

ORIGINAL RESEARCH

Higher mortality rates for large- and medium-sized mammals on plantation roads compared to highways in Peninsular Malaysia

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Abstract

The fragmentation of forests by agricultural expansion, urbanization, and road networks is an ongoing global biodiversity crisis. In Southeast Asia and other tropical regions, wildlife populations are being isolated into pockets of natural habitat surrounded by road networks and monoculture plantations. Mortality from wildlife–vehicle collisions (WVCs) is contributing to a decline in many species of conservation priority in human-modified landscapes. This study is the first in Malaysia to investigate factors affecting the occurrence of WVCs. We assessed roadkill data gathered by the Department of Wildlife and National Parks on small-, medium-, and large-sized mammals in Peninsular Malaysia. We examined the relationship between wildlife road accidents and several environmental factors. We found a total of 605 roadkill animals, involving 21 species, which included three species classified as Endangered. Road type (plantation road or highway), year, and distance of the road from continuous and fragmented forests were significant in determining mammal mortality. Unexpectedly, the majority of road mortality occurred on palm oil plantation roads compared to highways. Mortality of small- and medium-sized mammals was greater at locations further from continuous forest than those closer to fragmented forests. Segmentation of continuous forest by roads should be avoided wherever possible to reduce the threat of roads on crossing wildlife.

KEYWORDS

forest, fragmentation, palm oil, road type, roadkill, wildlife

1 | INTRODUCTION

Both vertebrate and invertebrate species occurring in forests are under increasing pressure from habitat loss, habitat fragmentation and hunting and/or illegal hunting, that is, poaching (Alroy, 2017;

Jamhuri et al., 2018; Newbold et al., 2014; Samantha et al., 2020; Tee et al., 2018). Using satellite imagery, Curtis et al. (2018) reported that 27% of global forest loss (~5 million hectares of forest a year), over a fifteen year period (2001–2015), can be attributed to deforestation through permanent land use change for commodity production,

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such as palm oil, mining, oil and gas production extractive industries, and urban expansion.

Estimates of global forest loss from 2013 to 2014 are ~18.7 million hectares or a 9% decline in forest cover, partly due to the expansion of plantations and linear infrastructure including roads, railways, and power lines (Butler, 2015). These anthropogenic threats are common in tropical and subtropical countries with high biodiversity and diverse ecosystems (Alamgir et al., 2017; Laurance & Arrea, 2017). Road construction, in particular, creates a myriad of problems for wildlife such as forest degradation, barriers to access critical resources, such as food, shelter and breeding opportunities, increased accessibility to intact landscapes for hunters, and mortality from vehicle collisions (Alamgir et al., 2019; Ascensão et al., 2017; Chen & Koprowski, 2016; Jaeger & Fahrig, 2004; Laurance et al., 2009, 2014; Santos & Tabarelli, 2002). Wildlife–vehicle collisions (WVCs) are globally considered to be one of the major threats to wildlife (van der Ree et al., 2011). For example, in the United States, Loss et al. (2014) estimated that between 89 and 340 million birds are killed each year from collisions with vehicles.

Roads expose wildlife to vehicle collisions, resulting in an injury or a mortality to both wildlife and humans and can influence environmental and economic loss (Grilo et al., 2018). Often where road networks border forested areas, WVCs are high due to poor visibility for drivers (Kang et al., 2016). The vulnerability of wildlife to vehicle collisions is related to a range of factors such as mobility, habitat specificity, reproductive rate, resource need, and home range (Laurance et al., 2006). Furthermore, increased traffic volume, high speed roads and more highways, and wildlife–vehicle collisions (WVCs) have become more frequent, particularly in developing countries (Grilo et al., 2018). In Malaysia, increased deforestation and conversion of land to monoculture plantations as well as increased road expansion and development are likely to lead to increased WVCs as forests become more fragmented by plantation roads and highways (Azhar et al., 2013, 2014; Clements et al., 2014; Kolowski & Nielsen, 2008; Wadey et al., 2018).

The aim of this study is to determine road-related and landscape factors that influence the incidence of WVCs using wildlife roadkill occurrence data. We investigated whether WVCs were affected by the distance of the road (and road type) to continuous and fragmented native forests. We compared the effect of two paved road types (Figure 1): (a) highways with two or four-lane roads and (b) plantation roads in palm oil production areas. We predicted that the WVCs would be greater in plantation roads due to their proximity to forest; as found in WVC studies in the United States, Brazil, and Italy (e.g., Eberhardt et al., 2013; Fabrizio et al., 2019; Grilo et al., 2018).

2 | METHODS

2.1 | Study area

The dataset for this study was collected from paved plantation roads and highways across Peninsular Malaysia (area of 130,598 km²;



FIGURE 1 Typical agricultural plantation road (top) and highway (bottom) on Peninsular Malaysia

Figure 1) with more than 50% of its area ~150 m AMSL (range = 69.6–95.3 m). The average daily temperature is ~26°C (range = 21–32°C), with average rainfall/year ~2,400 mm (range = 1,800–3,000 mm per year). The natural habitat of Peninsular Malaysia is high in biodiversity, comprising mostly tropical rainforests due its location along the equator, including lowland/hill dipterocarp and peat swamp forests. These include Endangered tree species such as *Shorea pauciflora*, *Vatica kanthanensis*, and *Dipterocarpus sarawakensis* (Kochummen et al., 1990; Magintan et al., 2017; Okuda et al., 2003; Yule, 2010). There are 223 mammal species in Peninsular Malaysia. Of these, four species are classified as Critically Endangered, 13 are Endangered, 28 are Vulnerable, and 26 are Near Threatened (DWNP, 2017).

2.2 | Data collection

Wildlife roadkill data were gathered over a five-year periods (2010–2014) by Department of Wildlife and National Parks (DWNP) personnel in Peninsular Malaysia. Data were gathered by road patrols for specific regions (i.e., 47 DWNP district offices in 11 states). These teams comprised two personnel (with one being the driver and the other detecting roadkill), who both had expertise in identifying wildlife species, and

in accordance with standard operation procedures established by the DWNP (DWNP, 2010). A mammal guide was also used (Francis, 2008) to further aid species identification. Patrols were conducted three times per week which encompassed most rural areas, with the vehicle driven at a constant speed (90 km/hr) on highways and plantation roads. We used distance patrolled by DWNP personnel from office to accident location as a measure of survey effort ($\bar{x} \pm SE = 20 \pm 0.60$ km).

Roadkill data were categorized according to typical body weight of the species into small- (<2 kg), medium- (2–15 kg), or large-sized (>15 kg) mammals (Francis, 2008) (see Table 1). The personnel also recorded the road type (plantation road or highway) and roadkill location (Figure 2). To prevent illegal harvesting of animal body parts and organs and also to avoid recounts, carcasses were immediately transferred from accident location to the nearest DWNP office.

2.3 | Measurement of landscape characteristics

We measured the distances of road from the nearest continuous forest (an area more than 10,000 ha) and from the nearest fragmented forest (an area less than 10,000 ha) and altitude at the roadkill location using the measurement tool in Google Earth (GE) Pro (Version

6) (Table 2). GE Pro provided the remote sensing imagery for the measurement of the above variables. The GE images were acquired between 1 June and 4 September 2014 and commonly had a spatial resolution of 15 m per pixel (Potere, 2008).

2.4 | Data analysis

We used generalized linear mixed models (GLMMs) (Schall, 1991) to quantify relationships among roadkill and landscape-level attributes (e.g., distance of road from fragmented forest), road type, and number of WVCs/year. Two additional models were developed to examine the effects of environmental variables on large- and medium-sized mammal roadkill. We did not analyze small-sized mammal roadkill due to insufficient sample size. We included five explanatory variables: distance of road from continuous forest (m), distance of road from fragmented forest (m), altitude (m), survey effort (m), road type (highways or plantation roads), and year. We used a Poisson distribution with a log-link function in the modeling process. WVC location was used as random factor. The dispersion parameter was fixed at 1.

To examine the potential challenge arising from multi-collinearity between predictor variables, we performed correlation tests

TABLE 1 List of small-, medium-, and large-sized mammal roadkill species in Peninsular Malaysia (2010–2014)

Mammal type	Species			Feeding guild	IUCN status	Number of roadkill	
	Common name	Scientific name	Family			Highways	Plantation roads
Large mammals (>15 kg)	Wild pig	<i>Sus scrofa</i>	Suidae	Omnivore	LC	58	18
	Asian tapir	<i>Tapirus indicus</i>	Tapiridae	Herbivore	EN	21	7
	Asiatic wild dog	<i>Cuon alpinus</i>	Canidae	Carnivore	EN	1	0
	Asian elephant	<i>Elephas maximus</i>	Elephantidae	Herbivore	EN	1	0
Medium mammals (2–15 kg)	Common palm civet	<i>Paradoxurus hermaphroditus</i>	Viverridae	Omnivore	LC	138	79
	Long-tailed macaque	<i>Macaca fascicularis</i>	Cercopithecidae	Omnivore	LC	148	7
	Leopard cat	<i>Prionailurus bengalensis</i>	Felidae	Carnivore	LC	28	23
	Dusky leaf monkey	<i>Trachypithecus obscurus</i>	Cercopithecidae	Herbivore	NT	14	0
	Malay civet	<i>Viverra zibetha</i>	Viverridae	Omnivore	LC	3	11
	Smooth-coated otter	<i>Lutrogale perspicillata</i>	Mustelidae	Carnivore	VU	7	7
	Malayan porcupine	<i>Hystrix brachyura</i>	Hystriidae	Omnivore	LC	4	7
	Pig-tailed macaque	<i>Macaca nemestrina</i>	Cercopithecidae	Omnivore	VU	3	2
	Bearcat/ binturong	<i>Arctictis binturong</i>	Viverridae	Omnivore	VU	3	1
	Banded leaf monkey	<i>Presbytis femoralis</i>	Cercopithecidae	Herbivore	NT	2	1
	Yellow-throated marten	<i>Martes flavigula</i>	Mustelidae	Carnivore	LC	2	0
	Javan mongoose	<i>Herpestes javanicus</i>	Herpestidae	Carnivore	LC	1	0
	Malayan pangolin	<i>Manis javanica</i>	Manidae	Carnivore	CR	1	0
	Large Indian civet	<i>Viverra zibetha</i>	Viverridae	Carnivore	NT	1	0
Small mammals (<2 kg)	Plantain squirrel	<i>Callosciurus notatus</i>	Sciuridae	Omnivore	LC	3	0
	Black giant squirrel	<i>Ratufa bicolor</i>	Sciuridae	Herbivore	NT	2	0
	Moonrat/gymnure	<i>Echinosorex gymnurus</i>	Erinaceidae	Carnivore	LC	1	0

Note: IUCN Status; IUCN Red List of Threatened Species: LC—Least Concern, VU—Vulnerable, NT—Near Threaten, CR—Critically Endangered.

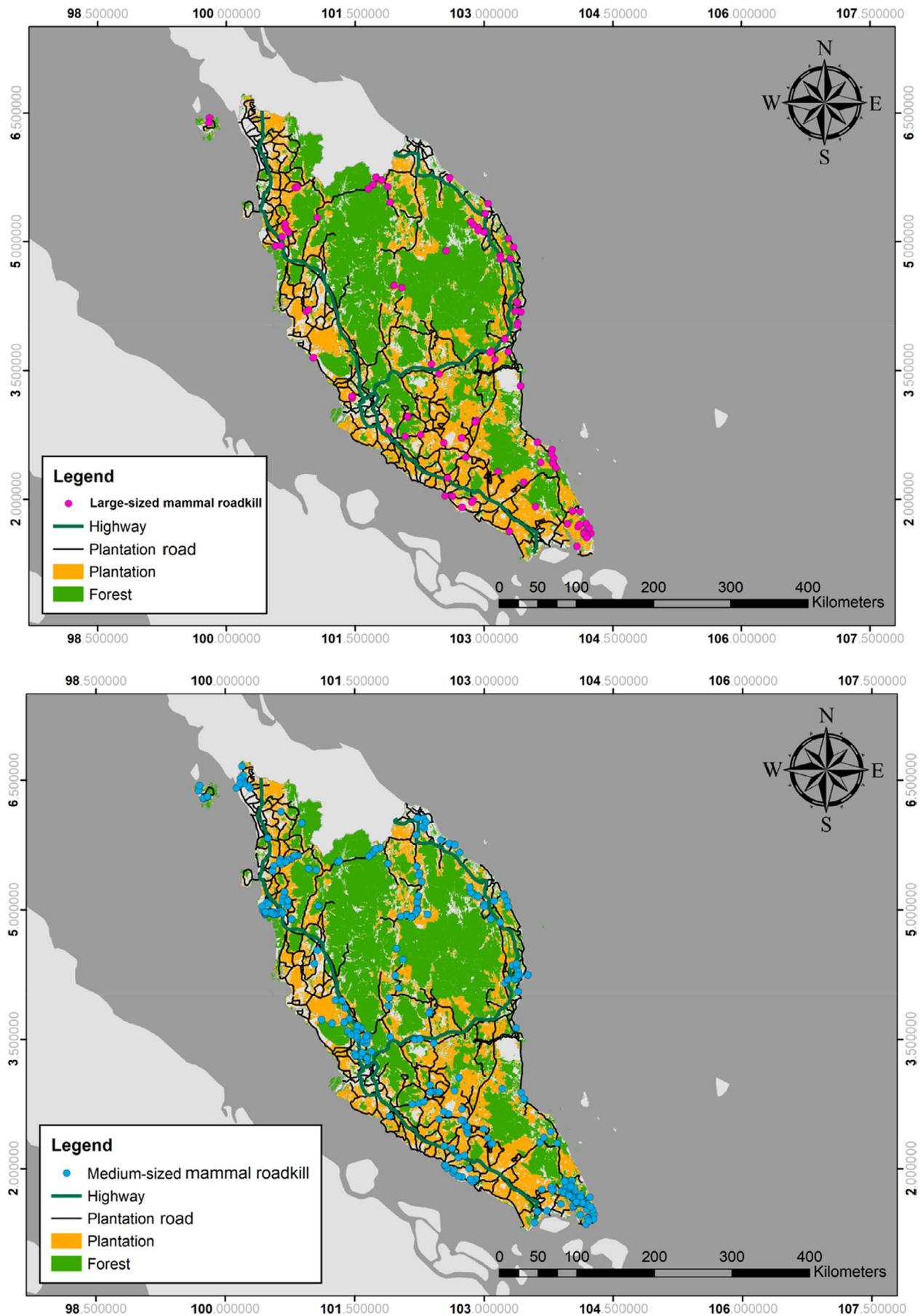


FIGURE 2 Locations of roadkills on Peninsular Malaysia (2010–2014)

among variables. No correlated variables were excluded as all variables were correlated below $|r| = 0.7$, the model distortion limit of Dormann et al. (2013). We fitted all possible regression models to select the final model (Schall, 1991). We followed Johnson and Omland (2004) by selecting data based on alternative hypotheses prior to data collection and analysis. We selected the most parsimonious models based on the minimum Akaike's information criterion (AIC) values (Anderson & Burnham, 2004). Since sample size (n), relative to the parameter (K), was large ($n/K = 456/6 = 76 > 40$) for at least one of the models, we did not use a corrected AIC (AICC) to compare the models (Anderson & Burnham, 2004). We reported the adjusted coefficient of regression, r^2 for the models. All analyses were performed in generalized linear models (GLMs) in GenStat 12th Edition (VSN International, Hemel Hempstead, UK).

TABLE 2 Summary statistics for distance between nearest continuous forest or fragmented forest and roadkill record location

Attribute	Mean	SE
Distances from the nearest continuous forest (km)	41.1	1.9
Distance from the nearest fragmented forest (km)	4.2	0.3

TABLE 3 Best subsets from candidate models

Response variable	Model	Explanatory variable	Adjusted R^2	AIC
Overall roadkill	1	Road type	20.40	205.81
	2	Model 1 + Distance from continuous forest	25.45	194.57
	3*	Model 2 + Year	28.14	194.17
	4	Model 3 + Distance from fragmented forest	28.77	194.19
	5	Model 4 + Altitude	28.94	195.38
	6	Model 5 + Survey effort	28.86	197.19
Large-sized mammal roadkill	1	Year	2.07	342.91
	2	Model 1 + Road type	3.50	339.33
	3*	Model 2 + Distance from fragmented forest	4.56	336.99
	4	Model 3 + Distance from continuous forest	4.66	337.96
	5	Model 4 + Altitude	4.98	338.16
	6	Model 5 + Survey effort	4.92	339.65
Medium-sized mammal roadkill	1	Road type	12.09	354.46
	2	Model 1 + Distance from continuous forest	15.42	342.47
	3	Model 2 + Year	19.04	333.21
	4*	Model 3 + Distance from fragmented forest	20.51	328.72
	5	Model 4 + Altitude	20.76	329.05
	6	Model 5 + Survey effort	20.63	330.85

Note: The most parsimonious model for each response variable (labeled with *) is determined based on a lowest AIC and complemented with an adjusted R^2 .

3 | RESULTS

3.1 | General patterns of wildlife roadkill occurrences

During the five-year period, the total survey effort was more than 9.1 million km (7.6 million km and 1.5 million km travelled on highways ($n = 388$ WVC locations) and plantation roads ($n = 68$ WVC locations), respectively). A total of 605 roadkill animals were recorded between 2010 and 2014 (Figure 2), with 106 large-, 493 medium-, and six small-sized mammal records. In terms of feeding guild, carnivore, herbivore, and omnivore had 72, 48, and 485 records, respectively. Twenty-one species were recorded, 11 of which are listed for protection under the Wildlife Conservation Act 2010 (Act 716). Three of the recorded species are listed as Endangered: the Malayan tapir (*Tapirus indicus*), Asian wild dog (*Cuon alpinus*), and Asian elephant (*Elephas maximus*). Three are listed as Vulnerable by the IUCN Red List (IUCN, 2017): the smooth-coated otter (*Lutrogale perspicillata*), pig-tailed macaque (*Macaca nemestrina*), and binturong (*Arctictis binturong*) (Table 1).

No small-sized mammal roadkill was recorded on plantation roads, but six records were detected on highways. No roadkill was recorded involving the large-sized carnivores in Peninsular Malaysia such as the Malayan tiger (*Panthera tigris*) and leopard (*P. pardus*). The common

Response variable	Explanatory variable	Slope	SE
Overall roadkill	Road type		
	Highways	0.000	
	Plantation road	0.424	
	Distance of road from continuous forest	3.620×10^{-6}	1.287×10^{-6}
	Year		
	2010	0.000	
	2011	-0.378	
	2012	-0.313	
	2013	-0.235	
	2014	-0.398	
Large-sized mammal roadkill	Road type		
	Highways	0.000	
	Plantation road	0.175	
	Distance of road from fragmented forest	2.188×10^{-5}	1.131×10^{-5}
	Year		
	2010	0.000	
	2011	0.212	
	2012	0.733	
	2013	0.631	
	2014	0.755	
Medium-sized mammal roadkill	Road type		
	Highways	0.000	
	Plantation road	0.454	
	Distance of road from continuous forest	5.225×10^{-6}	1.501×10^{-6}
	Distance of road from fragmented forest	-1.984×10^{-5}	9.310×10^{-6}
	Year		
	2010	0.000	
	2011	-0.462	
	2012	-0.469	
	2013	-0.364	
2014	-0.640		

TABLE 4 Coefficient of each explanatory variable in the most parsimonious models

palm civet (*Paradoxurus hermaphrodites*) had the highest number of mortality records (Table 1). Based on the available data, the exact time of the WVCs was unknown and hence it was impossible to determine whether most accidents occurred during the day or night. However, we can assume that some roadkill animals were nocturnal (seven species or 33%). Most of the roadkill (12 species or 57%) were forest-dependent species (Table 1), with the exception of wild pig, long-tailed macaque, plantain squirrel, and common palm civet, which can be found in a wide range of habitats including forests and agricultural areas (Azhar et al., 2014; Tee et al., 2019).

Our data also indicated that solitary animals and common species were the most likely to have WVCs, whereas large-sized conservation priority species such as the Asian elephant (*E. maximus*) and

Asiatic wild dog (*C. alpinus*) were the least likely. However, the numbers of wildlife roadkill involving animals that occur in large groups and common species such as long-tailed macaque (*Macaca fascicularis*), Common palm civet (*Paradoxurus hermaphrodites*), and wild pig (*Sus scrofa*) were moderately high.

3.2 | Factors associated with mammal roadkill occurrences

The most parsimonious model for predicting total mammal roadkill was one in which road type and distance of road from continuous forest were the explanatory variables (Table 3). Our results revealed

that the number of WVCs on the plantation roads was 0.42 times greater than the highways (Table 4). Plantation roads had higher WVCs irrespective of body size ($\bar{x} \pm SE = 2.338 \pm 0.326$ roadkill/location) than highways ($\bar{x} \pm SE = 1.149 \pm 0.0317$ roadkill/location). We found that the number of wildlife roadkill was higher in areas located further from continuous forests than fragmented ones (Table 4). Altitude, distance of road from fragmented forest, survey effort, and year had no significant effect on WVC occurrence. This model explained 28.14% of variation in wildlife roadkill across WVC locations (Table 3).

3.3 | Roadkill occurrences involving large-sized mammals

The most parsimonious model for large-sized mammal roadkill was one that included road type, distance from fragmented forest, and year (Table 3). Our results showed that the number of WVCs involving large-sized mammal on the plantation roads was 0.66 times greater than the highways (Table 4). Roadkill involving large-sized mammals were more likely to happen on plantation roads ($\bar{x} \pm SE = 0.368 \pm 0.0861$ roadkill/location) than highways ($\bar{x} \pm SE = 0.209 \pm 0.0222$ roadkill/location). Our results also revealed that the number of large-sized mammal roadkill was greater in areas located further away from forest fragments than those closer to the forests (Table 4). The number of large-sized mammal roadkill was significantly influenced by year (Table 4). The lowest WVC occurrence ($\bar{x} \pm SE = 0.118 \pm 0.0446$ roadkill/location) was in 2011, but the highest record ($\bar{x} \pm SE = 0.310 \pm 0.0511$ roadkill/location) was in 2014. We did not detect significant effects from altitude, survey effort, and distance from continuous forest on the number of large-sized mammal roadkill. The coefficient of determination, adjusted R^2 for this model, was 4.56% (Table 3).

3.4 | Roadkill occurrences involving medium-sized mammals

The most parsimonious model for explaining variations in medium-sized mammal roadkill was one in which road type, distance of road from continuous forest, distance from fragmented forest, and year were the explanatory variables (Table 3). Our results showed that the number of roadkill involving medium-sized mammals in the plantation roads was 0.4540 greater than the highways (Table 4). As with large-sized mammal roadkill, more medium-sized mammal roadkill were found on plantation roads ($\bar{x} \pm SE = 1.971 \pm 0.312$ roadkill/location) than highways ($\bar{x} \pm SE = 0.925 \pm 0.0343$ roadkill/location). The number of medium-sized mammal roadkill was more likely to increase in areas located further away from continuous forests than those closer to the forests (Table 4). In contrast, the number of medium-sized mammal roadkill decreased with distance from the nearest forest patch (Table 4). The number of medium-sized mammals was significantly attributed to year (Table 4). The highest

WVC occurrence ($\bar{x} \pm SE = 1.633 \pm 0.290$ roadkill/location) was in 2010 followed by 2013 ($\bar{x} \pm SE = 1.147 \pm 0.134$ roadkill/location) then 2011 ($\bar{x} \pm SE = 0.985 \pm 0.0491$ roadkill/location) and 2012 ($\bar{x} \pm SE = 0.958 \pm 0.0572$ roadkill/location) with the lowest record ($\bar{x} \pm SE = 0.888 \pm 0.0782$ roadkill/location) in 2014. Finally, roadkill occurrences involving medium-sized mammals were not influenced significantly by altitude and survey effort. This model explained 20.51% of the variation in medium-sized mammal roadkill across WVC locations (Table 3).

4 | DISCUSSION

This is the first study in Malaysia and perhaps Southeast Asia to quantitatively investigate factors affecting the occurrence of WVCs over large scales. We showed that 28 Malayan tapirs, an Asian elephant, and a wild dog were killed in WVCs over the study period. The mortalities of these endangered species from WVCs will likely make a marked impact on their already declining populations due to anthropogenic threats such as logging, agricultural expansion, poaching, and urbanization (IUCN, 2017) and should cause national and international concern. It should be noted that our study only includes WVCs discovered by wildlife department personnel and that the populations of these species, in Peninsular Malaysia, have been declining based on the population data from IUCN (2017). Therefore, the impact of WVCs on Malayan Tapir and Asian Elephant populations is likely to be underestimated.

While carnivores are considered to be less common roadkill than mammals with other diet types (Ford & Fahrig, 2007), our results revealed otherwise, with carnivores being more common roadkill than herbivores. This is likely due to carnivores having bigger home ranges than herbivores in tropical rainforests, requiring them to travel greater distances and cross both highways and plantation roads (Linkie & Ridout, 2011; Naha et al., 2016; Ripple et al., 2014). Furthermore, our results revealed that the number of roadkill for medium-sized mammals was higher compared than large-sized mammals, likely due to larger numbers of medium-sized mammals than large-sized mammals, whereas the population number of small-sized mammal species is probably larger than medium-sized and large-sized mammal, but detected less often, most likely due to the difficulty of detection as roadkill and the speed of patrol vehicle. Besides animal size, road type is another key factor that should be considered by wildlife agencies when implementing mitigation strategies or measures to reduce WVCs.

Our data can improve region-wide conservation planning for identifying hotspot locations of wildlife road accidents in Peninsular Malaysia. However, there are limitations to our study. First, data were unavailable to indicate whether DWNP personnel invested differential survey efforts on highways compared with plantation roads. However, accumulated distances travelled by personnel on plantation roads and highway were not available to correct the analysis for survey effort. Second, our data describe the number of roadkill at each WVC location but not the number

of roadkill/km/year. Third, the speed of the patrol vehicle (i.e., 90 km/hr) was likely too fast, resulting in some roadkill being undetected. And finally, the GE satellite imagery was acquired after data were collected, and therefore, landscape change during this survey period was not recorded.

4.1 | Factors influencing wildlife road accidents

Our study found roadkill were higher on plantation roads compared to highways; a finding consistent with Orłowski and Nowak (2006) who suggested road-related factors (e.g., road location and vehicle traffic volume) may influence roadkill patterns. The expansion of industrial-scale plantations in Malaysia, particularly palm oil monoculture around forest reserves and protected areas, is likely to increase road construction (for transporting oil palm from plantation to mill) and subsequently cause more WVCs. Some mammal species such as primates and civets may utilize forest patches inside palm oil plantations for foraging (Azhar et al., 2013, 2014; Bernard et al., 2014) and thus are likely to cross roads to access these areas. Transient mammals utilizing palm oil habitat such as wild boar, tapir, and pig-tailed macaque may cross roads in order to find food resources (Bernard et al., 2014; Sasidhran et al., 2016).

Forest-dependent mammals will come into increasing contact with roads as their habitat is fragmented and destroyed leading to the likelihood of an increase in the relative number of mammals involved in WVCs. Plantation roads may also function in a similar way as other linear clearings (e.g., along roads, power lines, or train tracks) whereby there is greater abundance and richness in this edge habitat. Cerboncini et al. (2016) reported a slight increase in small mammal richness at forest-railway edges in the Atlantic Forest of southern Brazil. Roadkill may also be higher on plantation roads than highways as plantation roads are generally narrower, with thicker vegetation at the road edge. Thicker roadside vegetation may muffle light and sound from vehicles causing wildlife to be unaware of the road presence (Goosem, 2007; Jaarsma et al., 2006; Siers et al., 2016).

Interestingly, the majority of roadkill occurred at higher altitude as oppose to low-lying or coastal areas, possibly due to the higher abundance of forest mammals present at this altitude. Furthermore, the majority of lowland forest habitat in Peninsular Malaysia has already been developed to establish agricultural areas or human settlements (Miettinen & Liew, 2010).

Medium-sized mammal roadkill were more likely to occur in areas furthest from continuous forest and near fragmented forest patches. This may be due to wildlife usually expanding their home range to forage and breed as their habitat is reduced and/or becomes more degraded. Furthermore, higher populations of herbivores in the forest patches are likely to be attributed to the lack of carnivores.

The number of WVCs varied year to year, which could be influenced by further deforestation and agricultural expansion. Malaysia lost 2.65 Mha (decreased by 17%) of humid primary forest from 2002 to 2019 (Global Forest Watch, 2020). Conversely, palm oil area has steadily increased from 5.74 Mha in 2016 to 5.90 Mha in 2019 (increased by 2.8%) (MPOB, 2020).

As palm oil plantations in Peninsular Malaysia expand in number and area, more new roads are being constructed that border intact forests and forest reserves. These areas are likely to result in increased roadkill ensuing roadkill hotspots, which require appropriate mitigation (Zimmermann Teixeira et al., 2017). Ultimately, a decline in wildlife will likely occur in biodiversity-rich areas (Fa et al., 2005).

4.2 | Management implications

Our study is the first to record mortality data and some of the variables that cause it. The study is a useful starting point for finding hotspots and guiding future mitigation. As the extent of road networks and the area of palm oil plantations are growing in biodiversity-rich countries in Southeast Asia, it is imperative that wildlife protection agencies impose measures that minimize the ecological impacts this causes, including the impact of WVCs. We suggest that roadkill hotspots should be used as an indicator of the sites for mitigation, particularly in palm oil plantations.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Jamaluddin Jamhuri: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); visualization (equal); writing – original draft (equal). **Mohd Anuar Edinoor:** Data curation (equal); investigation (equal); methodology (equal); resources (equal); writing – original draft (equal). **Norizah Kamarudin:** Conceptualization (equal); funding acquisition (equal); writing – original draft (equal); writing – review & editing (equal). **Alex M. Lechner:** Writing – review & editing (equal). **Adham Ashton-Butt:** Writing – review & editing (equal). **Badrul Azhar:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

Empirical data have been archived in DataDryad: <https://doi.org/10.5061/dryad.gtht76hh8>.

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REFERENCES

- Alamgir, M., Campbell, M. J., Sloan, S., Goosem, M., Clements, G. R., Mahmoud, M. I., & Laurance, W. F. (2017). Economic, socio-political and environmental risks of road development in the tropics. *Current Biology*, 27(20), R1130–R1140. <https://doi.org/10.1016/j.cub.2017.08.067>
- Alamgir, M., Campbell, M. J., Sloan, S., Suhardiman, A., Supriatna, J., & Laurance, W. F. (2019). High-risk infrastructure projects pose imminent threats to forests in Indonesian Borneo. *Scientific Reports*, 9(1), 140. <https://doi.org/10.1038/s41598-018-36594-8>
- Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences*, 114(23), 6056–6061. <https://doi.org/10.1073/pnas.1611855114>
- Anderson, D. R., & Burnham, K. (2004). *Model selection and multi-model inference* (2nd ed., p. 63). Springer-Verlag.
- Ascensão, F., Desbiez, A. L., Medici, E. P., & Bager, A. (2017). Spatial patterns of road mortality of medium–large mammals in Mato Grosso do Sul, Brazil. *Wildlife Research*, 44(2), 135–146. <https://doi.org/10.1071/WR16108>
- Azhar, B., Lindenmayer, D., Wood, J., Fischer, J., Manning, A., McElhinny, C., & Zakaria, M. (2013). Contribution of illegal hunting, culling of pest species, road accidents and feral dogs to biodiversity loss in established oil-palm landscapes. *Wildlife Research*, 40(1), 1–9. <https://doi.org/10.1071/WR12036>
- Azhar, B., Lindenmayer, D. B., Wood, J., Fischer, J., & Zakaria, M. (2014). Ecological impacts of oil palm agriculture on forest mammals in plantation estates and smallholdings. *Biodiversity and Conservation*, 23(5), 1175–1191. <https://doi.org/10.1007/s10531-014-0656-z>
- Bernard, H., Baking, E. L., Giordano, A. J., Wearn, O. R., & Ahmad, A. H. (2014). Terrestrial mammal species richness and composition in three small forest patches within an oil palm landscape in Sabah, Malaysian Borneo. *Mammal Study*, 39(October 2015), 141–154. <https://doi.org/10.3106/041.039.0303>
- Butler, R. A. (2015). *Global forest loss reached 46 million acres in 2014*. Retrieved 17 January 2015, from Mongabay.com/A Place Out of Time: Tropical Rainforests and the Perils They Face. <https://news.mongabay.com/2015/09/global-forest-loss-reached-46-million-acres-in-2014/>
- Cerboncini, R. A., Roper, J. J., & Passos, F. C. (2016). Edge effects without habitat fragmentation? Small mammals and a railway in the Atlantic Forest of southern Brazil. *Oryx*, 50, 460–467. <https://doi.org/10.1017/S0030605314001070>
- Chen, H. L., & Koprowski, J. L. (2016). Barrier effects of roads on an endangered forest obligate: Influences of traffic, road edges, and gaps. *Biological Conservation*, 199, 33–40. <https://doi.org/10.1016/j.biocon.2016.03.017>
- Clements, G. R., Lynam, A. J., Gaveau, D., Yap, W. L., Lhota, S., Goosem, M., Laurance, S., & Laurance, W. F. (2014). Where and how are roads endangering mammals in Southeast Asia's forests? *PLoS One*, 9(12), e115376. <https://doi.org/10.1371/journal.pone.0115376>
- Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science*, 361(6407), 1108–1111.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- DWNP (2010). *Prosedur Kualiti Pengurusan Konflik Hidupan Liar*. : Department of Parks and Wildlife of Peninsular Malaysia.
- DWNP (2017). *Red List of mammals for Peninsular Malaysia*. Department of Parks and Wildlife of Peninsular Malaysia.
- Eberhardt, E., Mitchell, S., & Fahrig, L. (2013). Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. *The Journal of Wildlife Management*, 77(7), 1353–1359. <https://doi.org/10.1002/jwmg.592>
- Fa, J. E., Ryan, S. F., & Bell, D. J. (2005). Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afro-tropical forests. *Biological Conservation*, 121(2), 167–176. <https://doi.org/10.1016/j.biocon.2004.04.016>
- Fabrizio, M., Di Febbraro, M., D'Amico, M., Frate, L., Roscioni, F., & Loy, A. (2019). Habitat suitability vs landscape connectivity determining roadkill risk at a regional scale: A case study on European badger (*Meles meles*). *European Journal of Wildlife Research*, 65(1), 7. <https://doi.org/10.1007/s10344-018-1241-7>
- Ford, A. T., & Fahrig, L. (2007). Diet and body size of North American mammal road mortalities. *Transportation Research Part D: Transport and Environment*, 12(7), 498–505. <https://doi.org/10.1016/j.trd.2007.07.002>
- Francis, C. (2008). *Field guide to the mammals of South-east Asia*. New Holland Publishers.
- Global Forest Watch (2020). Retrieved from <https://www.globalforestswatch.org/dashboards/global>
- Goosem, M. (2007). Fragmentation impacts caused by roads through rainforests. *Current Science*, 93, 1587–1595.
- Grilo, C., Coimbra, M. R., Cerqueira, R. C., Barbosa, P., Dornas, R. A. P., Gonçalves, L. O., Teixeira, F. Z., Coelho, I. P., Schmidt, B. R., Pacheco, D. L. K., Schuck, G., Esperando, I. B., Anza, J. A., Beduschi, J., Oliveira, N. R., Pinheiro, P. F., Bager, A., Secco, H., Guerreiro, M., & Kindel, A. (2018). Brazil road-kill: A data set of wildlife terrestrial vertebrate road-kills. *Ecology*, 99(11), 2625. <https://doi.org/10.1002/ecy.2464>
- IUCN (2017). *The IUCN red list of threatened species*. Retrieved from <http://www.iucnredlist.org/details/21472/0>
- Jaarsma, C. F., van Langevelde, F., & Botma, H. (2006). Flattened fauna and mitigation: Traffic victims related to road, traffic, vehicle, and species characteristics. *Transportation Research Part D: Transport and Environment*, 11(4), 264–276. <https://doi.org/10.1016/j.trd.2006.05.001>
- Jaeger, J. A., & Fahrig, L. (2004). Effects of road fencing on population persistence. *Conservation Biology*, 18(6), 1651–1657. <https://doi.org/10.1111/j.1523-1739.2004.00304.x>
- Jamhuri, J., Samantha, L. D., Tee, S. L., Kamarudin, N., Ashton-Butt, A., Zubaid, A., Lechner, A. M., & Azhar, B. (2018). Selective logging causes the decline of large-sized mammals including those in unlogged patches surrounded by logged and agricultural areas. *Biological Conservation*, 227, 40–47. <https://doi.org/10.1016/j.biocon.2018.09.004>
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19(2), 101–108.
- Kang, W., Minor, E. S., Woo, D., Lee, D., & Park, C. R. (2016). Forest mammal roadkills as related to habitat connectivity in protected areas. *Biodiversity and Conservation*, 25(13), 2673–2686. <https://doi.org/10.1007/s10531-016-1194-7>
- Kochummen, K. M., LaFrankie, J. V. Jr, & Manokaran, N. (1990). Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science*, 3, 1–13.
- Kolowski, J. M., & Nielsen, C. K. (2008). Using Penrose distance to identify potential risk of wildlife–vehicle collisions. *Biological Conservation*, 141(4), 1119–1128. <https://doi.org/10.1016/j.biocon.2008.02.011>
- Laurance, W. F., & Arrea, I. B. (2017). Roads to riches or ruin? *Science*, 358(6362), 442–444.
- Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Goosem, M., Venter, O., Edwards, D. P., Phalan, B., Balmford, A., Van

- Der Ree, R., & Arrea, I. B. (2014). A global strategy for road building. *Nature*, 513(7517), 229. <https://doi.org/10.1038/nature13717>
- Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P., & Ondzeano, C. (2006). Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, 20(4), 1251–1261. <https://doi.org/10.1111/j.1523-1739.2006.00420.x>
- Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24(12), 659–669. <https://doi.org/10.1016/j.tree.2009.06.009>
- Linkie, M., & Ridout, M. S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, 284(3), 224–229. <https://doi.org/10.1111/j.1469-7998.2011.00801.x>
- Loss, S. R., Will, T., & Marra, P. P. (2014). Estimation of bird–vehicle collision mortality on US roads. *The Journal of Wildlife Management*, 78(5), 763–771. <https://doi.org/10.1002/jwmg.721>
- Magintan, D., Nor, S. M., Ean, T. P., Lechner, A. M., & Azhar, B. (2017). The conservation value of unlogged and logged forests for native mammals on the East Coast of Peninsular Malaysia. *Journal for Nature Conservation*, 40, 113–119. <https://doi.org/10.1016/j.jnc.2017.10.005>
- Miettinen, J., & Liew, S. C. (2010). Degradation and development of peatlands in Peninsular Malaysia and in the islands of Sumatra and Borneo since 1990. *Land Degradation & Development*, 21(3), 285–296. <https://doi.org/10.1002/ldr.976>
- MPOB (2020). Retrieved from <https://www.mpob.gov.my>
- Naha, D., Jhala, Y. V., Qureshi, Q., Roy, M., Sankar, K., & Gopal, R. (2016). Ranging, activity and habitat use by tigers in the mangrove forests of the Sundarban. *PLoS One*, 11(4), e0152119. <https://doi.org/10.1371/journal.pone.0152119>
- Newbold, T., Hudson, L. N., Phillips, H. R., Hill, S. L., Contu, S., Lysenko, I., De Palma, A. (2014). A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792), 20141371. <https://doi.org/10.1098/rspb.2014.1371>
- Okuda, T., Suzuki, M., Adachi, N., Quah, E. S., Hussein, N. A., & Manokaran, N. (2003). Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. *Forest Ecology and Management*, 175(1–3), 297–320. [https://doi.org/10.1016/S0378-1127\(02\)00137-8](https://doi.org/10.1016/S0378-1127(02)00137-8)
- Orlowski, G., & Nowak, L. (2006). Factors influencing mammal roadkills in the agricultural landscape of south-western Poland. *Polish Journal of Ecology*, 54(2), 283–294.
- Potere, D. (2008). Horizontal positional accuracy of Google Earth's high-resolution imagery archive. *Sensors*, 8, 7973–7981. <https://doi.org/10.3390/s8127973>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 1241484. <https://doi.org/10.1126/science.1241484>
- Samantha, L. D., Tee, S. L., Kamarudin, N., Lechner, A. M., & Azhar, B. (2020). Assessing habitat requirements of Asian tapir in forestry landscapes: Implications for conservation. *Global Ecology and Conservation*, 23, e01137. <https://doi.org/10.1016/j.gecco.2020.e01137>
- Santos, A. M., & Tabarelli, M. (2002). Distance from roads and cities as a predictor of habitat loss and fragmentation in the caatinga vegetation of Brazil. *Brazilian Journal of Biology = Revista Brasileira De Biologia*, 62(4B), 897–905. <https://doi.org/10.1590/S1519-69842002000500020>
- Sasidhran, S., Adila, N., Hamdan, M. S., Samantha, L. D., Aziz, N., Kamarudin, N., Puan, C. L., Turner, E., & Azhar, B. (2016). Habitat occupancy patterns and activity rate of native mammals in tropical fragmented peat swamp reserves in Peninsular Malaysia. *Forest Ecology and Management*, 363, 140–148. <https://doi.org/10.1016/j.foreco.2015.12.037>
- Schall, R. (1991). Estimation in generalized linear models with random effects. *Biometrika*, 78(4), 719–727. <https://doi.org/10.1093/biomet/78.4.719>
- Siers, S. R., Reed, R. N., & Savidge, J. A. (2016). To cross or not to cross: Modeling wildlife road crossings as a binary response variable with contextual predictors. *Ecosphere*, 7(5), e01292. <https://doi.org/10.1002/ecs2.1292>
- Tee, S. L., Samantha, L. D., Kamarudin, N., Akbar, Z., Lechner, A. M., Ashton-Butt, A., & Azhar, B. (2018). Urban forest fragmentation impoverishes native mammalian biodiversity in the tropics. *Ecology and Evolution*, 8(24), 12506–12521. <https://doi.org/10.1002/ece3.4632>
- Tee, S. L., Solihhin, A., Juffiry, S. A., Putra, T. R., Lechner, A. M., & Azhar, B. (2019). The effect of oil palm agricultural expansion on group size of long-tailed macaques (*Macaca fascicularis*) in Peninsular Malaysia. *Mammalian Biology*, 94(1), 48–53. <https://doi.org/10.1016/j.mambio.2018.12.006>
- van der Ree, R., Jaeger, J. A., van der Grift, E., & Cleverger, A. (2011). Effects of roads and traffic on wildlife populations and landscape function: Road ecology is moving toward larger scales. *Ecology and Society*, 16(1). <https://doi.org/10.5751/ES-03982-160148>
- Wadey, J., Beyer, H. L., Saaban, S., Othman, N., Leimgruber, P., & Campos-Arceiz, A. (2018). Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biological Conservation*, 218, 91–98. <https://doi.org/10.1016/j.biocon.2017.11.036>
- Yule, C. M. (2010). Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. *Biodiversity and Conservation*, 19(2), 393–409. <https://doi.org/10.1007/s10531-008-9510-5>
- Zimmermann Teixeira, F., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, 54(5), 1544–1551. <https://doi.org/10.1111/1365-2664.12870>

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