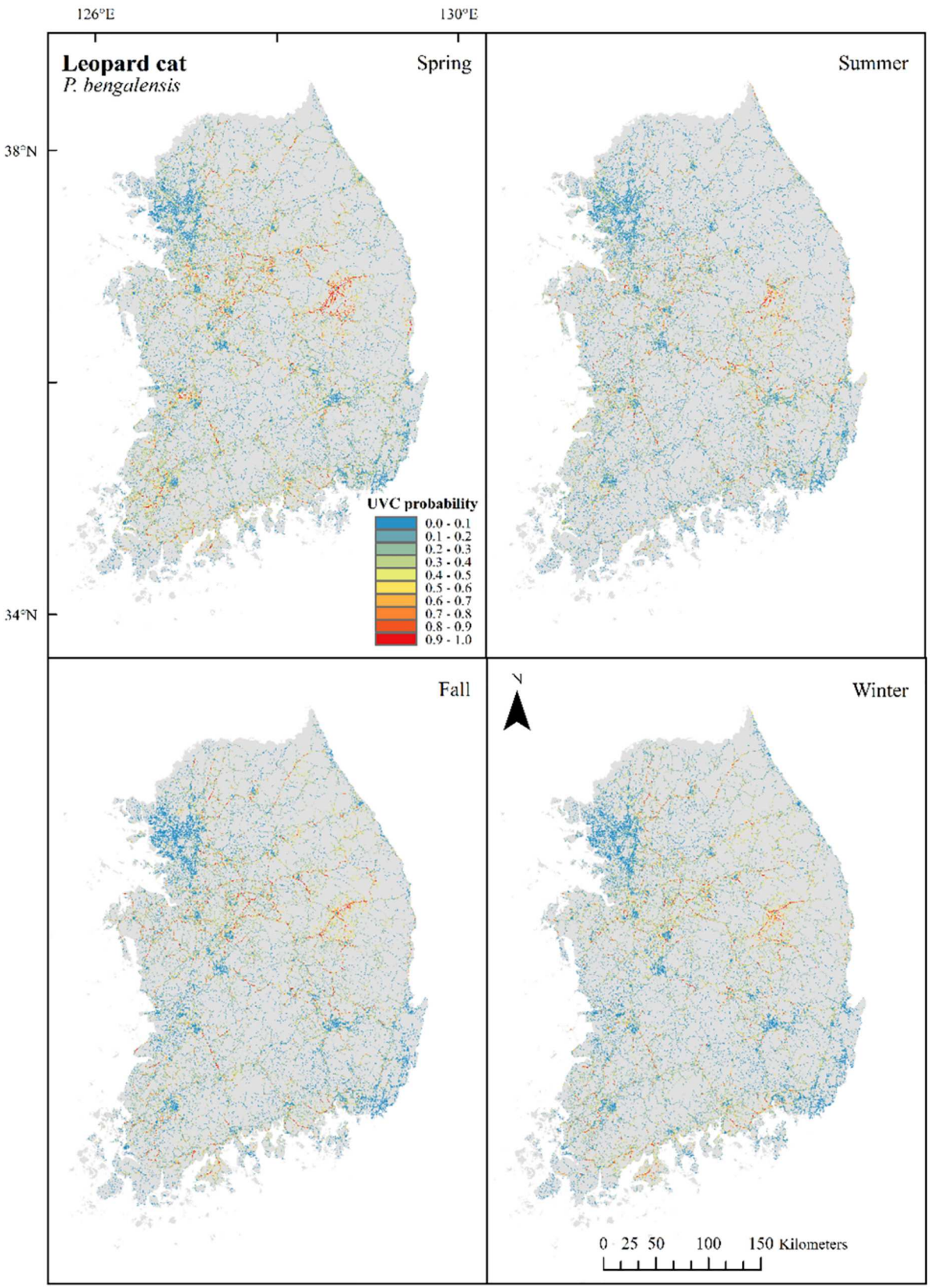


Figure 3. Season-based AVC probability predictions for *P. bengalensis* along roads using AVC data from 2019 to 2021 in the Republic of Korea. The red and blue colors indicate high and low probabilities of AVCs, respectively.

Table 4. Permutation importance (%) of each variable included in the seasonal models of *P. bengalensis* generated using AVC data between 2019 and 2021 in the Republic of Korea.

Category	Parameter	Spring	Summer	Fall	Winter
Bioclimatic	Annual mean temperature	0.4	0.0	0.7	1.2
	Annual precipitation	1.3	1.2	0.0	0.7
Landscape	Elevation	2.8	2.1	1.1	2.0
	Slope	0.9	3.8	0.7	2.1
	Ruggedness	0.2	0.7	1.7	1.3
	Landcover	7.4	6.6	0.8	4.7
	Forest distance	**13.1**	4.6	0.9	1.8
	Urban distance	7.1	**24.4**	1.8	6.6
	Water distance	2.5	2.2	1.2	1.6
	River distance	4.2	1.2	1.5	1.0
	River-coast distance	1.5	0.6	3.7	1.8
	Greenness	9.0	0.2	9.9	8.0
	Wetness	7.2	0.2	3.3	2.2
	Habitat suitability	**20.7**	**13.2**	**49.4**	**39.7**
Traffic	Corridor distance	0.8	2.3	3.0	0.5
	Max speed	**14.8**	**14.3**	6.6	**18.0**
	Lanes	6.0	**22.4**	**13.8**	6.8

Note: The highest values (>10) for each model are presented in bold.

Table 5. Permutation importance (%) of each variable included in the seasonal models of *L. lutra* generated using AVC data between 2019 and 2021 in the Republic of Korea.

Category	Parameter	Spring	Summer	Fall	Winter
Bioclimatic	Annual mean temperature	7.4	0.3	4.1	0.8
	Annual precipitation	5.7	4.4	4.2	**12.9**
Landscape	Elevation	**10.5**	2.8	**13.0**	1.3
	Slope	0.9	6.1	5.3	2.0
	Ruggedness	4.7	0.5	4.0	8.6
	Landcover	6.0	**16.9**	2.5	**10.5**
	Forest distance	9.7	0.9	1.3	3.8
	Urban distance	**20.4**	4.1	2.7	**14.0**
	Water distance	0.5	0.7	3.3	**13.5**
	River distance	2.3	4.4	2.6	4.4
	River-coast distance	0.2	**13.2**	2.9	0.2
	Greenness	3.3	2.3	5.3	0.6
	Wetness	2.4	5.0	**14.0**	5.6
	Habitat suitability	9.8	**24.4**	**17.0**	**11.0**
Traffic	Corridor distance	4.4	0.3	1.4	3.5
	Max speed	7.9	8.3	4.6	2.8
	Lanes	4.0	5.8	**11.8**	4.7

Note: The highest values (>10) for each model are presented in bold.

As habitat suitability increased, the likelihood of *L. lutra* AVC increased monotonically (Figure 6). In the summer, the AVC probability was high for both grassland and agricultural land. The AVC probability decreased slightly as the river-coast distance increased up to approximately 1 km, then gradually increased with greater distance. AVC probability peaked at low elevations, indicating a preference for lowland habitats that are typically in close proximity to water bodies. Additionally, areas with high wetness were more likely to experience AVC. Regarding road types, the AVC probability peaked on four-lane roads, indicating that large roads are more likely to have AVCs. In summary, the critical variables predicting the AVC of *L. lutra* varied seasonally, while habitat-related variables consistently influenced the predictive models across seasons.

Discussion

This study examined the spatiotemporal patterns of AVCs in two threatened mammalian species, *P. bengalensis* and *L. lutra*, within the Republic of Korea. By analyzing seasonal variations in AVC risk, we identified critical factors specific to each species associated with collision vulnerability. Our results demonstrate that AVC incidents involving the two species exhibit seasonal variation, with peaks corresponding to their active seasons. AVC frequencies peaked during the breeding and dispersal seasons in both species, a pattern consistent with previous studies (Seo et al. 2015). Juveniles, who generally have less experience with road hazards, may be more vulnerable to AVCs than adults (Kim et al. 2023). In addition, an expanded home range in the breeding season increases the risk of AVC by facilitating increased animal movement (Kim

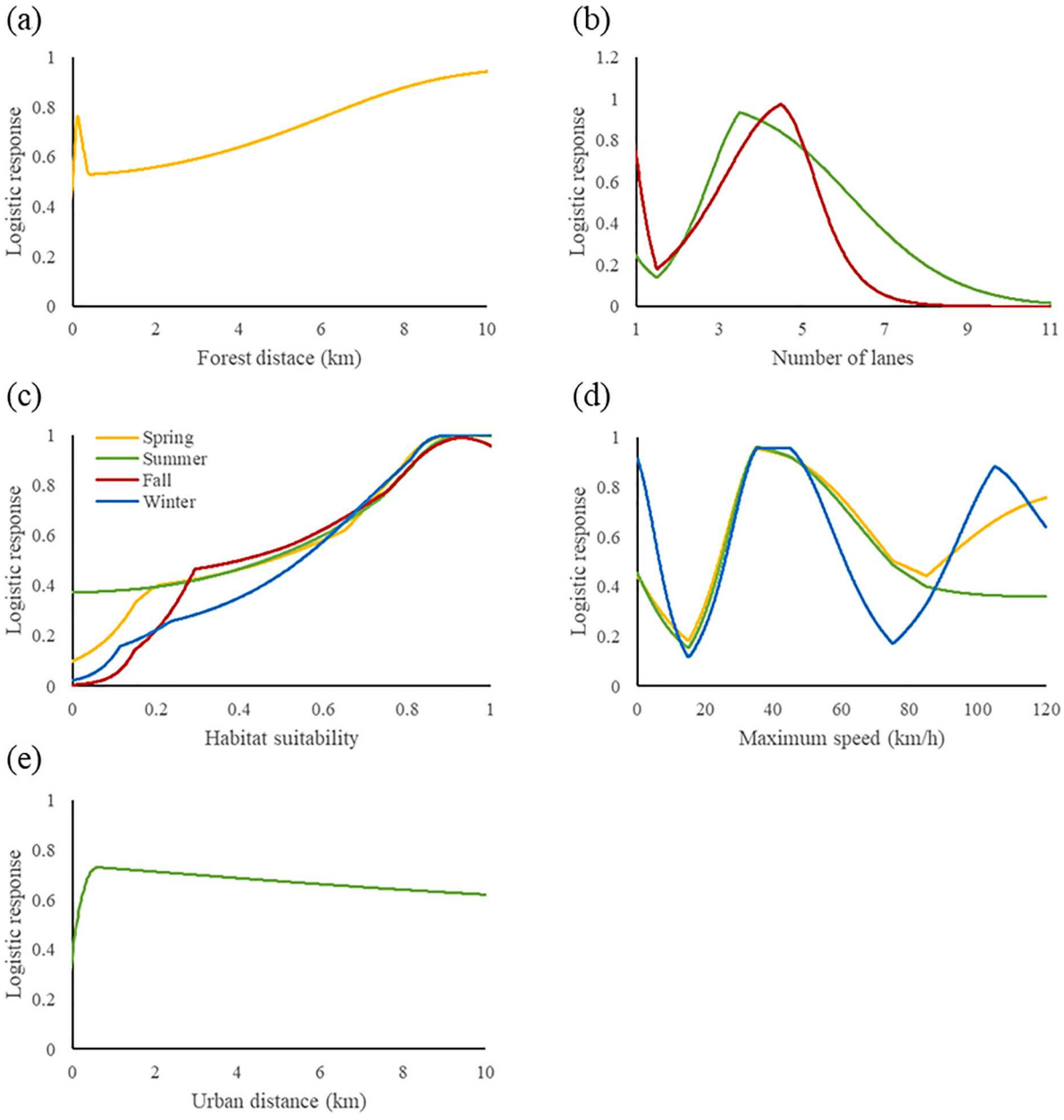


Figure 4. Response curves of variables with a permutation importance above ten in each season for *P. bengalensis*. Panels (a–e) correspond to (a) forest distance, (b) number of lanes, (c) habitat suitability, (d) maximum speed, and (e) urban distance. Each response curve for the predicted probability is independent of other variables in the models. The colors represent the seasons. AVC data were based on the KROS data from 2019 to 2021 in the Republic of Korea.

et al. 2019a). Therefore, high-activity seasons are correlated with elevated AVC rates, even in threatened species. These findings highlight the need to consider seasonally active behaviors for targeted conservation efforts to mitigate AVC risks.

The predictive power of the HSMs, as assessed by the AUC, was higher for *L. lutra* than for *P. bengalensis*. The lower AUC value of *P. bengalensis* likely indicates its status as a habitat generalist, occupying diverse environments without requiring specific environmental conditions for habitat selection (Jo et al. 2018). In contrast to habitat specialists that depend on specific environmental features, such as particular vegetation types or proximity to water, generalist species can adapt to a wide range of habitats, including forests and grasslands. This adaptability complicates the accurate prediction of their presence using HSMs. This broad ecological tolerance results in a lower model fit, as the distribution of species does not strongly align

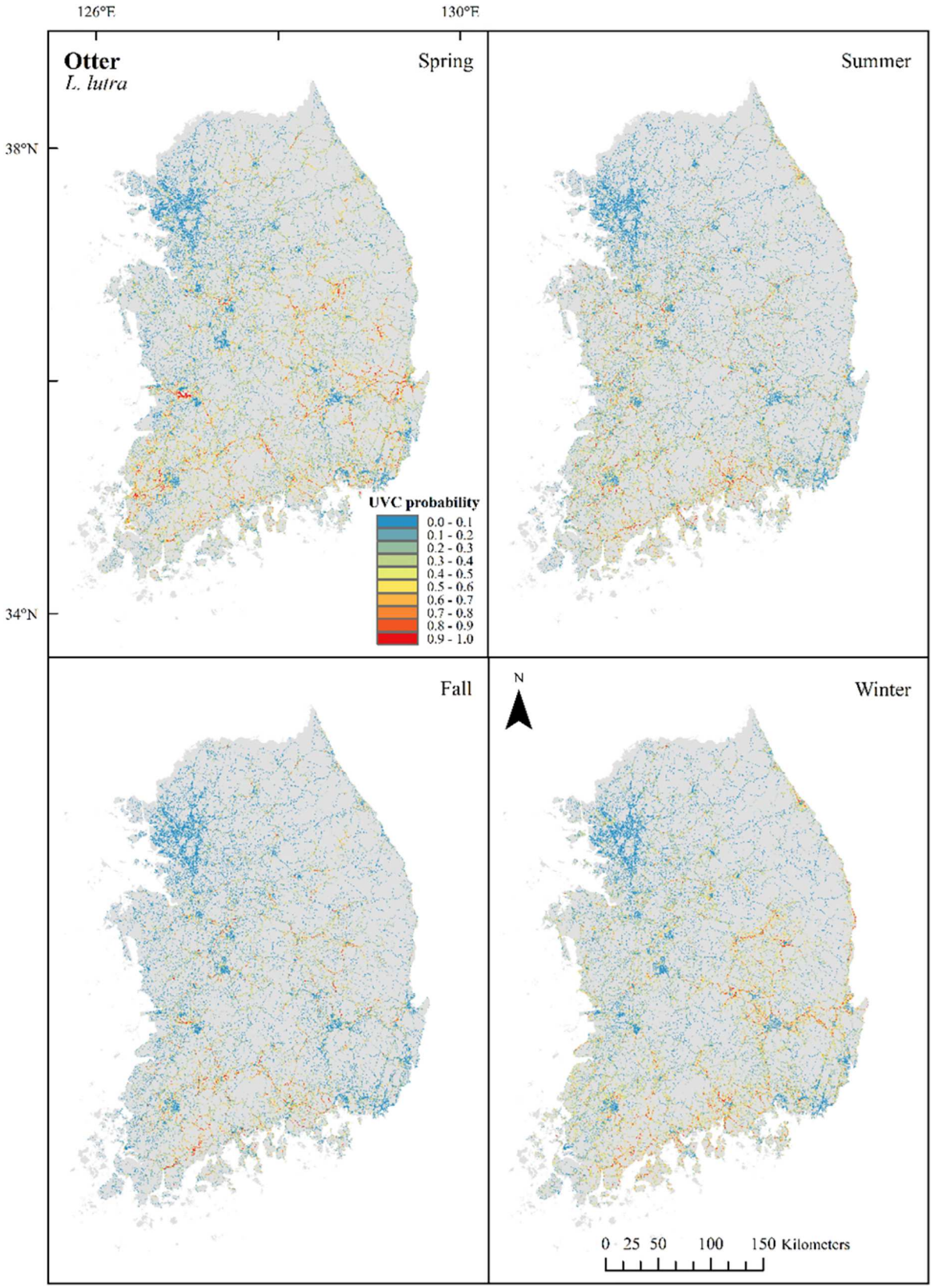


Figure 5. Season-based AVC probability predictions for *L. lutra* along roads using AVC data from 2019 to 2021 in the Republic of Korea. The red and blue colors indicate high and low probabilities of AVCs, respectively.

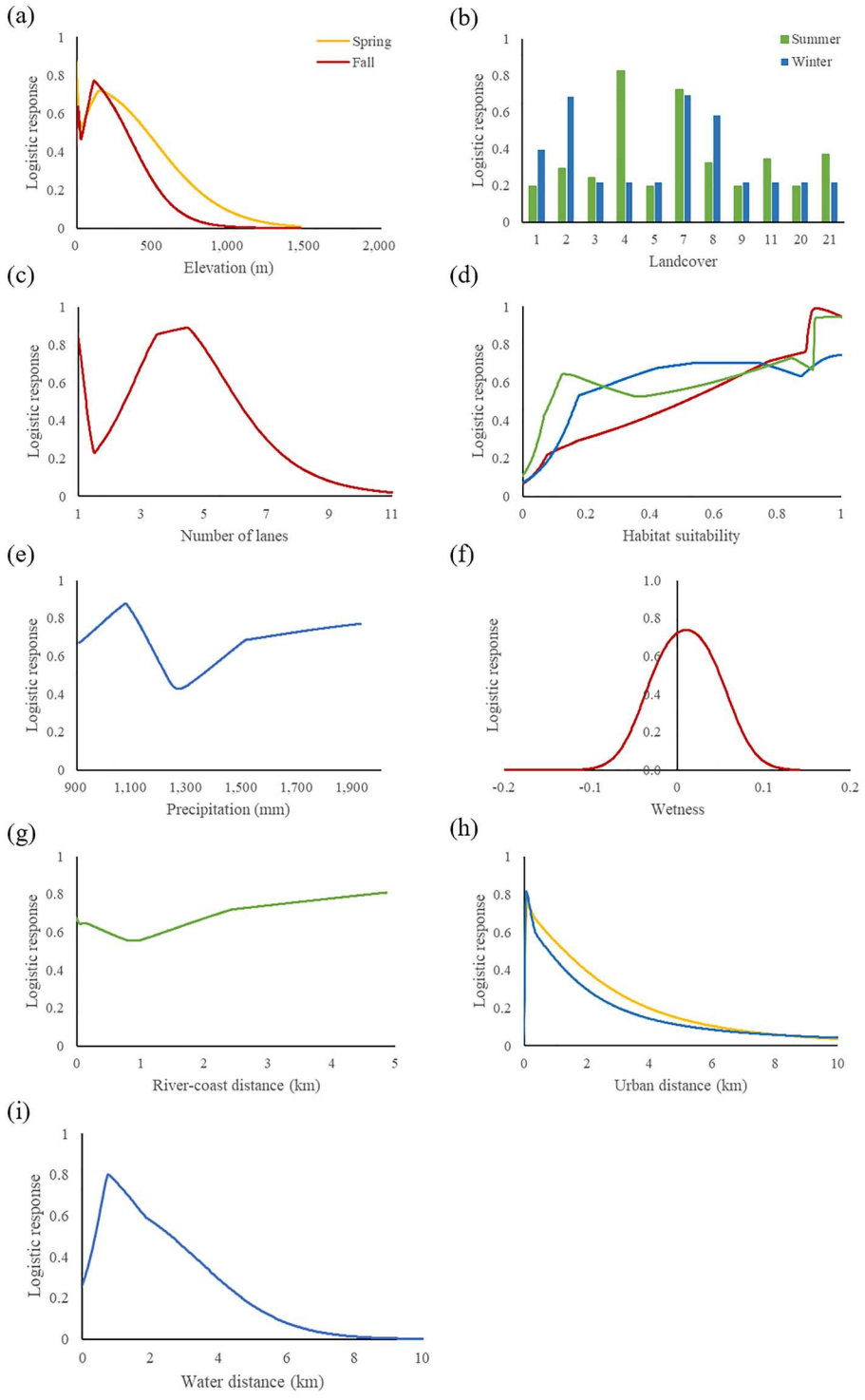


Figure 6. Response curves of variables with high permutation importance above ten by season for *L. lutra* in the Republic of Korea. Panels (a–i) correspond to (a) elevation, (b) landcover, (c) number of lanes, (d) habitat suitability, (e) urban distance, (f) precipitation, (g) wetness, (h) river – coast distance, and.(i) water distance. Each response curve of the predicted probability is independent of the other variables in the models. The colors represent the seasons. AVC data were based on the KROS data from 2019 to 2021 in the Republic of Korea.

with narrow environmental variables, a pattern noted in other generalist species (Peers et al. 2012; Hernandez et al. 2006). Therefore, the lower model fits for *P. bengalensis* are unlikely to undermine the validity of the models; instead, they highlight their generalist nature.

AVCs are particularly prone to occur in high-quality habitats according to AVC predictive models for both species. High-quality habitats are generally associated with increased animal activity due to abundant food and resources. These conditions facilitate increased population densities and promote frequent movements both within and between patches. This increased activity increases the likelihood of animal encounters with roads, particularly when high-quality habitats intersect with road networks. In fragmented landscapes, roads often intersect or border suitable habitats, further intensifying collision risk. For instance, a study on the golden jackal (*Canis aureus*) found that AVC risk was higher in areas with greater habitat suitability, suggesting that these animals are more prone to road crossings in regions where their preferred habitats are abundant (Frangini et al. 2022). These findings highlight the importance of habitat quality when developing effective AVC management.

Traffic factors and habitat characteristics were essential for predicting AVCs for *P. bengalensis* across all seasons. The highest collision risks occurred on four-lane roads, likely because they prevailed on national highways that intersect forest-agriculture boundaries and environments frequently used by this edge-dwelling species (Choi et al. 2012). Moreover, this is likely because most AVCs occurred on expressways and national highways, with four lanes being the most common (58.9%), followed by two (29.3%) and six lanes (7.9%) (Statistics Korea 2020). Additionally, roads with speed limits of 40–50 km/h and above 80 km/h were linked to elevated AVC probabilities, corresponding to small-scale roads in rural areas and national highways or expressways, respectively. These findings indicate that various aspects of road infrastructure and surrounding environments influence AVC risk in this species.

Habitat-related variables emerged as the most critical predictors in the AVC models of L. lutra, with key predictors including habitat suitability, water distance, elevation, and land cover. This species is susceptible to human disturbance (Jo et al. 2017), and its distribution is limited by prey abundance and availability (Ruiz-Olmo et al. 2001). Seasonal variability in key variables reflects L. lutra's susceptibility to changing environmental conditions. The strong association between water-adjacent environments and low-elevation areas suggests that AVCs involving *L. lutra* are strongly influenced by the availability and connectivity of aquatic habitats. Roads that intersect river corridors, particularly in lowland and coastal zones, may serve as major bottlenecks for movement, thereby increasing the likelihood of road crossings. Seasonal variation in key variables also reflects the species' changing spatial behavior, which is linked to breeding and dispersal demands.

In contrast to *P. bengalensis*, traffic-related variables exerted a limited influence on AVC risk in L. lutra, possibly because it relies on natural movement corridors and avoids open terrestrial habitats. However, other studies have indicated a positive correlation between AVCs involving *L. lutra* and traffic volume (Elmeros et al. 2006). This relationship could not be evaluated in the present study owing to a lack of data. Therefore, additional research is required to examine the impact of traffic on the AVC risk in this species.

Although both species exhibited seasonal variations in AVC frequency, the influencing factors differed. For *P. bengalensis*, AVC probability was associated with various road features and their surrounding environments, whereas for *L. lutra*, it was more directly related to aquatic habitat conditions. The observed contrasts illustrate the ecological differences between the species; *P. bengalensis* often inhabits edge habitats near human infrastructure, thereby increasing its exposure to roads, whereas *L. lutra* relies on continuous riparian systems and may be more susceptible to disruptions in habitat connectivity. Understanding these divergent patterns is crucial for developing effective mitigation strategies tailored to the ecological characteristics and behavioral patterns of each species.

This study provides valuable insights into the factors influencing AVC risks for these two threatened species. By identifying species-specific and seasonal patterns, this study highlights the critical periods and spatial factors that increase collision risks. These findings provide a scientific basis for designing effective and targeted mitigation strategies. Management strategies should incorporate habitat characteristics and seasonal behavioral patterns to prioritize road sections that intersect with high-quality habitats, especially during biologically active periods. For *P. bengalensis*, both habitat – and traffic-related features should be considered when identifying priority intervention areas. Roads near forest edges and segments with high habitat suitability and intermediate-to-high-speed limits warrant particular attention. Four-lane roads,

prevalent on expressways and national highways, are associated with elevated AVC rates and warrant targeted examination. Installing wildlife crossings and fencing along these roads can facilitate animal movement and minimize road access. In addition, implementing speed-reduction measures and installing warning signs near forests and urban areas may improve driver awareness. These actions are crucial during periods when the species demonstrates expanded ranging behavior associated with breeding and dispersal.

In the case of *L. lutra*, habitat-related variables were more influential in predicting the AVC risk. Management strategies should concentrate on roads adjacent to water bodies where suitable habitats and movement corridors are concentrated. Structures, including underpasses or tunnels at road-water intersections, enable safe passage between aquatic habitats. The fencing of these areas may further prevent road access. Restoring degraded riparian habitats and maintaining wet conditions near water bodies may mitigate AVC risks by supporting natural movement patterns. Mitigation efforts should account for periods of increased movement associated with breeding and juvenile dispersal, during which road-crossing frequency may intensify. Integrating spatial patterns of high AVC probability with species behavior and seasonal activity enables more effective management in reducing AVCs. These findings underscore the importance of incorporating ecological data into road planning and mitigation policies to facilitate the long-term conservation of threatened mammalian species in the Republic of Korea.

Although this study identified the key risk factors associated with AVCs involving the two threatened species, further research is required to address additional variables not included in this analysis. For instance, integrating road-related factors, such as traffic volume, road curvature, and nighttime lighting conditions, may enhance understanding of AVC dynamics. Incorporating landscape connectivity metrics into AVC models enhances the representation of movement corridors, which are essential for wildlife populations. Moreover, including variables that directly influence AVC risks, such as animal density, and incorporating individual-level information, such as age and sex when available, can improve model accuracy and predictive power. In addition to direct mortality, chronic exposure to anthropogenic disturbances such as roads may impose physiological stress on wildlife, potentially affecting immune responses and population resilience through inflammation-related pathways (Oh et al. 2025). These efforts are anticipated to support more effective and targeted mitigation strategies ultimately.

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No potential conflict of interest was reported by the author(s).

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Data availability statement

The datasets analyzed during the current study are available from the National Institute of Ecology on reasonable request.

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