

2021 Master's thesis

Human impacts on diel activity patterns of wild mammals
in the tourist area of Endau Rompin National Park, Peninsular Malaysia

半島マレーシアのエンダウ・ロンピン国立公園の観光利用地域における
野生哺乳類の日周活動パターンへの人為影響

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Abstracts

Wildlife tourism, which is the observation and interaction with local animal and plant life in their natural habitats, can provide economic incentives and motive for conservation of wildlife and their habitats. However, wildlife tourism could alter the physiology and behavior of wildlife, and cause them to adjust their activities to avoid contact with humans. For example, a previous study reported that wild mammals all over the world might adjust their diel activity patterns in response to human activities, and it results in more nocturnal behavior. In addition, changes in the diel activity patterns of wild mammals may affect inter-specific relationships. However, due to the lack of data on wildlife population, there is limited information on the effects of human activities, especially tourism, on the occurrence and the diel activity patterns of wild mammals and inter-specific interactions among them in national parks.

The aim of this study was to understand the human impacts on wild mammals and inter-specific interactions among wild mammal species in the tourist area of a national park with rainforests. In this study, to discuss human impacts on diel activity patterns of wild mammals in Endau Rompin National Park (ERNP), Peninsular Malaysia, I investigated (1) the detection rates and (2) the diel activity patterns of wild mammals using camera traps, and (3) the temporal overlap of diel activity patterns between some groups. Specifically, I tested whether there are differences in the diel activity patterns of wild mammals on the paved road, which were closer to the tourist centers in ERNP and were used relatively more by humans, and on the logging road, which are closer to the forest interior and have limited human use.

To investigate the detection rates and the diel activity patterns of wild mammals in ERNP, I conducted camera trapping survey. In total, 10 video cameras were installed for 250 days from July 8, 2019 to March 13, 2020. The detection rates of wild mammals were compared between the paved road and the logging road using generalized linear mixed models (GLMMs). The diel activity patterns of wild mammals were defined by comparing the number of independent records among the three time periods in a day (daytime, nighttime, twilight) using GLMMs, and were visualized by kernel density estimation. To discuss interspecific interactions of wild mammals, I analyzed the temporal overlap of diel activity patterns among guild groups and species of wild mammals.

My results showed that humans and vehicles were more frequently recorded significantly in the paved road than the logging road, indicating that human activity were significantly differed between the paved road and the logging road. In particular, heavy vehicle traffic was recorded, and so vehicle traffic would be the highest human activity on the road in ERNP. Both humans and vehicles showed clear diurnal activity patterns, indicating human activity in ERNP were conducted in daytime.

The detection rates and diel activity patterns of southern red muntjac (*Muntiacus muntjak*), wild boar (*Sus scrofa*), Malayan porcupine (*Hystrix brachyura*) and crab-eating macaque (*Macaca fascicularis*) did not differ between the paved road and the logging road. This result suggests that the human activity did not affect detection rates and the diel activity patterns of them. Therefore, the current

nonlethal tourism activities and park management in ERNP might be sustainable with no considerable negative impacts on these species. On the other hand, some species, such as bearded pig (*Sus barbatus*) and carnivores showed different detection rates and diel activity patterns between the two roads. This suggests that human activity may affect those species. If those species are under threat, urgent actions are needed. In addition, this study suggested human activity affected predator-prey interactions between carnivores and mouse deer (*Tragulus sp.*). Because carnivores were less active during the daytime on the paved road, mouse deer may change high level of diurnal activity to avoid overlapping carnivore activities. The change of diel activity patterns of predator species by human can potentially have indirect effects on interacting prey species that can ultimately have significant effects on the structure, function and biodiversity of the ecosystem.

In this study, I found that human activities affect the occurrence of wild mammals, diel activity patterns, and inter-specific interaction in a tourist area, but also that the degree of influence varied by species. Therefore, further studies on the ecology, behavior, and population density dynamics of each species and assessment of human impacts are needed for sustainable tourism and conservation management.

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Introduction

National parks, a category of protected areas, are required not only to protect biodiversity but also to use it sustainably through education and recreation (IUCN, 2021), and many of them have become important nature-based tourism destinations. According to the UNWTO Report, 7% of world tourism relates to wildlife tourism, a segment growing annually at about 3%. Moreover, a total of 14 countries in Africa are generating an estimated US\$ 142 million in entrance fees for protected areas (UNWTO, 2014). Wildlife tourism is the observation and interaction with local animal and plant life in their natural habitats (UNWTO, 2021). It includes tourism for the purpose of observing and encountering wildlife, visiting habitats, and catching wildlife such as hunting and fishing (Higginbottom, 2004). Wildlife tourism can provide economic incentives and motive for conservation of wildlife and their habitats (Higginbottom, 2004). However, wildlife tourism could alter the physiology and behavior of wildlife and increase the risk of extinction through increased mortality and decreased reproductive success (Higginbottom, 2004). Wild animals often perceive humans as a threat, which may cause them to adjust their activities to avoid contact with humans (Frid and Dill, 2002; Miller et al., 2020). Therefore, we need to assess and evaluate how wildlife responds to the long-term effects of tourism to manage protected area (Zhou et al., 2013).

The diel activity patterns of terrestrial mammals can generally be categorized as diurnal, nocturnal, crepuscular (active at twilight) or cathemeral (active throughout the day) (Bennie et al., 2014). However, diel activity patterns are highly variable among regions and across seasons, even within the same species (Ikeda et al., 2016). Many factors can affect activity patterns, such as day time length, temperature, precipitation, predator-prey or competitive interactions and human activities (Linkie and Ridout, 2011; Ross et al., 2013; Bennie et al., 2014; Ngoprasert et al., 2017; Gaynor et al., 2018a). Therefore, many wild mammals could change their diel activity patterns in response to human activities such as tourism and settlement (Gray and Phan, 2011; Gaynor et al., 2018b). For example, there is the report that mammals all over the world adjust their diel activity patterns in response to human activities occurring mainly during daylight hours by becoming more nocturnal (Gaynor et al. 2018a). In large carnivores and ungulates, which have a wide-ranging and plasticity in their behavior, such adjustments occur on a relatively fine spatiotemporal scale (Carter et al., 2012).

Especially, some of mammal species are often apex consumers and so could influence their associated ecosystems through top-down forcing and trophic cascades (Estes et al., 2011). Therefore, changes in diel activity patterns of wild mammals due to human impacts may affect inter-specific interactions of wild mammals. They often lead to myriad effects on other species and ecosystem processes, and so predator-prey or competitive interactions may be influenced by human activities. For example, in predator-prey interactions, predator avoidance of humans can lead to spatiotemporal proximity of prey to human in order to avoid predators, which can provide a shelter for prey from

predators using human presence as a shield (Berger, 2007; Muhly et al. 2011). In the montane ecosystem in southwest Alberta, Canada, prey appeared more abundant on roads and trails with more people (> 32 people/day), but predators did not appear as abundant on roads and trails with more than 18 people/day, even if more prey were present (Muhly et al., 2011). On two roads with different traffic volumes in Grand Teton National Park, USA, ungulates, which is prey species, increased their foraging behavior and decreased their anti-predator (vigilance) behavior near the road on the busy road compared to the less busy road (Shannon et al., 2014). Therefore, changes in the diel activity patterns of wild mammals due to human impacts may affect not only the diel activity patterns of that species, but also those of species that are interrelated to that species.

Tourism activity in national parks may affect the diel activity patterns of wild mammals. Leopards (*Panthera pardus*) tended to move more frequently and showed more diurnal activity patterns during periods of no tourism activity in a national park in Thailand (Ngoprasert et al., 2017). African elephants (*Loxodonta africana*) in a national park in Mozambique showed nocturnal activity patterns near park boundaries and on roads that are heavily used by humans due to the proximity of human settlements and plantations, and diurnal activity patterns inside park and off roads where human activities are relatively less affected (Gaynor et al., 2018b). Thus, differences in the period and space of tourist activity may affect the diel activity patterns of wild mammals. However, limited information is available on the effects of tourist activity on mammalian diel activity patterns, particularly along trails, at the population or community level (Ota et al., 2019). Large predators such as Felidae, and Ungulates are sometimes found to prefer using trails (Cusack et al., 2015). In the eastern United States, most species studied did not avoid trails, and predator species positively selected them, specifically at night (Kays et al., 2016). Therefore, there is limited information on the effects of human activities, such as tourism, on the occurrence and the diel activity patterns of wild mammals and inter-specific interactions among them in national parks. In particular, there are few studies that have evaluated how differences in the space of human activity in tourist areas affect mammals.

The aim of this study was to understand the human impacts on wild mammals and inter-specific interactions among mammal species in the tourist area of a national park with rainforests. In this study, to discuss human impacts on diel activity patterns of wild mammals in Endau Rompin National Park (ERNP), Peninsular Malaysia, I investigated (1) the detection rates of wild mammals and (2) the diel activity patterns of wild mammals using camera traps, and (3) the temporal overlap of diel activity patterns between some groups. Specifically, I tested whether there are differences in the detection rates and the diel activity patterns of wild mammals on the paved road, which were closer to the tourist centers in ERNP and were used relatively more by humans, and on the logging road, which are closer to the forest interior and have limited human use. The paved road was close to the residences of tourists and the village where local people live. The increased human traffic on the roads and their

proximity to human settlements have a negative impact on wild mammals (Gray and Phan, 2011; Zhou et al., 2013; Gaynor et al., 2018b), and the paved road in ERNP also may have a negative human impact on wild mammals than the logging road. Therefore, I hypothesized that the diel activity patterns of wild mammals to be more nocturnal on the paved roads, where human impact was greater than on the logging roads. In addition, large carnivores are typically more sensitive to human disturbance (Treves and Karanth, 2003), and therefore I hypothesized that less frequently records and more nocturnal on the paved road that are heavily used by humans. Conversely, humans can provide a shelter for prey from predators if prey are less sensitive to human disturbance than predators (Muhly et al., 2011).

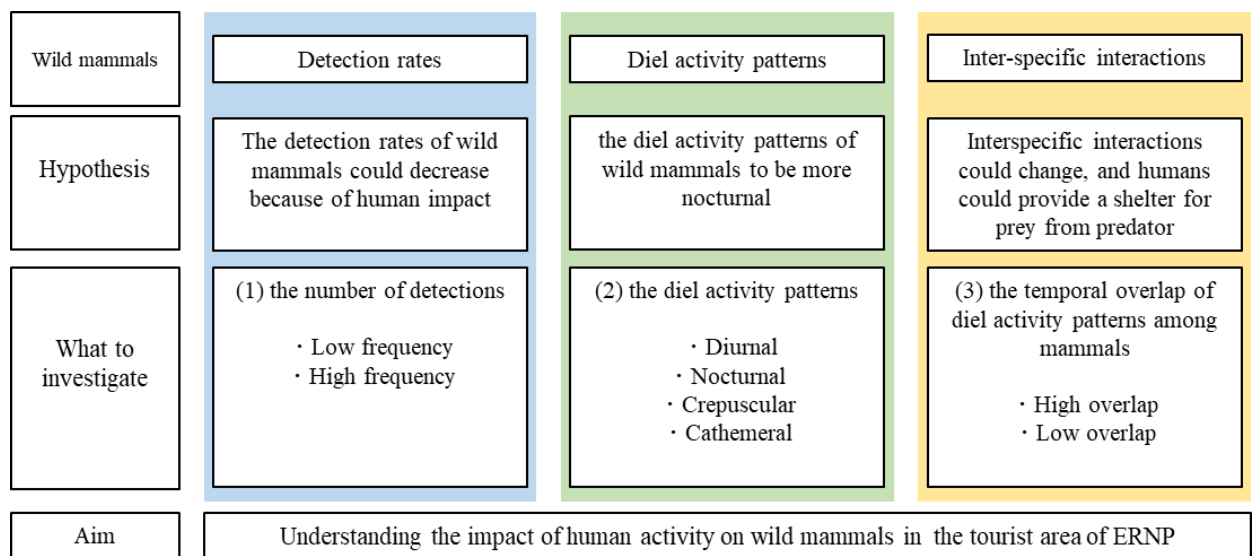


Fig. 1

Framework of this study.

Material and Methods

Study site

This study was conducted in ERNP, which is located at the border of the states of Johor and Pahang in Peninsular Malaysia (Fig. 2). In 1972, the Malaysian Federation Government decided to establish Endau Rompin as a national park to protect the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), and in 1989, 489.05 km² of virgin tropical rainforest was designated as Endau Rompin National Park. Currently, ERNP is managed by the semi-governmental Johor National Park Corporation (JNPC). The southern part of the park is managed by the state of Johor, and the northern part of the park is designated as Endau Rompin State Park and managed by the state of Pahang (Aihara et al., 2016). On the Johor side, there are two tourist areas: the Peta area (195.62 km²) and the Selai area (293.43 km²). The study was conducted in the Peta area of Johor state (2°31'N, 103°24'E, 40 m above sea level). ERNP has been open to public since September 1993. Approximately 2000 visitors entered Peta area each year (JNPC, undisclosed data).

The park provides various tourist activities such as camping, jungle trekking, night walking, swimming, canoeing, river rafting, and nature education. In the Peta area (Fig. 3), there is the Visitor Complex and Nature Education and Research Centre (NERC), which serve as a base for tourism, and there are three campsites at Kuala Jasin, Kuala Marong, and Batu Hampar. There is a village, Kampung Peta, of local aborigines (orang asli). Mainly tourists enjoy trekking along logging roads and nature trails from Kuala Jasin campsite to Kuala Marong campsite. Camping and trekking must be accompanied by a guide. Tourists are transported from the Visitor Complex to the Kuala Jasin Campsite either by a guide's car on a paved road or by boat up the Endau river.

The park comprises largely of a hilly landscape of mainly volcanic ignimbrite overlain in places by layers of shale and sandstone (Gumal et al. 2014). Two major rivers, Endau river and Rompin river, flow through the park, hence it became the name of the park. Much of the area is covered by tropical rainforest with an average annual temperature of 27 °C, rainfall of 3,400 mm, and humidity of 85 %. The tropical forests comprise lowland, hill mixed dipterocarp forest of Keruing–Red Meranti (*Dipterocarpus shorea*) and Kapur (*Dryobalanus*) types (Wong et al., 1987). The uniqueness of ERNP is that it is located in the “Riouw Pocket,” a meeting point of the western Borneo, Sumatran, and Malayan flora (Foo and Numata, 2019). It is characterized by a high degree of endemism, and a significant number of plant species that are locally endemic or restricted to the southern region of the peninsula are found in ERNP (Foo and Numata, 2019).

This ancient rainforest realm in north-eastern Johor is a treasure trove of biodiversity, and a critical habitat so important for the survival of the Malaysia globally-threatened megafauna, including Tiger, Malayan tapir and Asian elephant (JNPC). In total, 149 mammal species from 11 orders (Carnivore, Cetartiodactyla, Chiroptera, Dermoptera, Eulipotyphla, Perissodactyla, Pholidota, Primates, Proboscidea, Rodentia and Scandentia) were inhabited in ERNP (Aihara et al., 2016). For medium and large mammals, two critically endangered species (CR), i.e. Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and Sunda

pangolin (*Manis javanica*), ten endangered species (EN), i.e. Tiger (*Panthera tigris*), Flat-headed cat (*Prionailurus planiceps*), Sunda otter civet (*Cynogale bennettii*), Large-spotted civet (*Viverra megaspila*), Malayan tapir (*Tapirus indicus*), Southern pig-tailed macaque (*Macaca nemestrina*), Dukey leaf monkey (*Trachypithecus obscurus*), Lar gibbon (*Hylobates lar*), Slow loris (*Nycticebus coucang*) and Asian elephant (*Elephas maximus*) were listed in the IUCN Red List 2020-2 (IUCN). In ERNP, population estimation surveys of tigers and elephants were conducted for conservation purposes (Gumal et al., 2014; Saaban et al., 2020), and basic information on various wild mammals are being collected through camera trap surveys (Gumal et al., 2014; Aihara et al., 2016; Tan et al., 2018; Ota et al., 2019).

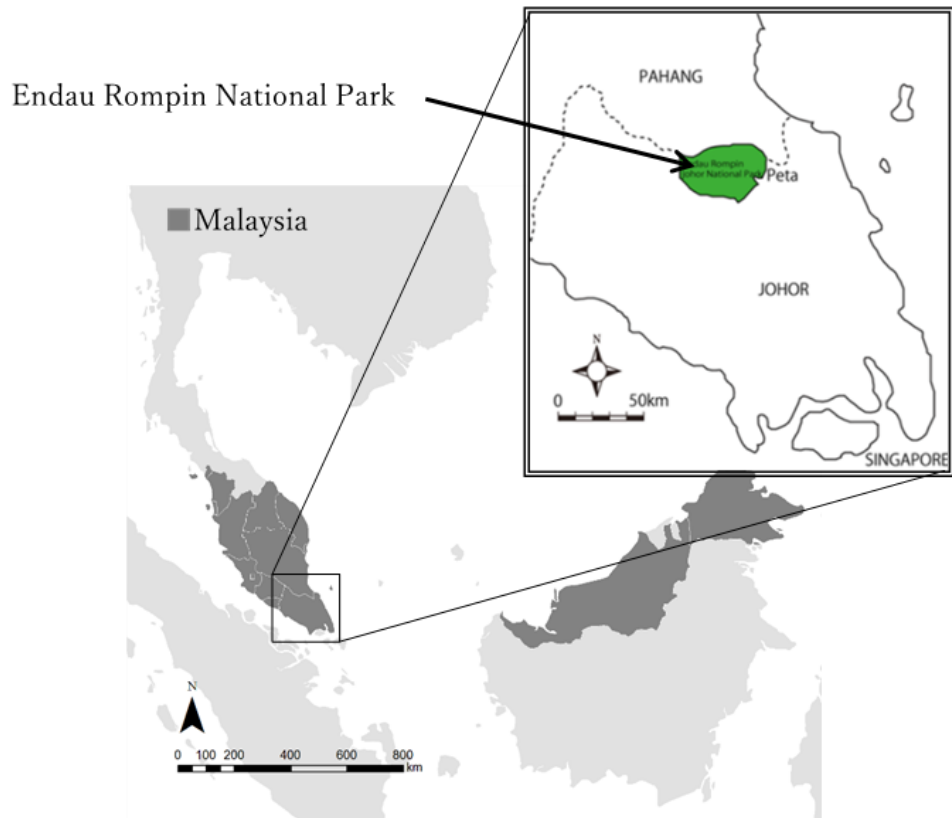


Fig. 2

Location of Endau Rompin National Park.

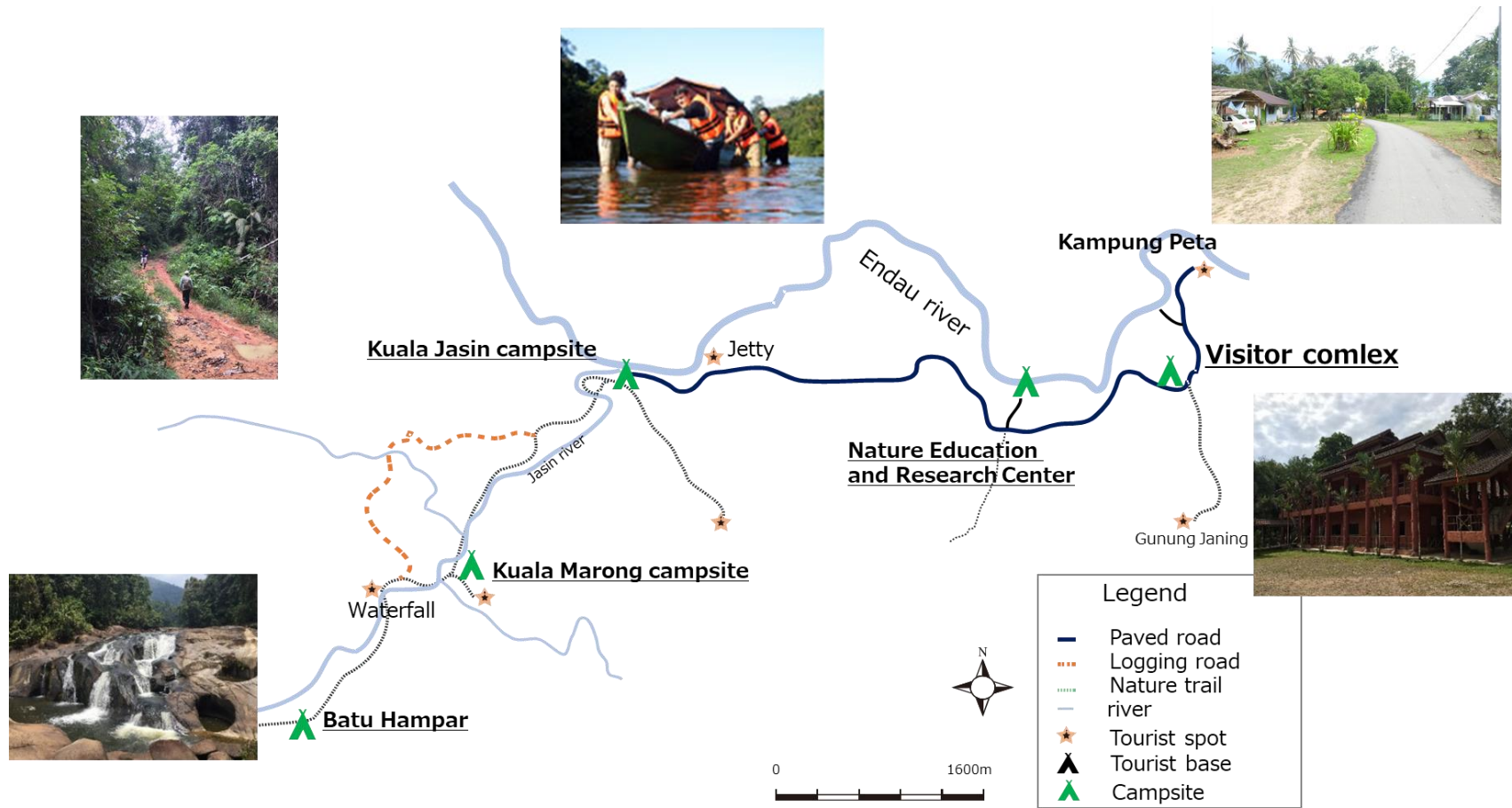


Fig. 3

The map of Peta site in Endau Rompin National Park.

Data collection

To investigate the detection rates and diel activity patterns of wild mammals in the Peta area of ERNP, I used high quality automatic day/night video cameras with multiple infrared sensors (Ltl Acorn 6210, Ltl Acorn 6310W). Camera traps have been used for wildlife surveys in the rainforests of Asia and Africa since the 1990s (Wemmer et al., 1996; Gimán et al., 2007). Camera trapping survey can minimize human disturbances and provide an inexpensive and time-efficient means of observing wildlife in tropical rainforests (Numata et al., 2005), and so diel activity patterns of wild mammals was examined by the camera traps data (Ikeda et al., 2016; Ota et al., 2019).

In total, 10 cameras were installed for 250 days from July 8, 2019 to March 13, 2020. The operation period of the cameras was different at each site due to the failure of equipment (Table 1). Data were collected and the batteries and SD cards were replaced in November 2019.

The camera traps were installed on two types of roads: a paved road between Visitor complex and Kuala Jasin campsite, and a logging road between Kuala Jasin campsite and Kuala Marong campsite (Fig. 4, Fig. 5). The paved road was about 7 km long, and was paved with asphalt. During the day, tourists and park staff move to the Kuala Jasin campsite where is the base for activities, by car or motor bike. As the tourist activity, night walking is conducted near the Visitor Complex and NERC. The 5 km long logging road was an unpaved road with a width of 5 to 10 meters, but it was passable by car. It is mainly used by tourists and park staff on foot. The cameras were installed at 6 points on the paved road (#A, #B, #C, #D, #E, #F) and 4 points on the forest road (#G, #H, #I, #J) for a total of 10 points with equal distance (approximately 1 km) between the points. The location of the camera traps was selected at the intersection of the road and the animal trail based on the animal sign, like footprint and dung.

The cameras were installed at a height of 0.5-1.5 m above the ground to record terrestrial medium and large mammals, and were oriented in such a way as to allow recording of animals walking along the road and those emerging from the animal trail. However, due to the large number of vehicles and people using the paved road, which exceeded the number of pictures the camera could take, the camera traps were installed at the six places on the paved road from November 5, 2019 to March 13, 2020, with the direction of the camera limited to the animal trail.

I recorded 15 seconds of video per record and set the minimum recording interval to 30 s (Ota et al., 2019). In addition, the date and time were recorded for all videos. Eight lithium batteries and a 32 GB SD card were used for the camera traps.

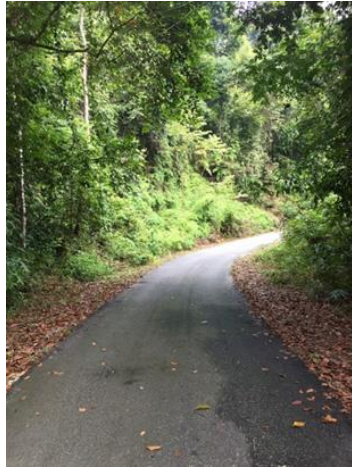


Fig. 4
(Above) Paved road, (below) Logging road.

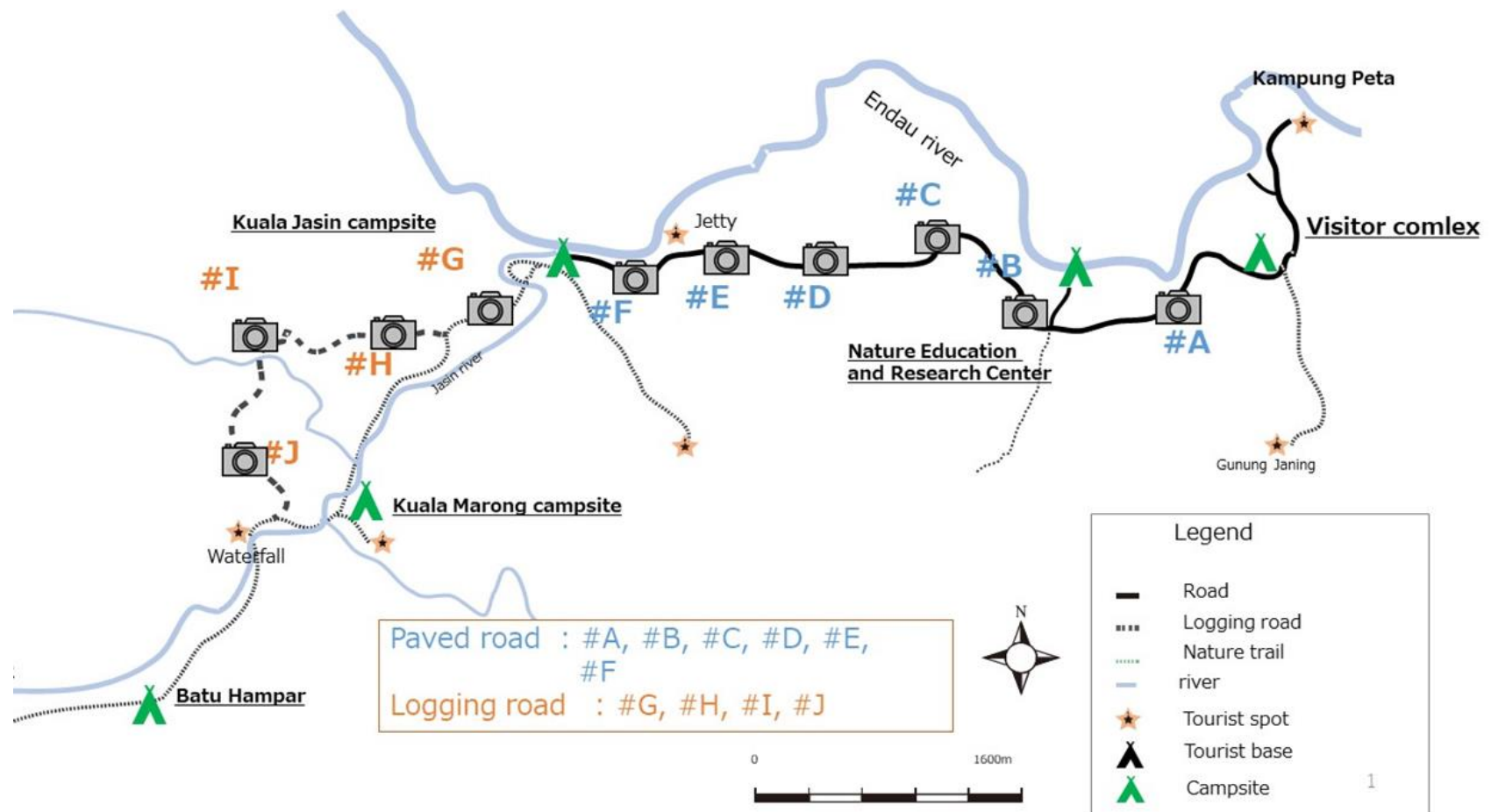


Fig. 5

Camera traps locations on the paved road (#A, #B, #C, #D, #E and #F), on the logging road (#G, #H, #I, #J).

Data analysis

The recorded videos were classified into wild mammals, humans walking, vehicles (cars or motorcycles), and others (birds, insects, reptiles, unidentified mammals). In order to eliminate duplicate records of the same individual or group, the number of records was counted as one independent record if the same species was recorded multiple times within 30 minutes (Yasuda, 2004).

Detection rates of wild mammals

The detection rates were defined as the number of records per 100 camera-day, and were calculated by mammal species and guild groups for all area, the paved road and the logging road, respectively. For species with > 10 independent records, I compared the number of independent records between the paved road and the logging road using generalized linear mixed models (GLMMs) with a Poisson distribution, in which road type (the paved road or the logging road) was included as a fixed effect, the number of operating days of the cameras was included as an offset term and each camera locations were considered as a random effect. P values were calculated by Wald chi-square tests using 'car' package (Fox and Weisberg, 2019). I compared the number of species of wild mammals recorded between the paved roads and the logging roads by using Two-sample t-test.

Diel activity patterns of wild mammals

To determine which of the four diel activity patterns (i.e., diurnal, nocturnal, crepuscular or cathemeral) was exhibited by each mammal species, I defined the twilight as ± 1 h from sunrise and sunset (Ota et al., 2019), and divided the day into three periods [daytime (08:00–18:00 h UTC+08:00), nighttime (20:00–06:00 h UTC+08:00), and twilight (06:00–08:00 h and 18:00–20:00 h UTC+08:00)]. The independent records of wild mammals were counted separately according to daytime, nighttime and twilight.

I compared the number of independent records among the three periods using GLMMs with a Poisson distribution, in which time period was included as a fixed effect, the length of operating hours of the cameras was included as an offset term and each camera locations were considered a random effect. P values were calculated by Wald chi-square tests using 'car' R package. Tukey's honestly significant difference (HSD) post hoc tests were done using 'multcomp' R package (Bretz et al., 2010), when time period was significant in GLMMs. I conducted that comparison by mammal species and guild groups for the paved road and the logging road, respectively.

Wild mammals that were recorded more than 10 times were defined as having diurnal, nocturnal, or twilight behavior if the number of records were significantly more during daytime, nighttime and twilight, respectively. I defined the species as cathemeral behavior when no significant differences were observed in the number of records among the three periods. The GLMM approach can be used as a standard method to evaluate diel activity patterns (Ikeda et al., 2016; Ota et al., 2019).

I investigated the diel activity patterns of wild mammals following the methods of Rowcliffe et

al. (2014) using the ‘overlap’ R package (Ridout and Linkie, 2009; Meredith and Ridout, 2020). The diel activity patterns of wild mammals were plotted using a von Mises kernel. This analysis was conducted on the individuals that were recorded more than 10 times, by mammal species and guild groups, for the paved road and the logging road, respectively.

To investigate differences in the diel activity patterns of mammals between the paved roads and the logging roads, I calculated the coefficient of overlap (the paved road vs the logging road) for each mammal using the ‘overlap’ R package function (Meredith and Ridout, 2020). The coefficient of the overlap ranges between 0 (no overlap) and 1 (complete overlap). To estimate the coefficient of overlap, I used \hat{D}_1 or \hat{D}_4 according to the sample size (Meredith and Ridout, 2020).

Overlap of the diel activity patterns of wild mammals (mammal vs mammal)

To discuss inter-specific interactions of wild mammals, I analyzed the temporal overlap of diel activity patterns among guild groups and species of wild mammals, and I calculated the coefficient of overlap (mammal vs mammal) for the paved road and the logging road, respectively. This method has been used to evaluate predator-prey or competitive interactions among sympatric wild mammals (Ridout and Linkie, 2009; Linkie and Ridout, 2011; Lynam et al., 2013).

Human activity in ERNP

To investigate human activity on the paved road and the logging road in ERNP, the detection rates of human activity (pedestrians and vehicles) on both roads were calculated from camera traps data from July 8, 2019 to November 5, 2019. As in the analysis of mammals, I compared the number of records of human walking and vehicles between the paved road and the logging road using GLMMs with a Poisson distribution, in which time period was included as a fixed effect, the number of operating days of the cameras was included as an offset term and each camera locations were considered a random effect. I analyzed the diel activity patterns of human activity using ‘overlap’ R package.

Overlap of the diel activity patterns of wild mammals and human (mammal vs human)

To analyze the temporal overlap of diel activity patterns between wild mammals and human, I calculated the coefficient of overlap (mammal vs human) for the paved road and the logging road, respectively.

Results

In total, mammals were recorded 774 times at 10 camera traps locations, of which medium and large mammals were recorded 686 times, and small mammals such as rats and squirrels were recorded 88 times. The total operation period of the camera trap was 1814 days (Table 1).

I recorded at least 21 species of medium and large mammals, which included one Critically endangered (CR) species, four Endangered (EN) species and six Vulnerable (VU) species (Table 2). Although two species, Lesser mouse deer (*Tragulus kanchil*) and Greater mouse deer (*Tragulus napu*), are reported to inhabit the study area (Aihara et al., 2016), it was difficult to identify them, so the two species were counted together as Mouse deer spp. (*Tragulus spp.*). Asian elephants were recorded at short intervals of 1 to 2 hours at camera locations on paved and logging roads. This suggests that Asian elephant were moving along the road, which may lead to repetitive counting of the number of records. Therefore, I did not include the data of Asian elephant in the analyses. The species recorded in this study were categorized into four guild groups: Carnivores, Ungulates, Primates, and Rodents (Table 3).

Table 1

Camera locations, number of independent events recorded by the camera trapping, camera-day.

Camera location		Mammals		Human (walking)	Vehicles	Others	Camera-day
		Medium & Large	Small				
Paved road	#A	73	49	40	2889	69	172
	#B	9	1	20	790	4	89
	#C	121	0	8	1826	14	142
	#D	36	26	4	1374	19	184
	#E	35	0	4	397	5	197
	#F	41	10	2	1031	4	114
Logging road	#G	68	0	27	116	4	249
	#H	149	1	12	73	35	244
	#I	90	1	6	82	32	174
	#J	64	0	9	72	4	249
Total		686	88	132	8650	190	1814

Table 2

List of Medium-Large mammal species recorded by camera trapping.

Order	Family	Scientific name	English name	Japanese name	IUCN Red List 2020-2
Carnivora	Felidae	<i>Catopuma temminckii</i>	Asiatic golden cat	アジアゴールデンキヤット	NT
Carnivora	Felidae	<i>Neofelis nebulosa</i>	Clouded leopard	ウンピョウ	VU
Carnivora	Felidae	<i>Panthera pardus</i>	Leopard	ヒョウ	VU
Carnivora	Felidae	<i>Panthera tigris</i>	Tiger	トラ	EN
Carnivora	Felidae	<i>Pardofelis marmorata</i>	Marbled cat	マーブルキヤット	NT
Carnivora	Felidae	<i>Prionailurus bengalensis</i>	Leopard cat	ベンガルヤマネコ	LC
Carnivora	Mustelidae	<i>Aonyx cinerea</i>	Asian small-clawed otter	コツメカワウソ	VU
Carnivora	Mustelidae	<i>Martes flavigula</i>	Yellow-throated marten	キエリテン	LC
Carnivora	Mustelidae	<i>Prionodon linsang</i>	Banded linsang	オビリンサン	LC
Carnivora	Ursidae	<i>Helarctos malayanus</i>	Sun bear	マレーグマ	VU
Carnivora	Viverridae	<i>Viverra zangalunga</i>	Malay civet	ジャワジャコウネコ	LC
Cetartiodactyla	Cervidae	<i>Muntiacus muntjak</i>	Southern red muntjac	ホエジカ	LC
Cetartiodactyla	Tragulidae	<i>Tragulus sp.</i>	Mouse deer spp.	マメジカ	-
Cetartiodactyla	Suidae	<i>Sus barbatus</i>	Bearded pig	ヒゲイノシシ	VU
Cetartiodactyla	Suidae	<i>Sus scrofa</i>	Wild boar	イノシシ	LC
Perissodactyla	Tapiridae	<i>Tapirus indicus</i>	Malayan tapir	マレーバク	EN
Pholidota	Manidae	<i>Manis javanica</i>	Sunda pangolin	マレーセンザンコウ	CR
Primates	Cercopithecidae	<i>Macaca fascicularis</i>	Crab-eating macaque	カニクイザル	VU
Primates	Cercopithecidae	<i>Macaca nemestrina</i>	Southern pig-tailed macaque	ミナミブタオザル	EN
Proboscidae	Elephantidae	<i>Elephas maximus</i>	Asian elephant	アジアゾウ	EN
Rodentia	Hystriidae	<i>Hystrix brachyura</i>	Malayan porcupine	マレーヤマアラシ	LC

Table 3

Guild groups categorized from mammal species recorded by camera traps.

Guild groups	Species
Carnivores	Asiatic golden cat, Clouded leopard, Leopard, Tiger, Marbled cat, Leopard cat, Asian small-clawed otter, Yellow-throated marten, Banded linsang, Malay civet, Unidentified Feridae, Unidentified Viverridae, Unidentified Carnivore
Ungulates	Southern red muntjac, Bearded pig, Wild boar, Mouse deer spp., Malayan tapir, Sus spp.
Primates	Crab-eating macaque, Pig-tailed macaque
Rodents	Malayan porcupine, Rat sp., Squirrel sp.

Detection rates of wild mammals

I calculated the detection rates (the number of records per 100 camera-day) by mammal species and guild groups in the paved road, and the logging road (Table 4, Fig. 6). For species and guild groups with >10 records (Southern red muntjac, Bearded pig, Wild boar, Mouse deer, Crab-eating macaque, Malayan porcupine, Leopard cat, Malay civet, Carnivores, Ungulates, Primates and Rodents), the number of records on paved and logged roads was compared by GLMMs. As a result, the number of records of bearded pig, crab-eating macaque and primates were significantly differed between the paved road and the logging road (Table 4). Bearded pigs were recorded significantly more on the logging road ($\chi^2 = 17.6$, $df = 1$, $p < 0.001$). Crab-eating macaque were recorded significantly more on the paved road ($\chi^2 = 7.7$, $df = 1$, $p = 0.006$). By guild groups, primates were recorded significantly more on the paved road ($\chi^2 = 6.4$, $df = 1$, $p < 0.05$). The number of species of wild mammals recorded were not significantly differed between the paved roads and the logging roads (Fig. 7).

Table 4

The number of independent records per 100 camera-day for medium-large mammals on all study area and on the paved road and on the logging road, the result of GLMMs and Wald chi-square test.

	No. of independent records	No. of independent records/ 100 camera-day			P value
		All area	Paved road	Logging road	
<i>All medium-large mammals</i>	654	36.05	33.52	38.54	0.42
<i>Guilds</i>					
Camivores	121	6.67	8.80	4.59	0.79
Ungulates	471	25.96	19.93	31.88	0.11
Primates	33	1.82	3.34	0.33	0.01 *
Rodents	115	6.34	10.91	1.86	0.18
<i>Species</i>					
Southern red muntjac	175	9.65	9.91	9.39	0.60
Bearded pig	102	5.62	1.22	9.93	<0.001 ***
Wild boar	100	5.51	5.12	5.90	0.60
Mouse deer spp.	85	4.69	3.56	5.79	0.57
Asian elephant	32	-	-	-	-
Crab-eating macaque	31	1.71	3.34	0.11	0.01 **
Malayan porcupine	27	1.49	1.34	1.64	0.74
Leopard cat	24	1.32	2.34	0.33	0.14
Malay civet	19	1.05	1.56	0.55	0.73
Unidentified Feridae	18	-	-	-	-
Unidentified Viverridae	18	-	-	-	-
Unidentified Camivore	13	-	-	-	-
Asiatic golden cat	10	0.55	0	1.09	-
<i>Sus spp.</i>	8	-	-	-	-
Leopard	7	0.39	0	0.76	-
Banded linsang	3	0.17	0	0.33	-
Yellow-throated marten	3	0.17	0.33	0	-
Southern pig-tailed macaque	2	0.11	0	0.22	-
Sunda pangolin	2	0.11	0.11	0.11	-
Tiger	2	0.11	0	0.22	-
Asian small-clawed otter	1	0.06	0	0.11	-
Clouded leopard	1	0.06	0	0.11	-
Malayan tapir	1	0.06	0.11	0	-
Marbled cat	1	0.06	0.11	0	-
Sun bear	1	0.06	0.11	0	-

Wald-chisq test *P<0.05, **P<0.01, ***P<0.001

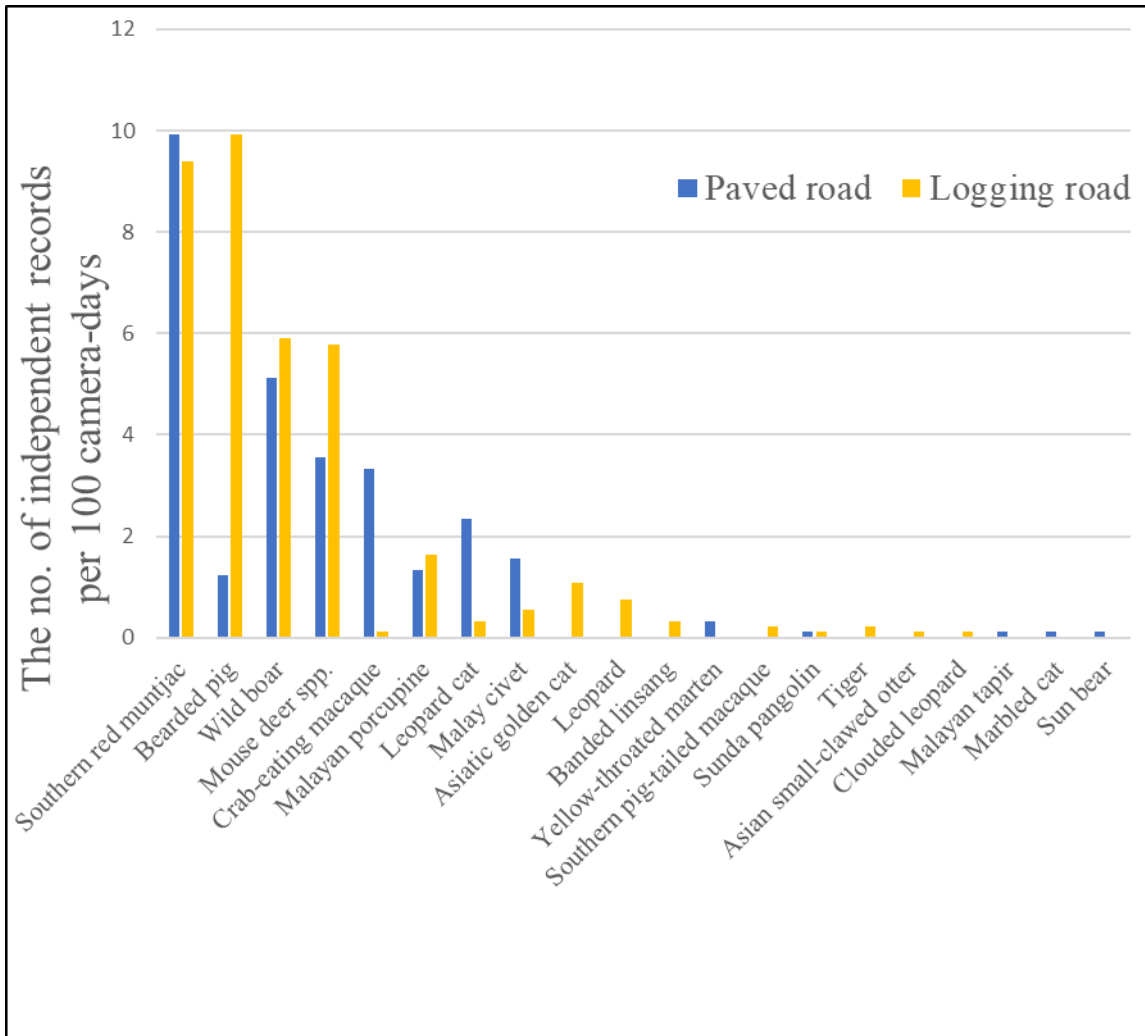


Fig. 6

The number of independent records per 100 camera-days for medium-large mammal species on the paved road and on the logging road.

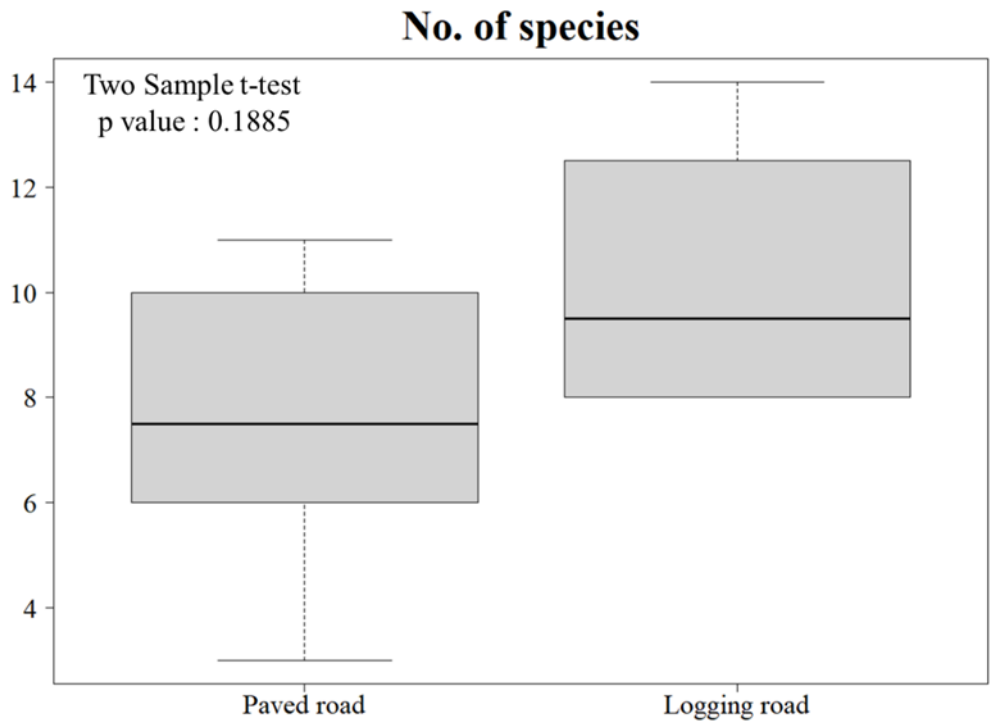


Fig. 7

The number of species recorded by cameras on the paved road (n=6) and on the logging road (n=4).

Diel activity patterns of wild mammals

I compared the number of independent records among daytime, nighttime and twilight using GLMMs for species and guild groups which were recorded more than 10 times on each road (Table 5). Moreover, Fig. 10-12 shows the diel activity patterns of wild mammals visualized by kernel density estimation. The trend of diurnal activity patterns differed among species. Moreover, the activity patterns of mouse deer and carnivores differed between the paved road and the logging road, even within the same species or guild groups (Fig. 10-e, Fig. 12-a).

Diel activity patterns of species

Southern red muntjac was recorded significantly more in the daytime and at twilight than during the nighttime on both the paved road and the logging road (paved road; $\chi^2 = 29.0$, $df = 2$, $p < 0.001$, logging road; $\chi^2 = 30.5$, $df = 2$, $p < 0.001$) (Table 5). This species displayed two activity peaks around 8:00 and 18:00 (Fig. 10-a) on both two roads, with 96.6% of independent records of the paved road and 91.9% of independent records of the logging road being recorded during the daytime and twilight (Fig. 8, Fig. 9). This indicated that southern red muntjac had diurnal or crepuscular activity patterns on both roads. Southern red muntjac had a high degree of overlap between the paved road and the logging road (0.85) (Table 6, Fig. 10-a).

Bearded pig was recorded significantly more in the daytime and at twilight than during the nighttime on the logging road ($\chi^2 = 32.4$, $df = 2$, $p < 0.001$) (Table 5). Although there was no significant difference in the number of independent records on the paved road among time periods, it could be due to the low sample size. This species displayed diurnal activity patterns on both the paved road and the logging road (Fig. 10-b), with 72.7% of independent records of the paved road and 72.5% of independent records of the logging road being recorded during the daytime (Fig. 8, Fig. 9). This indicated that bearded pig had diurnal activity patterns on both two roads. Bearded pig had a high degree of overlap between the paved road and the logging road (0.79) (Table 6, Fig. 10-b).

Wild boar was recorded significantly more in the daytime and at twilight than during the nighttime on both the paved road and the logging road (paved road; $\chi^2 = 11.7$, $df = 2$, $p < 0.01$, logging road; $\chi^2 = 19.0$, $df = 2$, $p < 0.001$) (Table 5). This species displayed diurnal activity patterns on both two roads (Fig. Fig. 10-c), with 63.0% of independent records of the paved road and 72.2% of independent records of the logging road being recorded during the daytime (Fig. 8, Fig. 9). This indicated that wild boar had diurnal activity patterns on both the paved road and the logging road. Wild boar had a high degree of overlap between the paved road and the logging road (0.83) (Table 6, Fig. 10-c).

There was no significant difference in the number of independent records of mouse deer. on the paved road among time periods, while mouse deer was recorded significantly more in the nighttime than during the daytime on the logging road ($\chi^2 = 6.3$, $df = 2$, $p < 0.05$) (Table 5). This species displayed various activity throughout the day on both the paved road and the logging road (Fig. 10-d). The ratio of

the number of records on the paved road during the daytime, twilight, and nighttime was 46.9%, 25.0%, and 28.1%, respectively (Fig. 8), while the ratio of the number of records on the logging road during the daytime, twilight, and nighttime was 24.5%, 20.8%, and 54.7%, respectively (Fig. 9). This indicated that mouse deer had cathemeral activity pattern on both roads, but tended to be diurnal on the paved road and nocturnal on the logging road. Mouse deer had 65% overlap in their diel activity patterns between the paved road and the logging road (Table 6, Fig. 10-d).

Malayan porcupine displayed an activity peak around 1:00 and nocturnal activity (Fig. 10-e), and all of independent records being recorded during the nighttime (Fig. 8, Fig. 9). This indicated that Malayan porcupine had nocturnal activity pattern on both the paved road and the logging road. Malayan porcupine had a high degree of overlap between the paved road and the logging road (0.88) (Table 6, Fig. 10-e)

Crab-eating macaque displayed two activity peaks around 8:00 and 16:00 on the paved road (Fig. 11-a), with 86.7% of independent records being recorded during the daytime (Fig. 8). This indicated that crab-eating macaque had diurnal activity pattern on the paved road.

Leopard cat displayed an activity peak around 24:00 and nocturnal activity (Fig. 11-b), with 95.2% of independent records being recorded during the nighttime (Fig. 8). This indicated that leopard cat had nocturnal activity pattern on the paved road.

Malay civet displayed an activity peak around 23:00 and nocturnal activity (Fig. 11-d), and all of independent records being recorded during the nighttime (Fig. 8). This indicated that Malay civet had nocturnal activity pattern on the paved road.

Asiatic golden cat displayed various activity throughout the day (Fig. 11-c), with 40%, 30% and 30% of independent records being recorded during the daytime, twilight and nighttime, respectively (Fig. 9). This indicated that Asiatic golden cat had cathemeral activity pattern on the paved road.

Diel activity patterns of guild groups

Carnivores was recorded significantly more in the nighttime than during the daytime and at twilight on the paved road ($\chi^2 = 36.0$, $df = 2$, $p < 0.001$) (Table 5). Carnivores on the paved road displayed an activity peak around 23:00 and nocturnal activity, while on logging road, displayed various activity throughout the day (Fig. 12-a). This indicated that carnivores had different activity pattern between the paved road and the logging road. Carnivores had 69% overlap in their diel activity patterns between the paved road and the logging road (Table 6, Fig. 12-a).

Ungulates was recorded significantly more in the daytime and at twilight than during the nighttime on both the paved road and the logging road (paved road; $\chi^2 = 54.0$, $df = 2$, $p < 0.001$, logging road; $\chi^2 = 70.0$, $df = 2$, $p < 0.001$) (Table 5). Ungulates displayed two activity peaks around 8:00 and 18:00 on both roads (Fig. 12-b). This indicated that ungulates had diurnal activity patterns on both the paved road and the logging road. Ungulates had a high degree of overlap between the paved road and

the logging road (0.91) (Table 6, Fig. 12-b).

Rodents was recorded significantly more in the nighttime than during the daytime and at twilight on the paved road ($\chi^2 = 34.1$, $df = 2$, $p < 0.001$) (Table 5). Rodents displayed an activity peak around 1:00 and nocturnal activity (Fig. 12-c). This indicated that rodents had nocturnal activity patterns on both the paved road and the logging road. Rodents had a high degree of overlap between the paved road and the logging road (0.74) (Table 6, Fig. 12-c).

Table 5

Number of independent records in all area and on the paved road and on the logging road, the result of GLMMs and Tukey's HSD test.

	No. of independent records	No. of independent records /100 camera-days					
		Paved road			Logging road		
		Daytime	Twilight	Nighttime	Daytime	Twilight	Nighttime
<i>All medium-large mammals</i>	654	36.61 ab	41.43 b	27.26 a	49.52 a	51.75 a	22.27 b
<i>Guilds</i>							
Carnivores	121	0.80 a	5.35 b	18.17 c	3.14	4.59	6.03
Ungulates	471	28.86 b	33.41 b	5.61 a	45.59 b	47.16 b	12.05 a
Primates	33	6.95	2.67	0	0.79	0	0
Rodents	115	5.35 a	4.68 a	18.98 b	0	0	3.93
<i>Species</i>							
Southern red muntjac	175	14.97 b	20.04 b	0.80 a	13.36 b	18.34 b	1.83 a
Bearded pig	102	2.14	1.34	0.27	17.29 b	12.45 b	1.57 a
Wild boar	100	7.75 b	6.68 b	1.87 a	10.22 b	7.21 b	1.05 a
Mouse deer spp.	85	4.01	5.35	2.41	3.41 a	7.21 ab	7.60 b
Crab-eating macaque	31	6.95	2.67	0	0.26	0	0
Malayan porcupine	27	0	0	3.21	0	0	3.93
Leopard cat	24	0.27 a	0 ab	5.35 b	0.52	0	0.26
Malay civet	19	0	0	3.74	0	0	1.31
Unidentified Feridae	18	0	0.67	4.54	0	0	0
Unidentified Viverridae	18	0	1.34	3.21	0	0.66	0.79
Unidentified Carnivore	13	0	1.34	1.34	0	0	1.57
Asiatic golden cat	10	0	0	0	1.05	1.97	0.79
Sus spp.	8	0	0	0	1.31	1.97	0
Leopard	7	0	0	0	1.31	1.31	0
Banded linsang	3	0	0	0	0	0	0.79
Yellow-throated marten	3	0.53	0.67	0	0	0	0
Southern pig-tailed macaque	2	0	0	0	0.52	0	0
Sunda pangolin	2	0	0	0.27	0	0	0.26
Tiger	2	0	0	0	0.26	0	0.26
Asian small-clawed otter	1	0	0	0	0	0.66	0
Clouded leopard	1	0	0	0	0	0	0.26
Malayan tapir	1	0	0	0.27	0	0	0
Marbled cat	1	0	0.67	0	0	0	0
Sun bear	1	0	0.67	0	0	0	0

Value with different letters within a row are significantly different (Tukey's HSD test, $P < 0.05$)

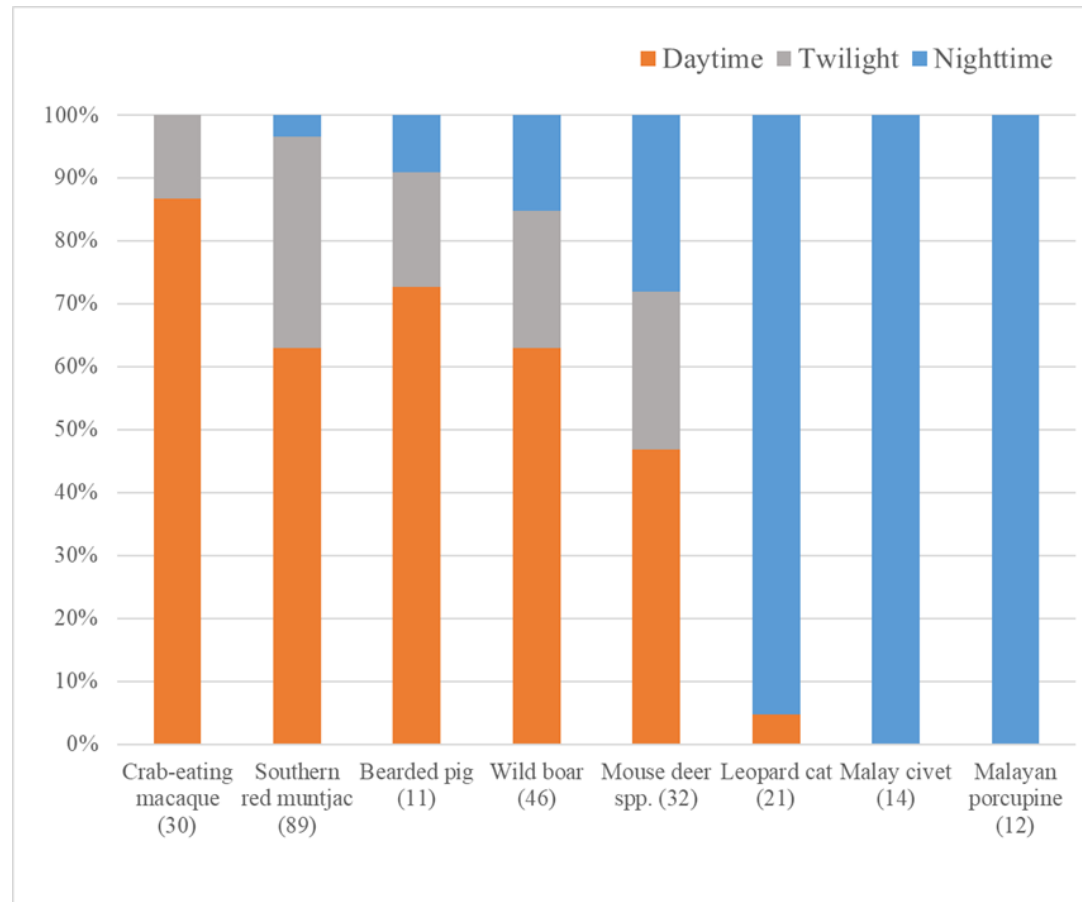


Fig. 8

Activity time period for 9 species (with $n > 9$) on the Paved road. Orange bar indicates percent frequency of independent records taken during the day time (0800-1800 h); Grey bar indicates percent frequency of independent records taken in twilight (0600-0800 h and 18:00-2000 h); Blue bar indicates percent frequency of independent records taken during the night time (2000-0600 h). Numbers in parentheses indicate sample size.

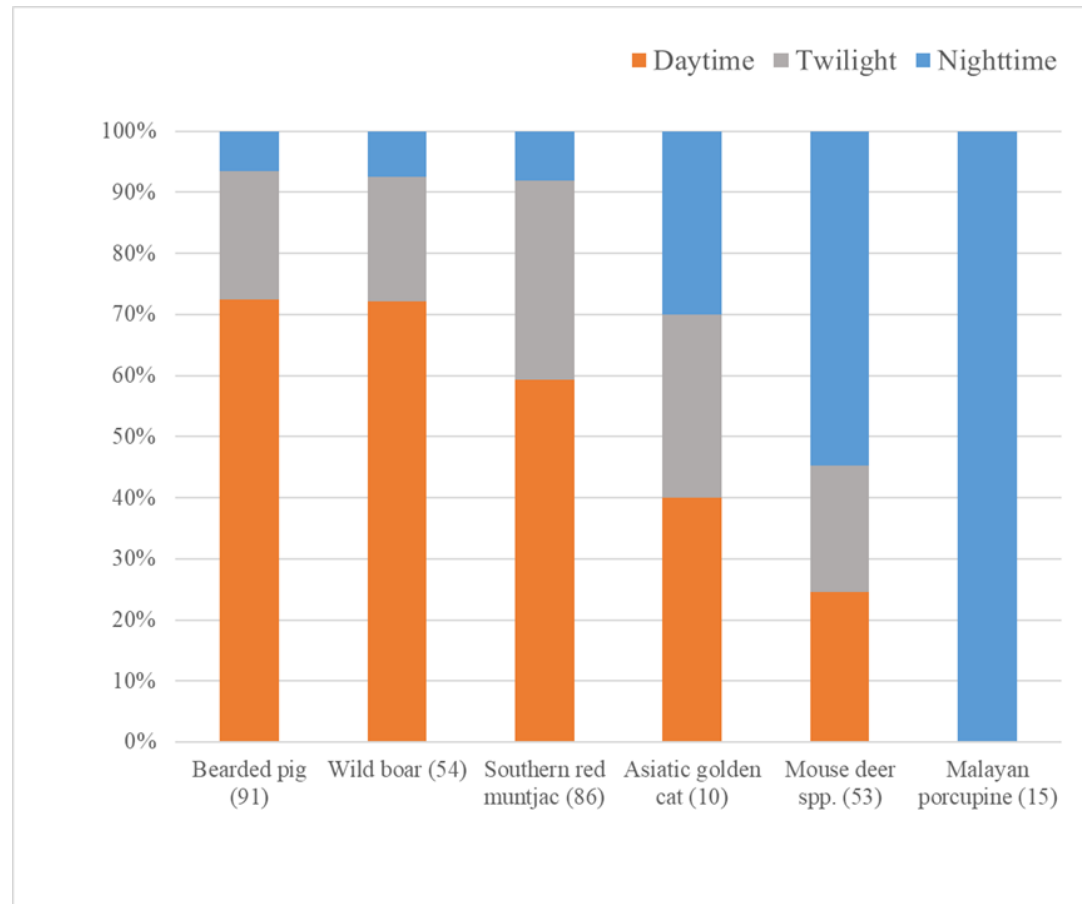


Fig. 9

Activity time period for 9 species (with n >9) on the Logging road. Orange bar indicates percent frequency of independent records taken during the day time (0800-1800 h); Grey bar indicates percent frequency of independent records taken in twilight (0600-0800 h and 18:00-2000 h); Blue bar indicates percent frequency of independent records taken during the night time (2000-0600 h). Numbers in parentheses indicate sample size.

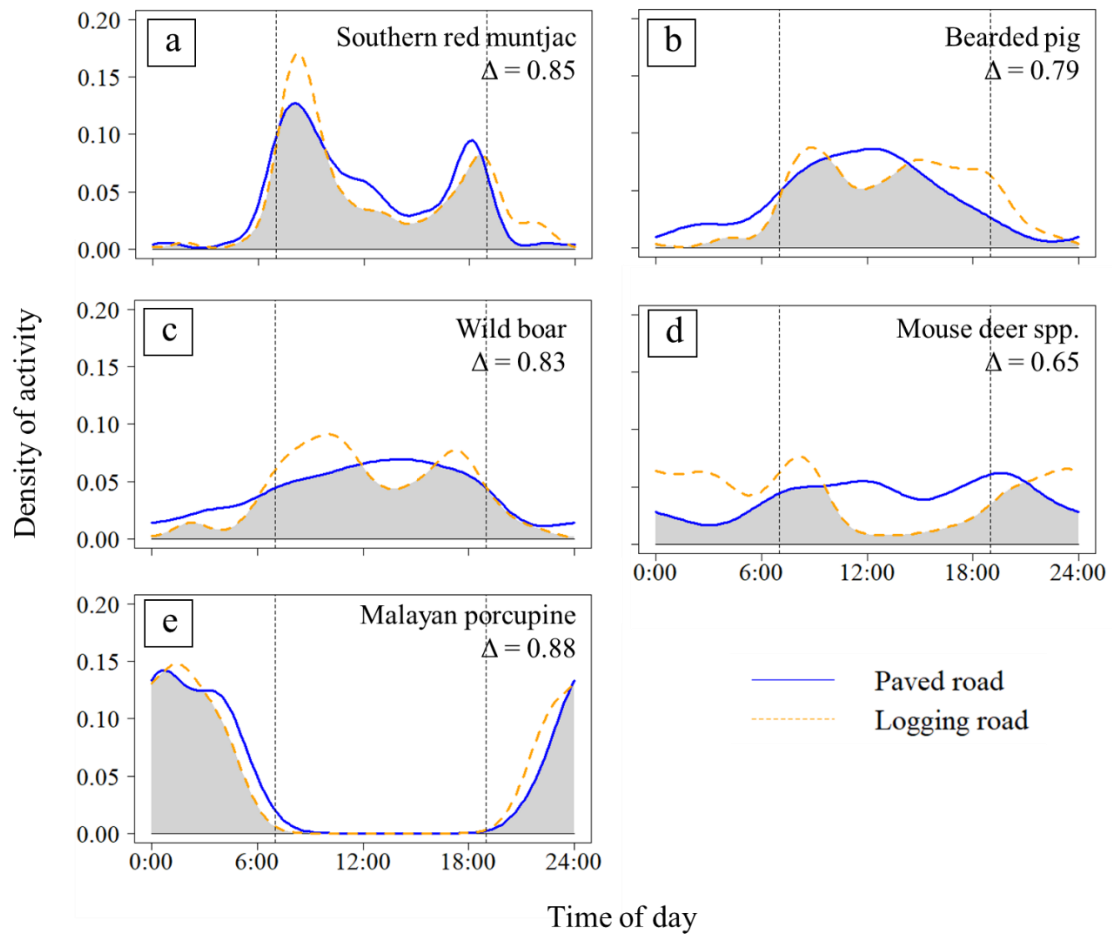


Fig. 10 (a, b, c, d, e)

Density estimates of the diel activity patterns of Southern red muntjac, Bearded pig, Wild boar, Mouse deer and Malayan porcupine (the paved road vs on the logging road). The grey area indicates the overlap between the two roads. Δ indicates the coefficient of overlap. The black dashed line indicates the time of sunrise (0700h) and sunset (1900 h).

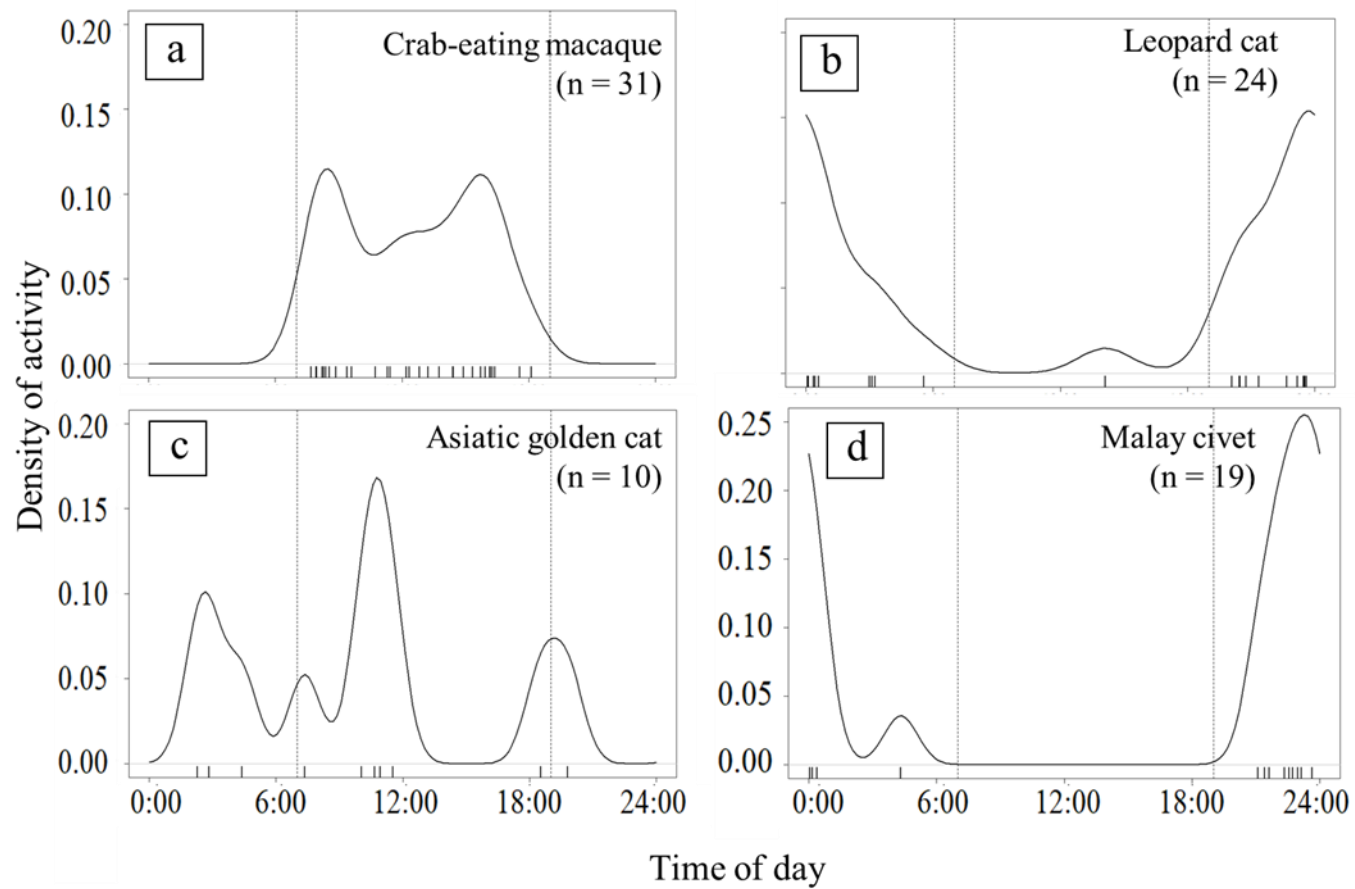


Fig. 11 (a, b, c, d)

Density estimates of the diel activity patterns (Crab-eating macaque, Leopard cat, Malay civet) on the paved road, (Asiatic golden cat) on the logging road. The black dashed line indicates the time of sunrise (0700h) and sunset (1900 h).

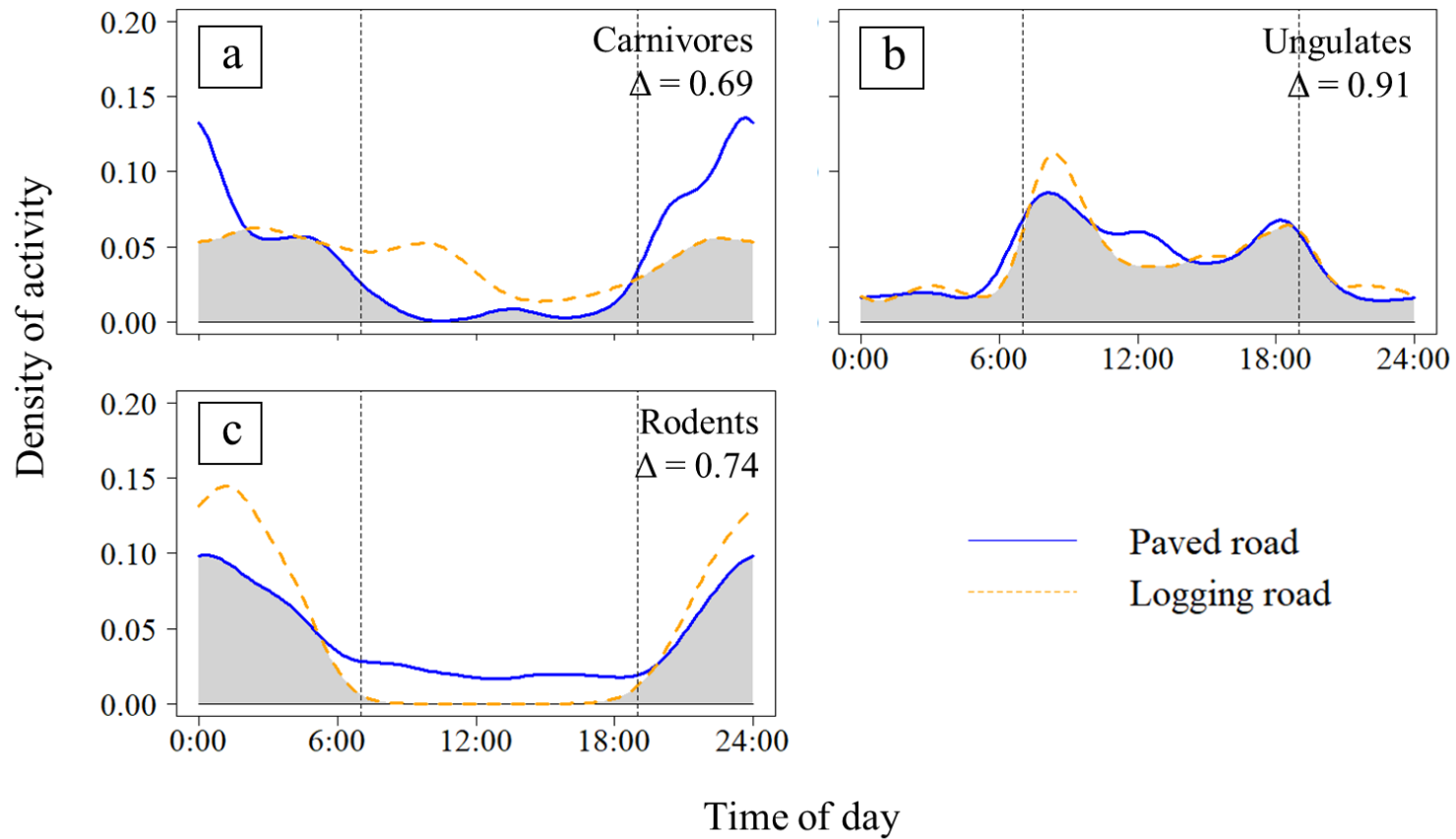


Fig. 12 (a, b, c)

Density estimates of the diel activity patterns of Carnivores, Ungulates and Rodents (the paved road vs on the logging road). The grey area indicates the overlap between the two roads. Δ indicates the coefficient of overlap. The black dashed line indicates the time of sunrise (0700h) and sunset (1900 h).

Table 6

The coefficients of overlap (Paved road vs Logging road) with approximate 95% bootstrap confidence intervals in parentheses.

$n \geq 10$	The coefficients of overlap
Carnivores	0.69 (0.55-0.82)
Ungulates	0.91 (0.85-0.95)
Rodents	0.74 (0.59-0.85)
Southern red muntjac	0.85 (0.78-0.90)
Bearded pig	0.79 (0.59-0.95)
Wild boar	0.83 (0.69-0.93)
Mouse deer spp.	0.65 (0.59-0.71)
Malayan porcupine	0.88 (0.66-1.03)

Bold value indicates high degree of temporal overlap (≥ 0.75).

Overlap of the diel activity patterns among mammal species

On the paved road, carnivores had a high degree of overlap with rodents (0.78) and Malayan porcupine (0.70), while it had a low degree of overlap with ungulates (0.33), southern red muntjac (0.18), bearded pig (0.28) and wild boar (0.35) (Table 7). Two carnivore species (leopard cat and Malay civet), which were both nocturnal, showed 0.69 of the coefficient of overlap. Crab-eating macaque had a high degree of overlap with southern red muntjac, bearded pig and wild boar (> 0.70). Four ungulates species (southern red muntjac, bearded pig, wild boar and mouse deer) had a high degree of overlap mutually (> 0.69). On the logging road, carnivores showed a high degree of overlap with mouse deer (0.88) (Table 8, Fig. 13). Three ungulates species (southern red muntjac, bearded pig and wild boar) showed a high degree of overlap mutually (> 0.70).

Table 7

The coefficients of overlap (Mammal vs Mammal) on the paved road.

Paved road	Carnivores	Ungulates	Primates	Rodents	Southern red muntjac	Bearded pig	Wild boar	Mouse deer spp.	Crab-eating macaque	Malayan porcupine	Leopard cat	Malay civet
Ungulates	0.33											
Primates	0.11	0.70										
Rodents	0.78	0.46	0.27									
Southern red muntjac	0.18	-	0.72	0.32								
Bearded pig	0.28	-	0.77	0.43	0.72							
Wild boar	0.35	-	0.73	0.49	0.71	0.86						
Mouse deer spp.	0.48	-	0.59	0.57	0.69	0.74	0.83					
Crab-eating macaque	0.11	0.70	-	0.27	0.72	0.77	0.73	0.59				
Malayan porcupine	0.70	0.21	0.04	-	0.10	0.18	0.23	0.29	0.04			
Leopard cat	-	0.31	0.09	0.73	0.17	0.25	0.31	0.44	0.09	0.66		
Malay civet	-	0.15	0.01	0.48	0.05	0.15	0.15	0.26	0.01	0.49	0.69	
Asiatic golden cat	-	-	-	-	-	-	-	-	-	-	-	-

Bold value indicates high degree of temporal overlap (≥ 0.75).

Table 8

The coefficients of overlap (Mammal vs Mammal) on the logging road.

Logging road	Carnivores	Ungulates	Primates	Rodents	Southern red muntjac	Bearded pig	Wild boar	Mouse deer spp.	Crab-eating macaque	Malayan porcupine	Leopard cat	Malay civet
Ungulates	0.64	-										
Primates	-	-										
Rodents	0.57	0.24	-									
Southern red muntjac	0.53	-	-	0.13	-							
Bearded pig	0.52	-	-	0.12	0.74							
Wild boar	0.55	-	-	0.14	0.74	0.85						
Mouse deer spp.	0.88	-	-	0.59	0.51	0.48	0.52					
Crab-eating macaque	-	-	-	-	-	-	-	-				
Malayan porcupine	0.54	0.22	-	-	0.11	0.10	0.12	0.56	-			
Leopard cat	-	-	-	-	-	-	-	-	-	-		
Malay civet	-	-	-	-	-	-	-	-	-	-	-	
Asiatic golden cat	-	0.54	-	0.48	0.48	0.50	0.56	0.55	-	0.34	-	-

Bold value indicates high degree of temporal overlap (≥ 0.75).

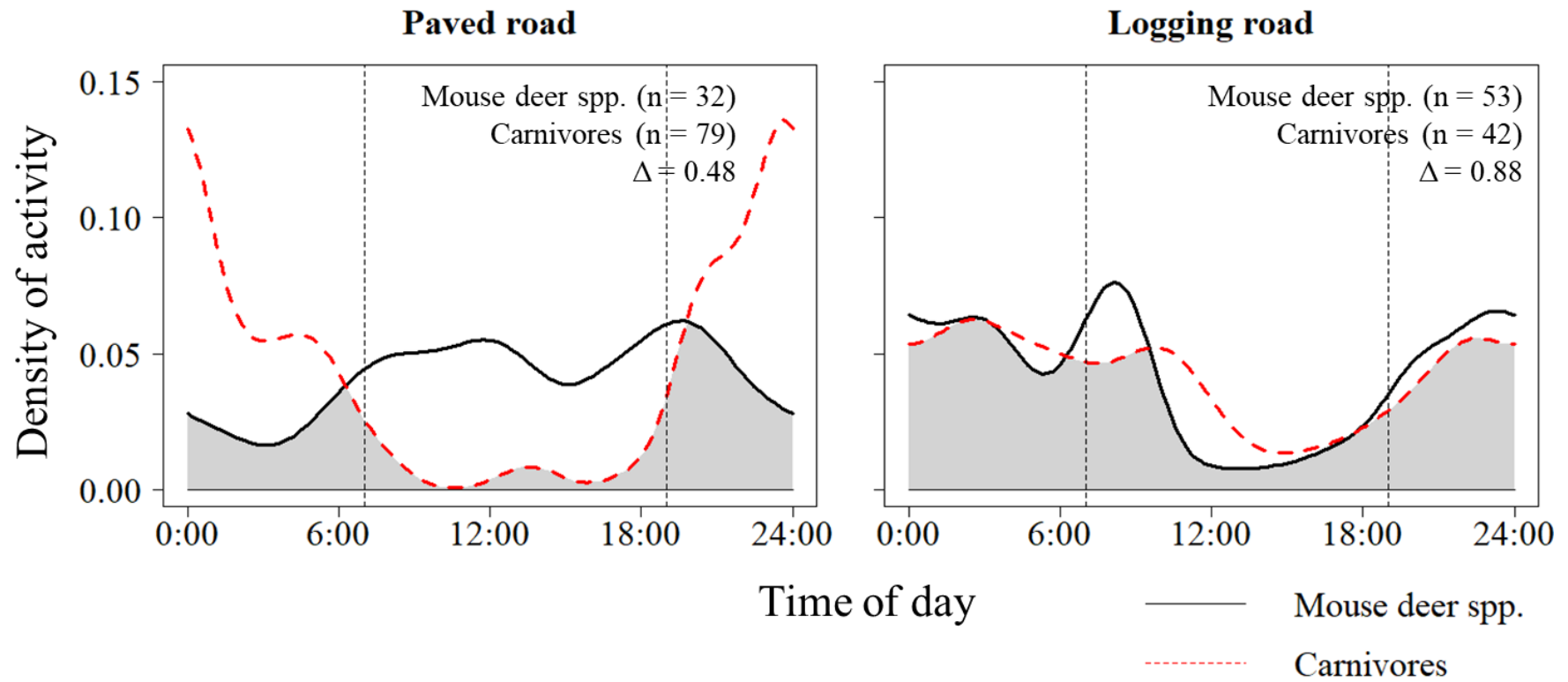


Fig. 13

Overlap of the diel activity patterns of Mouse deer spp. and Carnivores on the paved road and on the logging road. The grey area indicates the overlap between the two roads. Δ indicates the coefficient of overlap. The black dashed line indicates the time of sunrise (0700h) and sunset (1900 h).

Human activity in ERNP

The number of records per camera-day of humans (walking) and vehicles in all study area were 0.12 and 9.80, respectively. The detection rates of humans and vehicles on the paved road were 0.18 and 20.81, respectively. The detection rates of humans and vehicles on the logging road were 0.07 and 0.57, respectively. As a result of comparing the number of records between the paved road and the logging road by GLMMs, there was no significant difference in the number of records of humans, but there was the significant difference in the number of records of vehicles (Table 9). I calculated the detection rates of humans and vehicles for each location (Fig. 14 (a, b, c)Fig. 14). For humans, the detection rate was relatively high at locations close to sightseeing spots (#A, #B) on the paved road, tourists were recorded for bird-watching and night-walking (Fig. 14-a). On the logging road, humans were recorded, the detection rate was relatively high at locations close to entrance of a nature trail tourist often use (#G). This road was used by tourists for trekking, and also by park administrators for transportation in park maintenance. For vehicles, the detection rate was relatively high at locations close to sightseeing spots (#A) on the paved road (Fig. 14-b). Both humans and vehicles showed clear diurnal activity patterns (Fig. 15-a, b, c). They had a high degree of overlap between the paved roads and the logging roads (0.86) (Fig. 15-d).

Table 9

The detection rates of human walking and vehicles recoded from July 8 2019 to November 5 2019, the result of GLMMs (Paved road vs Logging road) and Wald chi-square test.

	No. of independent records/camera-day			P value
	All area	Paved road	Logging road	
Human (walking)	0.12	0.18	0.07	0.3156
Vehicles	9.80	20.81	0.57	< 0.001 ***
Human (walking) & Vehicles	9.92	20.99	0.64	< 0.001 ***

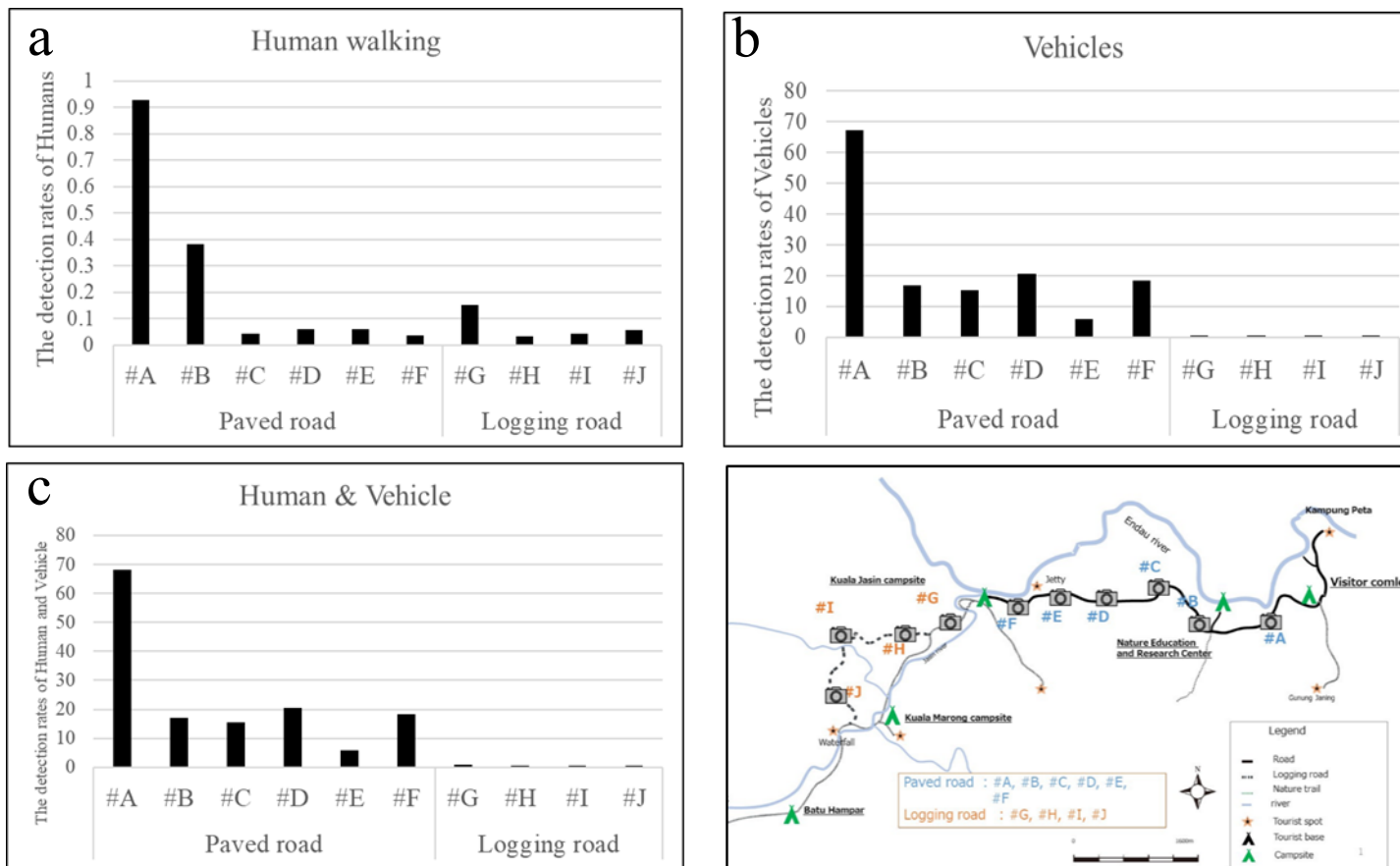


Fig. 14 (a, b, c)

The detection rates of human walking and vehicles recoded from July 8 2019 to November 5 2019

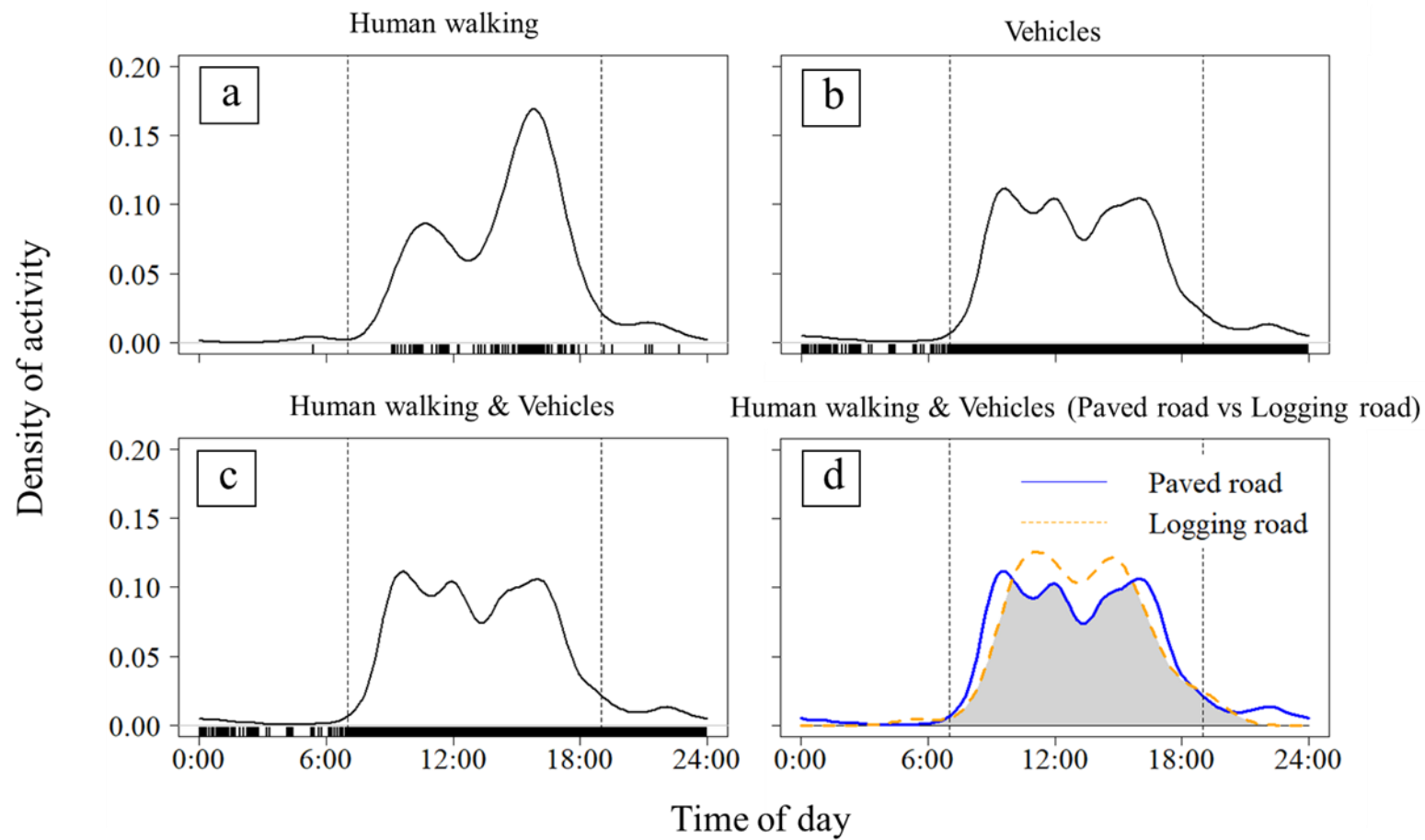


Fig. 15 (a, b, c, d)

Density estimates of the diel activity patterns (Human on walking, Vehicles, Human walking and Vehicles), overlap of activity patterns of Human walking and Vehicles on the paved road and on the logging road. The black dashed line indicates the time of sunrise (0700h) and sunset (1900 h).

Overlap of the diel activity patterns between mammal species and human

On the paved road, carnivores and rodents, which displayed nocturnal activity, had a low degree of overlap with human activity (< 0.30), bearded pig and crab-eating macaque had a high degree of overlap with vehicles (> 0.75) (Table 10). On the logging road, bearded pig and wild boar had a moderate overlap with human activity (0.60-0.69), while other species had a low degree of overlap with human activity (< 0.50) (Table 10).

Table 10

The coefficients of overlap (Mammal vs Human, Vehicle).

	The coefficients of overlap								
	All area			Paved road			Logging road		
	Human	Vehicle	Human/Vehicle	Human	Vehicle	Human/Vehicle	Human	Vehicle	Human/Vehicle
Medium-Large mammals	0.49	0.56	0.56	0.53	0.54	0.54	0.45	0.49	0.49
Carnivores	0.20	0.23	0.23	0.16	0.14	0.14	0.31	0.36	0.36
Ungulates	0.54	0.62	0.62	0.61	0.64	0.64	0.48	0.52	0.51
Primates	0.76	0.85	0.85	0.72	0.83	0.83	NA	NA	NA
Rodents	0.23	0.26	0.26	0.30	0.29	0.29	0.01	0.05	0.04
Southern red muntjac	0.50	0.59	0.59	0.57	0.62	0.62	0.40	0.45	0.45
Bearded pig	0.70	0.77	0.77	0.66	0.78	0.78	0.64	0.68	0.68
Wild boar	0.68	0.73	0.73	0.68	0.72	0.72	0.61	0.66	0.66
Mouse deer spp.	0.36	0.42	0.42	0.58	0.58	0.58	0.19	0.25	0.24
Crab-eating macaque	0.76	0.82	0.82	0.72	0.83	0.83	NA	NA	NA
Malayan porcupine	0.05	0.06	0.06	0.08	0.07	0.07	0.01	0.03	0.03
Leopard cat	0.21	0.22	0.22	0.17	0.14	0.14	NA	NA	NA
Malay civet	0.05	0.06	0.06	0.08	0.06	0.06	NA	NA	NA
Asiatic golden cat	0.37	0.42	0.42	NA	NA	NA	0.32	0.47	0.45

Bold value indicates high degree of temporal overlap (≥ 0.75).

Discussion

The present study evaluated the detection rates and the diel activity patterns of wild mammals in the tourist use area of ERNP using camera traps. In total 21 different species of medium and large mammals including 11 carnivore species and 6 ungulate species were recorded by the camera traps (Table 2). Ota et al. (2019) recorded at least 22 species of medium and large wild mammals in camera trap surveys with camera-days comparable to this study (1728 days) on a logging road and nature trails in ERNP. The point where the road and the animal trail cross were suitable for this type of camera-trap survey, and the cameras were able to capture medium and large mammals of various groups, such as Carnivores and Ungulates, although records of small, arboreal or flying mammals such as rodents and bats were limited. In addition, during the survey period of this study, the direction of the camera installed on the paved road was changed to face animal trail because many humans and vehicles used this road and it would exceed the capacity of the SD card quickly. This may have resulted in a lost opportunity to record wild mammals moving along the road. Especially, carnivore have a habit of moving along roads (Cusack et al., 2015). Therefore, it should be noted that the detection rates and number of species of wild mammals recorded on the paved road in this study may have been affected by the change in camera direction. However, the diel activity patterns of the wild mammals were estimated from the time when the videos were recorded, and thus was not affected.

Compared to the logging road, humans and vehicles were recorded significantly more on the paved road (Table 9), suggesting that human activities were significantly differed between the paved road and the logging road. In particular, heavy vehicle traffic was recorded frequently, and so vehicle traffic was the highest human activity on the road in ERNP. Both humans and vehicles showed clear diurnal activity patterns, indicating human activity in ERNP were conducted in daytime. The increased human traffic on roads had a negative effect on occurrence of wild mammals (Zhou et al., 2013). In addition, Muhly et al. (2011) reported that predator species did not occur in large numbers on roads and trails where human use exceeded 18 (times/ day). In this study, the number of records of humans and vehicles on the paved road was 20.99 (times/day) (Table 9). It was suggested that human traffic on the paved road in ERNP may have a significant impact on wild mammals.

Human impact on detection rates of mammals

There was no significant difference in the number of independent records of some species (southern red muntjac, wild boar, mouse deer, Malayan porcupine, leopard cat and Malay civet) between the paved road and the logging road (Table 4), indicating that the detection rates of these species may not differ on both roads. It suggested that human impact did not affect on the detection rates of these species. However, the number of records of bearded pig and crab-eating macaque were significantly differed between the paved road and the logging road (Table 4). Bearded pig were recorded significantly more on the logging road, indicating significant occurrence on the logging road. This may indicate that the logging

road was a preferable habitat of bearded pig, or that they avoided the paved road because of high human activity. Crab-eating macaque were recorded significantly more on the paved road. They are common near human settlements such as forests, parks, tourist attractions, and temples in Southeast Asia, and can be frequently observed around tourist sites in ERNP. Crab-eating macaque occurred along roads and trails to be provisioned with human food by commuters and tourists (Hansen et al., 2019). In ERNP also, they may have occurred more frequently on the paved road because of the supply of food from human.

In addition, the carnivore species that appeared on the two types of roads might be different (Table 4). Four medium-large carnivores (Asiatic golden cat, clouded leopard, leopard and tiger) were recorded only on the logging road, indicating some carnivores preferred the logging road or avoid the paved road. Leopards preferred more forest interior in protected areas (Ngoprasert et al., 2007). Schuette et al. (2013) also showed that distance to human settlements is the most important factor of human disturbance affecting carnivore occupancy in Kenya. Therefore, the finding that some carnivores avoided the paved road, which were closer to the tourist centers and human activity relatively high, suggested that human impact may affect the occurrence of them in ERNP. In this study, however, the number of records of each carnivorous species were small, so it was not possible to discuss their detection rates and their diel activity patterns. In order to assess human impact of these carnivore species, further studies are needed to accumulate camera trap data and to use GPS to reveal the behavioral activity patterns of individual in more detail.

Human impact on diel activity patterns of wild mammals

In this study, I examined the diel activity patterns of nine mammalian species. Bearded pig, wild boar and crab-eating macaque showed diurnal activity, southern red muntjac showed diurnal or crepuscular activity, leopard cat, Malay civet and Malayan porcupine showed nocturnal activity, mouse deer and Asiatic golden cat showed cathemeral activity. The diel activity patterns of these species that were recorded in this study were similar to previous studies of these species using camera-trapping techniques in tropical forest in Peninsular Malaysia (Mohd-Azlan, 2006; Gumal et al., 2014; Tan et al., 2018; Ota et al., 2019), Borneo (Colon, 2002; Bernard et al., 2013, Ross et al., 2013), Sumatra (Linkie and Ridout, 2011), Thailand (Kitamura et al., 2010; Lynam et al., 2013) and Cambodia (Gray and Phan, 2011) (Table 11).

Despite the paved road had high human activity compared to the logging road, the diel activity patterns of southern red muntjac, bearded pig, wild boar and Malayan porcupine did not differ between the paved road and the logging road. It suggested that there were no significant human impacts on their diel activity patterns. Particularly, bearded pig and wild boar showed diurnal activity, their activity patterns had a high degree of overlap with human. Previous studies have reported that human activity had negative effects on wild mammal activity; for example, Davinson (2019) showed that the diel activity patterns of bearded pig shifted from diurnal to nocturnal due to the influence of human activities, however, in this study bearded pig did not change their activity from diurnal to nocturnal. In addition, Ota et al. (2019)

reported the diel activity patterns of southern red muntjac and bearded pig and were not differed between the open and closed seasons in ERNP, these were not affected by human activity. Therefore, these findings of my study suggested that current human activities have not had a significant negative impact on the diel activity patterns of these mammals in ERNP, either temporally or spatially.

Mouse deer had cathemeral activity pattern on both roads, but tended to be diurnal on the paved road and nocturnal on the logging road, and this species had 65% overlap in their diel activity patterns between the paved road and the logging road (Fig. 10-d, Table 6). It indicated that the diel activity patterns of mouse deer differed between the two roads. Furthermore, it suggested that mouse deer changed their diel activity patterns within the tourist area, becoming diurnal on the paved road with high human activity and nocturnal on the logging road in the forest interior. This may be due to the inter-specific interaction with carnivore species, and the details are discussed later.

By guild groups, carnivores had different their diel activity patterns between the paved road and the logging road. They had nocturnal activity pattern on the paved road and had cathemeral activity on the logging road, indicating that they were more nocturnal on the paved road with high human activity than on the logging road. It suggested that the diel activity patterns of carnivores changed because of human activity on the paved road. It was reported wild mammals changed their diel activity patterns from diurnal to nocturnal due to human impact (Gaynor et al. 2018a). However, it needs to be careful with this interpretation. As I pointed out previously, the carnivore species that appeared on the two types of roads might be different. The main carnivore species recorded on the paved road were leopard cat and Malay civet, which were nocturnal activity as in previous studies. Furthermore, these two species were frequently recorded on the paved road compared to the logging road, suggesting that human impact may not change the diurnal activity patterns of leopard cat and Malayan civet.

Human impact on inter-specific interactions

I evaluated inter-specific interactions by examining the overlap in the diel activity patterns of each species and guild groups. Carnivores had 78% overlap with rodents on the paved road in this study. High level of the overlap of activity patterns between carnivores and rodents may suggest the predator-prey interaction because activities at the same time period of day are expected to increase the encounter between species. Especially, leopard cat, which recorded most frequently on the paved road, prey commonly on rodents such murids (Grassman et al., 2005). In order to verify this hypothesis, it would be desirable to collect carnivores scat samples to analyze the composition of prey species, but scats collection is difficult in tropical forests due to low population densities and high scat decay rates. Therefore, in the absence of difficult-to-collect dietary data, examining temporal overlap among wild mammals, as in this study, can provide needed insight into predator-prey interactions (Linkie and Ridout, 2011).

Interestingly, the overlap of activity patterns of carnivores and mouse deer were clearly differed between the paved road and the logging road (Fig. 13), indicating that the predator-prey interactions would

be influenced by human activities. Prey may become spatiotemporally close to humans in their activities to avoid predators, and that roads can be a shelter for non-predators from predators using human presence as a shield in predator-prey interactions (Berger, 2007; Muhly et al., 2011). Therefore, I hypothesized the temporal avoidance of carnivores may cause the activity patterns of mouse deer. The diel activity patterns of mouse deer differed between the two roads, and were more diurnal activity on the paved road with high human activity than on the logging road. The diel activity patterns of mouse deer had high overlap with carnivores on the logging road (89%), but moderate overlap on the paved road (48%). Because carnivores were less active during the daytime on the paved road, mouse deer may show high level of diurnal activity to avoid overlapping activity patterns of carnivores. However, further studies are needed to verify the hypothesis because the mouse deer showed various diurnal activity patterns in different studies; diurnal (Kitamura et al., 2010), nocturnal (Ross et al., 2013), crepuscular (Tan et al., 2018; Ota et al., 2019) and cathemeral (Bernard et al., 2013). This may suggest that this species may change its activity patterns relatively easily.

Implications for tourism and conservation

In this study, human impacts on detection rates and diel activity patterns of wild mammals and inter-specific interactions among mammals on the two types of roads with different human use in a tourist area of ERNP were discussed. The detection rates and the diel activity patterns of southern red muntjac, wild boar, Malayan porcupine and crab-eating macaque were not affected by human activity. The findings suggest that the current nonlethal tourism activities and park management (e.g. trekking and transportation by car) in ERNP are sustainable with no negative impact on these species. In ERNP, lethal human activities (e.g. hunting) are strictly prohibited and tourists are required to follow guides to enter the park. These protection methods are effective in preventing tourists from having any significant negative effects on the diel activity patterns of the mammals that inhabit ERNP (Ota et al., 2019).

On the other hand, this study suggested that human activity may affect the detection rates and the activity patterns of some species and guild groups such as bearded pig and carnivores. If they are species of conservation concern, such as endangered species, urgent actions are needed. In particular, large carnivores are likely to be a target for conservation as the top of the food chain (Kuranth and Chellam, 2009). In addition, this study suggested human activity affected predator-prey interactions between carnivores and mouse deer. Just as the direct impact of predators can have an indirect impact on vegetation and biodiversity in general, the change of diel activity patterns of predator species by human can potentially have indirect effects on interacting prey species that can ultimately have significant effects on the structure, function and biodiversity of an ecosystem (Muhly et al., 2011; Shannon et al., 2014).

Although conservation policies vary depending on the species and groups to be conserved, information on mammal occurrence, diel activity patterns, and inter-specific interactions, as I conducted in this study, is expected to be useful in conservation efforts. For example, approaches such as "temporal

zoning" (analogous to spatial zoning), could be considered, which restricts certain human activities to times when species of conservation concern are most active or when the likelihood of negative human-wildlife encounters is highest (Gaynor et al., 2018a).

The information on the occurrence and diel activity patterns of mammals can also be used for tourism purposes. For example, in this study, southern red muntjac showed peaks of activity in the morning and evening. The activities at the time may provide opportunities for direct observation of that species by tourists. It may also help to avoid unexpected encounters between tourists and dangerous animals such as Asian elephants. In addition, a tourism program called "Virtual Hunting" is currently underway to enable indirect observation of wildlife using camera traps. The accumulation of basic information on the occurrence and the diel activity patterns of wildlife and the understanding of human impact on wildlife could not only enable sustainable tourism activities, but it could also lead to the creation of new tourism activities.

In this study, I found that human activities affect the occurrence of wild mammals, diel activity patterns, and inter-specific interaction in a tourist area, but also that the degree of influence varied by species. Because this study was conducted over a period of about eight months, I could not take into account the effects of the wet and dry seasons and the opening and closing of a national park on the diel activity patterns of wild mammals. Wild mammals may change their diel activity patterns due to fluctuations in the number of tourists throughout the year. Sensitivity of wild mammals against human may vary with breeding season (Berger, 2007). In addition, it reported that the population densities of mammals have varied among seasons and years as a result of changes in factors such as food resources, rainfall and temperature (Hancock et al., 2005). Therefore, further studies on the ecology, behavior, and population density dynamics of each species and assessment of human impacts are needed for sustainable tourism and conservation management.

Acknowledgements

I would like to express my appreciation to Professor Dr. Shinya Numata for giving me the opportunity to conduct this study and his thoughtful guidance. I am also grateful to Dr. Mazlan Bin Hashim, Dr. Dyana, Ms. Nadiah and Mr. Tarfic for their cooperation in my research in Malaysia. A special gratitude I give to Ms. Shima, park guides and staff of Johor National Parks Corporation for their support to my survey in ERNP. Finally, many colleagues at Human-Nature Laboratory and Environmental Management Unit of Department Tourism Science of Tokyo Metropolitan University kindly provided their productive comments and a lot of encouragement.

Table 11

Comparison of diel activity patterns among previous studies. Diurnal, nocturnal, crepuscular and cathemeral activity patterns indicated with D, N, Cr and Ca.

Common name	This study	Colon, 2002	Mohd-Azlan, 2006	Kitamutra et al., 2010	Gray and Phan, 2011	Linkie and Ridout, 2011	Bernard et al., 2013	Ross et al., 2013	Lynam et al., 2013	Gumal et al., 2014	Tan et al., 2018	Ota et al., 2019
Asiatic golden cat	Ca		Ca	Ca					D	Cr		
Leopard cat	N		Ca	N	Ca				N	N		Ca
Malay civet	N	N	N				N					
Southern red muntjac	D or Cr		D	Ca	Ca	D	D	D			Cr	D
Mouse deer spp.	Ca		Ca	D, Ca			Ca	Cr, N			Cr	Cr
Bearded pig	D						Ca	Ca			Cr	D
Wild boar	D		D	D	Ca	D					Cr	D
Crab-eating macaque	D						D					
Malayan porcupine	N		N		N		N					N

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