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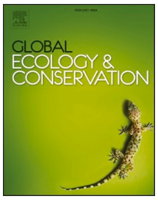

Original Research Article

Behavioral response of Bornean ungulates, including bearded pigs and sambar deer, to anthropogenic disturbance in Sabah, Malaysia

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ABSTRACT

Understanding wildlife behavioral responses to anthropogenic disturbance is crucial for assessing its effects and managing protected areas. We used camera traps to investigate the behavioral responses of two of the most frequently hunted Bornean ungulate species, bearded pigs (*Sus barbatus*) and sambar deer (*Rusa unicolor*), to anthropogenic disturbance in three protected areas in Sabah, Malaysia, that have varying levels of human activity. We found that human activities generally influence the activity patterns of both ungulates, albeit with variations among the sites. Temporal activity levels of both species would be affected by anthropogenic disturbance; temporal activity levels of bearded pigs were generally low where poaching of this species is reported and both species reduced their activity during daytime, the period of highest probability of encountering humans. Bearded pigs approached plantations during times of low human activity, presumably to forage, indicating that they adjust their spatiotemporal activity patterns to minimize human contact. Conversely sambar deer approached plantations when humans were active during the daytime, suggesting acclimation to non-lethal human contact to maximize energy intake. We observed a reduction in active times for both species at sites of high anthropogenic disturbance. Despite these challenges, both species demonstrated behavioral adaptability to anthropogenic disturbance by utilizing artificial environments such as roads and oil palm plantations probably as foraging places, thereby potentially compensating for reduced active times especially for feedings. Our study underscores the negative impact of human activities on the activity patterns of these two ungulate species. Meanwhile, they showed behavioral plasticity to anthropogenic disturbance by utilizing food resources in artificial environments efficiently. Our

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findings highlight the need for additional research into the behavioral responses of ungulates in Southeast Asia.

1. Introduction

Loss of species diversity is a serious environmental issue, given the functional roles of every organism in each ecosystem (Srivastava et al., 2012). Mammals are a useful indicator of global biodiversity loss because of their diverse ecological niches (Ceballos and Ehrlich, 2002). Of 173 mammalian species examined, more than 70 % experienced the contraction of their geographic ranges in the past 200 years, mainly due to anthropogenic disturbances (Ceballos and Ehrlich, 2002). Human activities, including overhunting and habitat destruction have immense negative impacts on wildlife (Tilman et al., 2017; Andermann et al., 2020; Brodie et al., 2015).

Wildlife often show physiological and behavioral responses to anthropogenic stimuli; such responses can be broadly categorized as attraction, avoidance, and habituation (Whittaker and Knight, 1998, Bejder et al., 2009), causing behavioral changes (Bejder et al., 2009). These include changes in spatial distribution, temporal activity patterns, feeding behavior, reproduction, and social structure (Bejder et al., 2009). Adjusting spatial and temporal activity patterns is a common response of wildlife to avoid encountering humans (Ciuti et al., 2012; Gaynor et al., 2018). The fear response of some wildlife to humans exceeds that to natural predators (Ciuti et al., 2012; Visscher et al., 2023). Among the various human activities, hunting can directly affect wildlife abundance and mammals may change their ecological characteristics in response to human activities (Stankowich, 2008; Tilman et al., 2017). Globally, most species at threat from hunting are in Africa and Southeast Asia (Ripple et al., 2016). The extinction risk of terrestrial mammals is particularly high in Southeast Asia (Ceballos and Ehrlich, 2002; Tilman et al., 2017), where regional population decline of most large species has occurred within the past 50–100 years (Corlett, 2007). On the island of Borneo, a remarkable level of wildlife habitat loss has largely been caused by rapid deforestation and the conversion of forests to monocultural plantations (Ocampo-Peñuela et al., 2020). However, hunting rather than logging is the main threat to medium- to large mammals (Brodie et al., 2015). Given that hunting pressures including poaching are not fully controlled and depend on differences in accessibility and intensity of active enforcement even within protected areas (Corlett, 2007), and because hunting has direct (abundance) and indirect (behavior) impacts on wildlife (Ripple et al., 2016), monitoring wildlife populations and their behavior is necessary to assess and control hunting/poaching in a given area.

Ungulates often show apparent vigilance for anthropogenic disturbance including hunting (Stankowich, 2008; Ciuti et al., 2012; Cromsigt et al., 2013). They change temporal and spatial land-use patterns in response to human disturbance depending on various factors such as the season, the presence of offspring, the level of exposure to humans, and their physical condition (Stankowich, 2008). One significant behavioral response to human disturbance is an increase in nocturnality to avoid detection (Gaynor et al., 2018). This shift in activity patterns is also influenced by environmental factors such as moonlight, which regulates the brightness at night (Kyba et al., 2017). Therefore, the visibility and movement at night of some ungulate species are affected by the lunar illumination levels (Prugh and Golden 2014; Ampeng et al., 2018; Colino-Rabanal et al., 2018; Gordigiani et al., 2021). In Southeast Asia, they have long been targeted by hunters, and many ungulate species are now threatened due to overhunting and habitat loss (Corlett, 2007). In Malaysian Borneo, ungulates including bearded pigs (*Sus barbatus*) and sambar deer (*Rusa unicolor*) account for up to 80 % of hunted animals (Bennett et al., 2000; Yi and Mohd-Azlan, 2020; Saikim et al., 2023). Given that the behavioral responses of ungulates show intraspecific variation and differ according to the level of anthropogenic disturbance (Stankowich, 2008), it is important to assess behavioral responses of different populations of ungulates to human stimuli, to evaluate anthropogenic disturbance level and the management of protected areas. Also, given that most hunting/poaching activity occurs at night in Malaysian Borneo (Wong et al., 2004), these ungulates may show differences in response to anthropogenic stimuli by the time and the presence of humans. Despite knowledge of behavior being central to wildlife management, along with long-term monitoring of population dynamics (Crosmary et al., 2012), relatively little attention has been paid to assessing the effect of anthropogenic disturbance on animal behavior (Burton et al., 2022).

Here, we investigated behavioral responses of two ungulate species, bearded pigs and sambar deer, to anthropogenic disturbance in three protected areas under different levels of disturbance in Sabah, Malaysia. Although both species are listed as vulnerable on the IUCN Red List (Timmins et al., 2015, Luskin et al., 2017), hunting and selling meats of these species is permitted with appropriate licenses issued by the Sabah Wildlife Department outside the protected areas in Sabah (Wildlife Conservation Enactment, 1997). Camera trapping is an efficient means of estimating wildlife behavior (Caravaggi et al., 2020), and it can facilitate regional comparisons of wildlife behavioral responses (Burton et al., 2022). Therefore, we compared the temporal activity levels of the two ungulate species and the effect of artificial environments such as oil palm plantations and gravel roads on their activities across sites, using camera trap data obtained over a three-year period between 2010 and 2016. We also assessed the effects of the lunar phase on their nocturnal activities in relation to their approach to artificial environments. We predict that these two ungulate species would exhibit differences in temporal activity levels by sites, depending on the level of human disturbance, and would stay away from the artificial environments depending on the level and timing of human activity and nighttime visibility.

2. Materials and methods

2.1. Study sites

The Danum Valley Conservation Area (hereafter called DVCA) (4° 50’–5°05’ N, 117°30’–117°48’ E, Fig. 1) is a forest reserve covering 438 km^2. DVCA is conserved primarily for the maintenance of forest essential for climatic or physical reasons (Forest Enactment, 1968). Most of the area comprises mature lowland evergreen dipterocarp forest (Marsh and Greer, 1992). The study area consists of old-growth forest surrounding a tourist lodging facility (5°01' N, 117°44'E). There was only one gravel road leads to the facility (Fig. 2a).

The Lower Kinabatangan Wildlife Sanctuary (hereafter called LKWS) (5° 10'–5° 50' N, 117° 40' –118° 30' E, Fig. 1) is located along the Kinabatangan River, which reaches 560 km inland. LKWS comprises 10 forest blocks totaling an area of 270 km^2, including seasonal and tidal swamp forests, permanent freshwater swamps, mangrove forests, and lowland dipterocarp forests (Abram et al., 2014). LKWS is conserved primarily for the protection of nature and the maintenance of wildlife habitat (Wildlife Conservation Enactment, 1997). The southern area of the study site is extensively covered by secondary forests. The northern area has been deforested for oil palm plantations, except for a protected zone along the river (Fig. 2bII).

The Tabin Wildlife Reserve (hereafter called TWR) (5°05'–5°22'N, 118°30'–118°55'E, Fig. 1) covers approximately 1225 km^2. It is surrounded by large oil palm plantations. TWR is conserved primarily for protection of wildlife and wildlife habitat (Forest Enactment, 1968). Most of TWR was heavily logged for timber in the 1970s and 1980s, leaving mainly regenerating mixed dipterocarp tropical rainforest (Mitchell, 1994). The study area was located on the western boundary of TWR (5°11'N, 118° 30'E) (Fig. 2c).

There was little to no poaching around the study area in DVCA (Hearn et al., 2017; Wong et al., 2004), due to various geographical and administrative factors, such as being 50 km from the nearest village and having just one access road with a government-controlled access gate. Conversely, poaching has been reported in LKWS (Hearn et al., 2017; Love et al., 2017); even within protected areas, ungulate population density, especially sambar deer, may occasionally be affected by poaching (Matsuda et al., 2015). However, as local communities are of Muslim faith, they do not consume bearded pigs (Bennett and Robinson, 2000; Kurz et al., 2021), so the population density of bearded pigs is generally high with possibly little impact on their behavior (Matsuda et al., 2015) at the time of data collection. TWR is surrounded by oil palm plantations and relatively close to the human settlements where poaching predominantly occurs (Saikim et al., 2023). In the TWR study area, there was sporadic poaching (Hearn et al., 2017). Sambar deer are a target species for poachers in both LKWS and TWR. Although poaching occurred in LKWS and TWR, bearded pigs and sambar deer were relatively common around these sites during the study period (Nakabayashi et al., 2014; Bernard et al., 2022). The photographic encounter rate (± SD) of presumed poachers during 2007–2013 in DVCA, LKWS, and TWR were 0.000 ± 0.000, 0.434 ± 1.138, and 0.381 ± 2.366, respectively (Hearn et al., 2017), although poaching intensity may not correlate with these rates when poachers avoided cameras (Brodie et al., 2015). We encountered or recorded presumed poachers in the sites except for DVCA during the study period.

The natural predator of the two ungulate species is the Sunda clouded leopard (*Neofelis diardi*) (Ross et al., 2013), and the presence of these natural predators can potentially affect the behavior and movement of these species (Ross et al., 2013). We recorded 4 photos of the Sunda clouded leopard at all three sites during the study period (Nakabayashi et al., 2021). However, the sample size was not sufficient to use the records for analysis. Given that the difference in sampling area (1–4 km^2) among the three sites was almost negligible compared to the home-range size of the Sunda clouded leopard (16.1 km^2, Hearn et al., 2013), the natural predator density

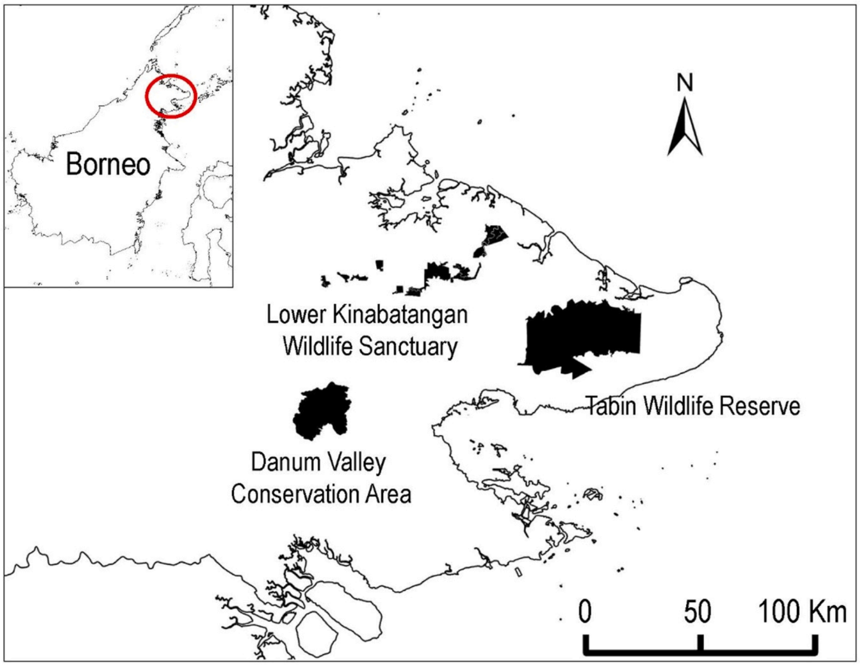


Fig. 1. Location of the three study sites in Sabah, Malaysia.

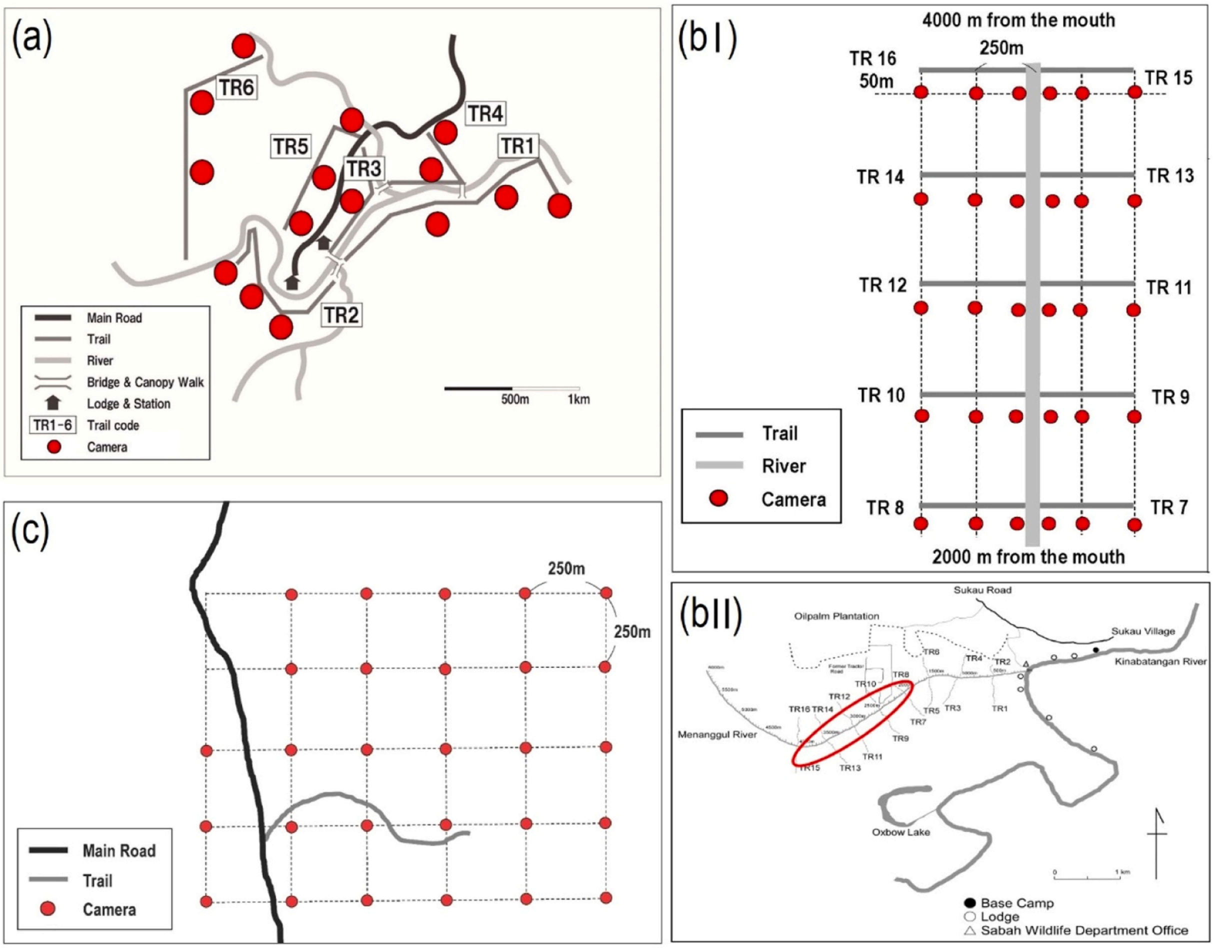


Fig. 2. Maps of camera locations at each study site. (a) camera stations at DVCA, (bI) trails and camera stations and (bII) trail locations at LKWS, (c) camera stations at TWR.

is likely comparable (Hearn et al., 2017). Therefore, we considered the effect of the presence of natural predators to be similar across sites. During the study period, June to September 2010, a masting season was observed at each study site (Kanamori et al., 2017, Matsuda et al., 2019).

The minimum and maximum daily temperatures and annual precipitation did not differ greatly among the study sites (annual temperature: 22–33 ℃, annual precipitation 2400–3100 mm; Mitchell, 1994; Matsuda et al., 2019; South East Asia Rainforest Research Partnership Unpublished data. https://www.searrp.org/).

2.2. Data collection

We set up 15, 30, and 28 infrared-triggered sensor cameras (Bushnell, Trophy CamTM) in DVCA (July 2010–August 2011 and May 2014–December 2016), LKWS (July 2010–December 2014), and TWR (May 2010–June 2012), respectively. The cumulative number of camera operation days in DVCA, LKWS, and TWR were 14,134, 18,265, and 4980, respectively, totaling 37,379 days. The camera operating days in DVCA, LKWS, and TWR were 942.2 ± 152.0 (mean ± SD, range = 682–1229), 608.8 ± 531.4 (range = 28–1315), and 177.9 ± 123.2 (range = 26–539), respectively.

We defined non-independent photo-capture events as consecutive photos of the same or different individuals of the same species taken within a 30-minute interval and removed these photos from our analysis (Yasuda, 2004; Ridout and Linkie, 2009; Monterroso et al., 2014). Because of the terrain and level of regulations (e.g. establishing new transects) to conduct this study differed by the study site, we employed different layouts of camera stations at each study site (along trails in DVCA and grid like patterns in LKWS and TWR, Fig. 2).

In DVCA, we placed 15 cameras along six forest trails, which were established and maintained by the tourist lodging facility. Because it was prohibited to establish new trails and to place cameras at sites where tourism activity would be disturbed in the study area, the trails that were longer than 1 km and relatively easily accessible were selected as camera locations to maintain consistency of trail characteristics. Cameras were placed on each trail at least 200 m intervals, alternating right and left to avoid bias of photo-capture frequency caused by terrain differences. Each station was at least 196 (average 1197) m away from each other on the different trails (Fig. 2a).

In the LKWS, we had planned to install 30 cameras, but a maximum of only 27 cameras were in operation during the study period, probably owing to malfunctions caused by high humidity and rain in the tropical rainforest. All cameras were placed on the trails in the riverine forest along the Menanggul River. In the LKWS, trails 200–500 m long and 1 m wide were established at 500 m intervals on both sides of the river. Of the 16 trails, we selected ten trails that were all 500 m long and placed three cameras at the points from the riverbank to the inland forest in each trail, that is, 10 m, 250 m and 500 m from the riverbank; cameras were set up 50 m away from the trails (Fig. 2bI).

In the TWR, we placed 28 cameras on camera stations created by overlaying a 750 × 500 m grid in May and August 2010. Cameras were placed at each grid point at 250 m intervals (Fig. 2c).

2.3. *Spatiotemporal activity analysis*

We conducted three analyses; multinomial logistic regression analysis, Wald chi-squared test, and generalized linear mixed models (GLMMs) to evaluate the effect of presence of young on active time of day, differences in the activity levels by time of day among the sites, and the effect of artificial environments and nocturnal visibility on spatial activity by time of day, respectively. To define time of day, we divided a day into three periods: nighttime (19:00–04:59 h local time (GMT + 8)); daytime (07:00–16:59 h); and twilight (05:00–06:59 h and 17:00–18:59 h). During the study period, twilight hours essentially corresponded to 1 hour between sunset and sunrise, at 05:54–06:25 and 17:50–18:25 in DVCA, 05:51–06:23 and 17:47–18:25 in LKWS, and 05:50–06:21 and 17:46–18:22 in TWR (data from https://www.timeanddate.com).

First, we needed to clarify whether the presence of young affects the active period (night, day, twilight) because maternal care behavior may affect the movements of the study species (Caldecott, 1991) and bearded pigs change activity patterns when infants and juveniles are present (Love et al., 2017). We applied multinomial logistic regression analysis to assess the effect of the presence of young on the photo-recorded periods (night, daytime, and twilight) of the study species at each study site, using the R package "mlogit" (Croissant, 2020) in R version 4.2.2 (R Development Core Team 2022). We set the presence of young as a fixed effect and the camera operating days as a weight. There were few photos of sambar deer with young; therefore, we did not conduct this analysis for this species. Based on the results of this analysis, we separately treated the ungulate species depending on the presence or absence of young in the following analyses.

Then we tested for site differences in activity level estimates during each active period (night, day, twilight). We fitted a circular kernel density distribution estimated by 1000 bootstrap resampling to the radian time data (Lashley et al., 2018) after converting the time data of each photo-capture event into radians. For species with fewer than 200 photos, we estimated errors by bootstrapping with sampling from the fitted probability density distribution. For the other cases, we sampled from the data (Rowcliffe, 2023). We used the Wald chi-squared test with Bonferroni post hoc correction on each pairwise comparison of the estimated circular kernel density distribution of both species using the function compareAct in the R package "activity". We selected this analysis because it allows for more accurate comparison of site differences by directly evaluating the activity level estimates derived from circular kernel probability distributions at specific times of day (e.g. nighttime) rather than using the number of photos recorded during each period.

We estimated the effects of artificial environments and nocturnal visibility on the spatiotemporal activity of the two species during each active period (daytime, twilight, and nighttime) using GLMMs in the R package "lme4" (Bates et al., 2023). We set the number of independent photo-capture events for each period as the response variable, the distance from oil palm plantations or gravel roads to each camera as a fixed variable, and year and month as random effects, with the number of camera operation days as an offset term. For nocturnal activity, we included the ratio of the illuminated portion of the moon as an additional fixed variable because poaching generally occurs at night in Sabah (Wong et al., 2004) and lunar illuminations could affect nocturnal movements in some ungulates including wild boar (*Sus scrofa*) and deer (Prugh and Golden 2014; Colino-Rabanal et al., 2018). The variables used for each period are shown in Table 1. We conducted Wald chi-square tests for the significance of fixed effects using 'car' package (Fox et al., 2023). We used ArcGIS Pro (ESRI, Redland, CA) to measure the shortest linear distance (m) from each camera to the oil palm plantations in LKWS and TWR as an indicator of anthropogenic disturbance. We used the same measurement method for the gravel road in DVCA. In LKWS and TWR, both oil palm plantations and gravel roads were present in the vicinity of the study areas (Fig. 2bII, 2c). Once we confirmed the multicollinearity between these two parameters by calculating the variance inflation factor (VIF) (VIF > 10), we selected oil palm plantations as the index of anthropogenic effect, given the larger number of humans present and their greater impact. We checked the

Table 1
Explanation of variables used in GLMM analyses to estimate the effects of anthropogenic disturbance on the spatiotemporal activity of bearded pigs and sambar deer during each period of the day.

variable	daytime, twilight	nighttime
response variable	number of independent photo-capture events	number of independent photo-capture events
fixed variable	distance (m) from oil palm plantations (LKWS and TWR) or gravel roads (DVCA) to each camera	distance (m) from oil palm plantations (LKWS and TWR) or gravel roads (DVCA) to each camera, ratio of the illuminated part of moon
random effect	year, month	year, month

ratio of the illuminated portion of the moon (https://www.arachne.jp/onlinecalendar/mangetsu/) and used this as an indicator of nighttime brightness.

3. Results

3.1. Sampling effort

We recorded 4825 and 713 independent photos of bearded pigs and sambar deer, respectively. Bearded pigs were present in 1747, 2090, and 988 and sambar deer were present in 411, 89, and 213 photos in DVCA, LKWS, and TWR, respectively (Fig. 3). The number of photos of bearded pigs with young was 193, 126, and 33 in DVCA, LKWS, and TWR, respectively (Fig. 3).

3.2. Effect of the presence of young on activity patterns in bearded pigs

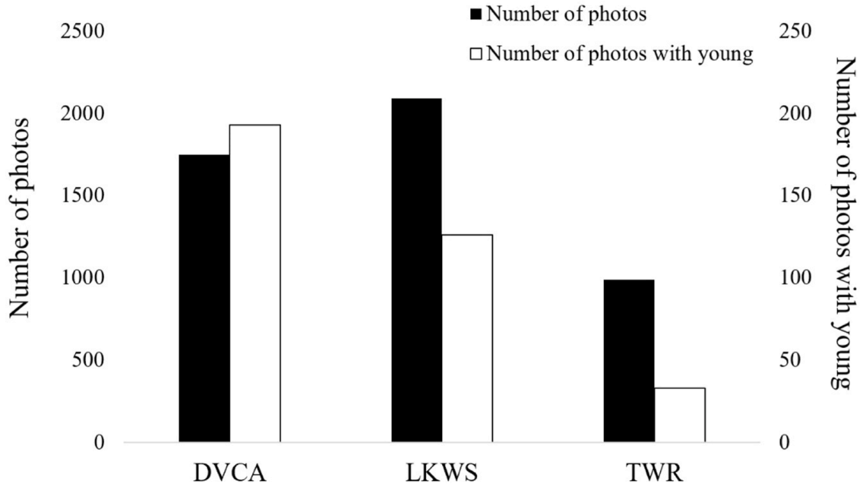
Table 2 shows the multinomial logistic regression analysis results In LKWS, bearded pigs with young were more active during the day than during the night ($z = 3.12$ $p < 0.01$) but there were no significant differences between the twilight and the night ($z = 0.82$, $p = 0.41$). In DVCA and TWR, bearded pigs with young were more active in both the daytime ($z = 0.26$, $p < 0.01$ and $z = 3.07$, $p < 0.01$, respectively) and twilight periods ($z = 2.37$ $p = 0.02$, $z = 2.13$, $p = 0.03$, respectively) compared with nighttime. These results indicated that the activities of bearded pigs at all sites were affected by the presence of young. Therefore, we subsequently conducted separate analyses of bearded pig activity depending on the presence or absence of young.

3.3. Differences in activity level estimates among the study sites

The among-site comparison of activity level estimates is shown in Figs. 4 and 5. Due to the small sample size, we sampled from the fitted probability density distribution of bearded pigs with young and sambar deer to estimate bootstrapping errors with sampling. For bearded pigs with young, there were no statistical differences in activity levels during any period across the sites (Fig. 4, Table SI1). However, for bearded pigs without young, significant differences in activity levels were found for all periods (Fig. 4, Table SI1). At night, the activity levels of individuals in DVCA were higher than those in TWR ($p < 0.01$). The activity levels of individuals in TWR were lower than those in both DVCA and LKWS during the daytime (both $p < 0.01$) and twilight ($p < 0.01$, $p = 0.01$, respectively). For sambar deer, individuals in TWR were more active in daytime activity levels than in LKWS ($p = 0.016$; Fig. 4, Table SI1). There were no significant differences for the other combinations.

3.4. Effects of anthropogenic disturbance and nocturnal visibility on diel activity patterns

Due to the small sample size of bearded pigs with young in TWR, we could not analyze them for all sites. During twilight and daytime periods, the GLMM results of the effects of anthropogenic disturbance during twilight and daytime periods indicated that both



Poaching	little to no	Y	Y
Poaching of bearded pigs	little to no	little	Y

Fig. 3. Number of photos used for the analyses and poaching status at each study site. Y in the table indicates "reported".

Table 2
Results of multinomial logistic regression analysis for the effect of the presence of young in bearded pigs on periods of activity. The nighttime period was the base outcome. Significant values are shown in bold.

site	variables	daytime			twilight		
		estimated coefficient	degree of freedom	p-value	estimated coefficient	degree of freedom	p-value
DVCA	Intercept	1.09	1743	< 0.01	0.18	1743	0.02
	presence of young	**2.11**		< 0.01	**1.06**		0.02
LKWS	Intercept	1.42	2086	< 0.01	0.46	2086	< 0.01
	presence of young	**1.21**		< 0.01	0.37		0.41
TWR	Intercept	-0.06	984	0.44	-0.04	984	0.63
	presence of young	**1.99**		< 0.01	**1.44**		0.03

species responded similarly to oil palm plantations as explained in the subsequent sentences. In LKWS and TWR, when bearded pigs without young were closer to plantations, they were significantly more active during twilight ($p < 0.01$, $p = 0.017$, respectively; Fig. 5, Table SI2). For all other cases, there were no significant differences (Fig. 5, Table SI2). In contrast, in DVCA, when individuals without young were farther from the gravel road, they were significantly more active during the daytime ($p < 0.01$; Fig. 5, Table SI2). Similar to bearded pigs, sambar deer in LKWS and TWR were significantly more active during twilight the closer they were to plantations ($p < 0.01$, $p = 0.049$, respectively; Fig. 5, Table SI2). In TWR, they were more active during the daytime, as they were close to the plantation ($p < 0.01$; Fig. 5, Table SI2). There were no tendencies between the photo numbers and the distance from the road in the individuals in DVCA during daytime and twilight ($p = 0.65$, 0.22, respectively; Fig. 5, Table SI3).

The GLMM results showed that during the nighttime, there were differences in the effects of the brightness of the moon and the distance from oil palm plantations or a gravel road on nocturnal activity, depending on species and study site (Fig. 6, Table SI3). In LKWS, bearded pigs tended to be more active the larger the area of the moon ($p = 0.05$; Fig. 6, Table SI3). In LKWS and TWR, the nocturnal activity of bearded pigs also increased the closer they were to oil palm plantations ($p < 0.01$, $p = 0.01$, respectively; Fig. 6, Table SI3). Unlike bearded pigs in LKWS, sambar deer in TWR were more active on nights when the moon was less illuminated ($p < 0.01$; Fig. 6, Table SI3). Sambar deer in TWR tended to be more active at night when they were close to oil palm plantations, although the significant differences were marginal ($p = 0.06$; Fig. 6, Table SI3). On the other hand, in DVCA, the degree of illumination of the moon and the distance from the gravel road had no effect on the levels of activity of either bearded pigs ($p = 0.52$, 0.89, respectively; Fig. 6, Table SI3) or sambar deer ($p = 0.70$, 0.82, respectively; Fig. 6, Table SI3).

4. Discussion

Our results indicate that activities of both bearded pigs and sambar deer were negatively associated with human activities. The activity level differences of these species among the study sites suggest that they change their activities in response to the environment, including anthropogenic disturbances. Responses to human-modified environments also varied across the sites and species, suggesting that such differences might be related to the level of anthropogenic disturbance. The small photo number of bearded pigs with young in TWR and sambar deer in LKWS suggests that, in these sites, these species may be less abundant or have moved away from the study areas, which were relatively close to anthropogenically disturbed zones such as plantations. However, note that the relatively short distance between the cameras (196–250 m) may lead to spatial autocorrelation which potentially compromise statistically independence of data (Kays et al., 2010).

4.1. *Bearded pigs*

4.1.1. *Temporal activity levels*

The activity levels of bearded pigs during daytime and twilight were the lowest among the three sites when they travel with young (Fig. 4). Their temporal activity patterns in TWR statistically differed from the other two sites; it was predominantly crepuscular in TWR where poaching for bearded pigs is reported while in DVCA and LKWS where poaching of this species is less frequent it was consistently diurnal, irrespective of the presence or absence of young (Fig. SI1, Table SI4). As the active period of individuals in TWR overlaps with that of Sunda clouded leopards (Ross et al., 2013), factors other than predation pressure may be shaping their activity patterns. Crepuscular activity patterns are, for example, often explained as helping to avoid high temperatures (Davison et al., 2019). Indeed, irrespective of the presence of young, individuals in TWR reduce their activity during the hottest part of the day (12:00–16:00, Table SI5). However, considering that individuals in the logged forest at other sites, i.e., LKWS, exhibit diurnal activity patterns, the effect of air temperature on the distinct crepuscular activity pattern of individuals in TWR is likely to be low. The vegetation structure and composition generally affect resource use such as foods and nests and provide hiding places for wildlife including ungulates (DeWalt et al., 2003; García-Marmolejo et al., 2015). Given that vegetation of TWR and LKWS is relatively similar, i.e., of the top 10 families discovered in the secondary forests of LKWS and TWR areas in each vegetation survey plot (covering 70.9 % and 80.5 % of the overall tree species in each location, respectively), half of them overlap in five families, which cover 45.6 % and 52.5 % of the total tree species, respectively (calculated from Mitchell, 1994 and Matsuda et al., 2019), the effect of vegetation differences on their behavior could also be low.

One plausible explanation for such a difference in TWR could be anthropogenic disturbance. Given that the regular operating hours

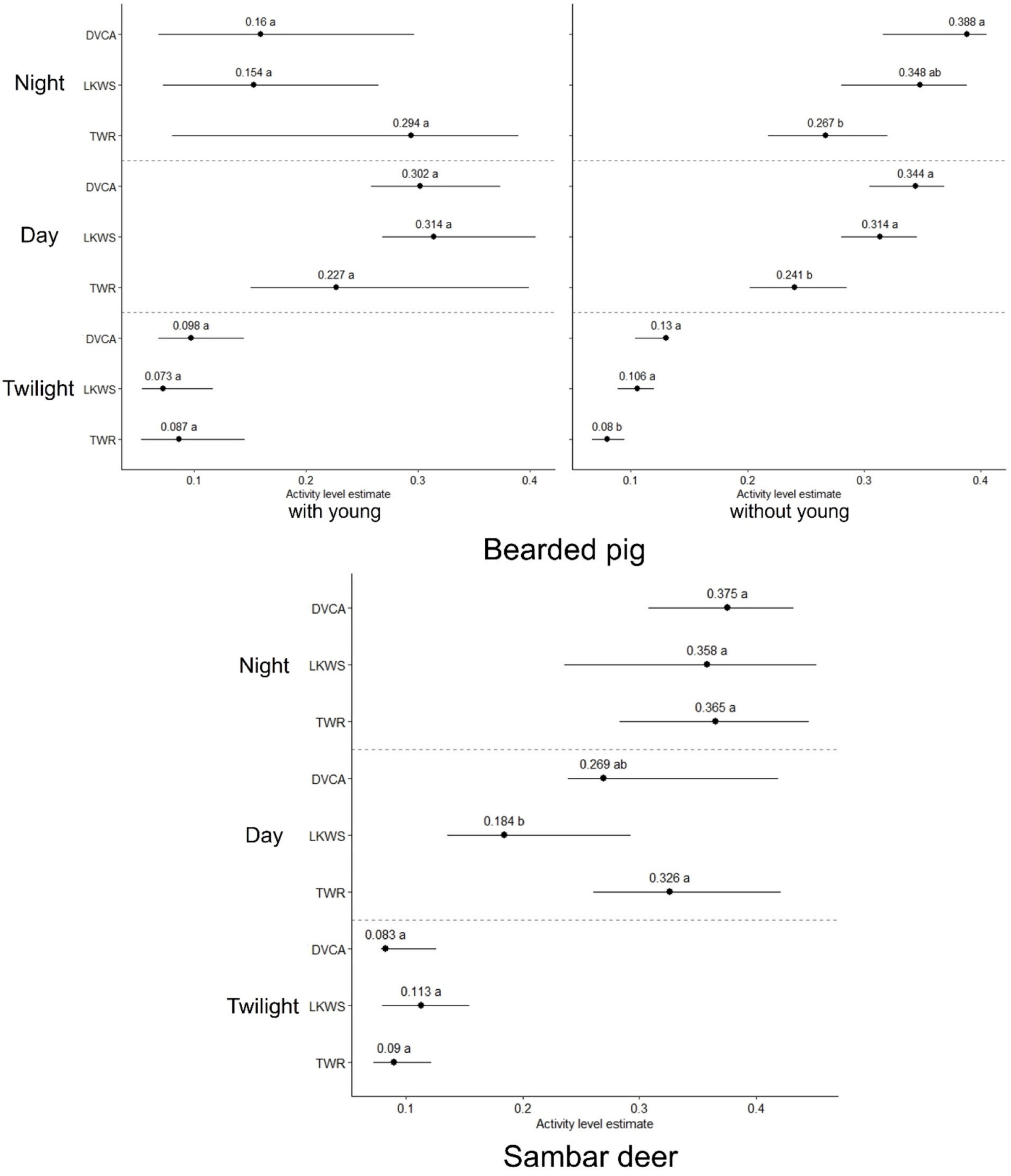


Fig. 4. Plots of activity level estimates and 95 % confidence limits of the Wald-test pairwise comparisons of activity levels of bearded pigs and sambar deer during each period among the study sites. Different alphabets indicate significant differences between the estimates.

of oil palm plantations in Sabah are from 06:00–18:00 (Davison et al., 2019), the highest probability of encountering humans is during the daytime. Thus, the activity pattern of bearded pigs, where oil palm plantations form part of their ranging area, has been reported to shift to nocturnal activity (Luskin et al., 2014; Davison et al., 2019; Love et al., 2017). This is consistent with becoming nocturnal as a general response of wildlife to avoid encounters with humans (Gaynor et al., 2018). By contrast, poaching typically occurs at night in Sabah (Wong et al., 2004). For individuals in TWR, where poaching of this species likely occurs most frequently among the study sites (Hearn et al., 2017), the twilight period may be more suitable for their activities because they are less likely to encounter plantation

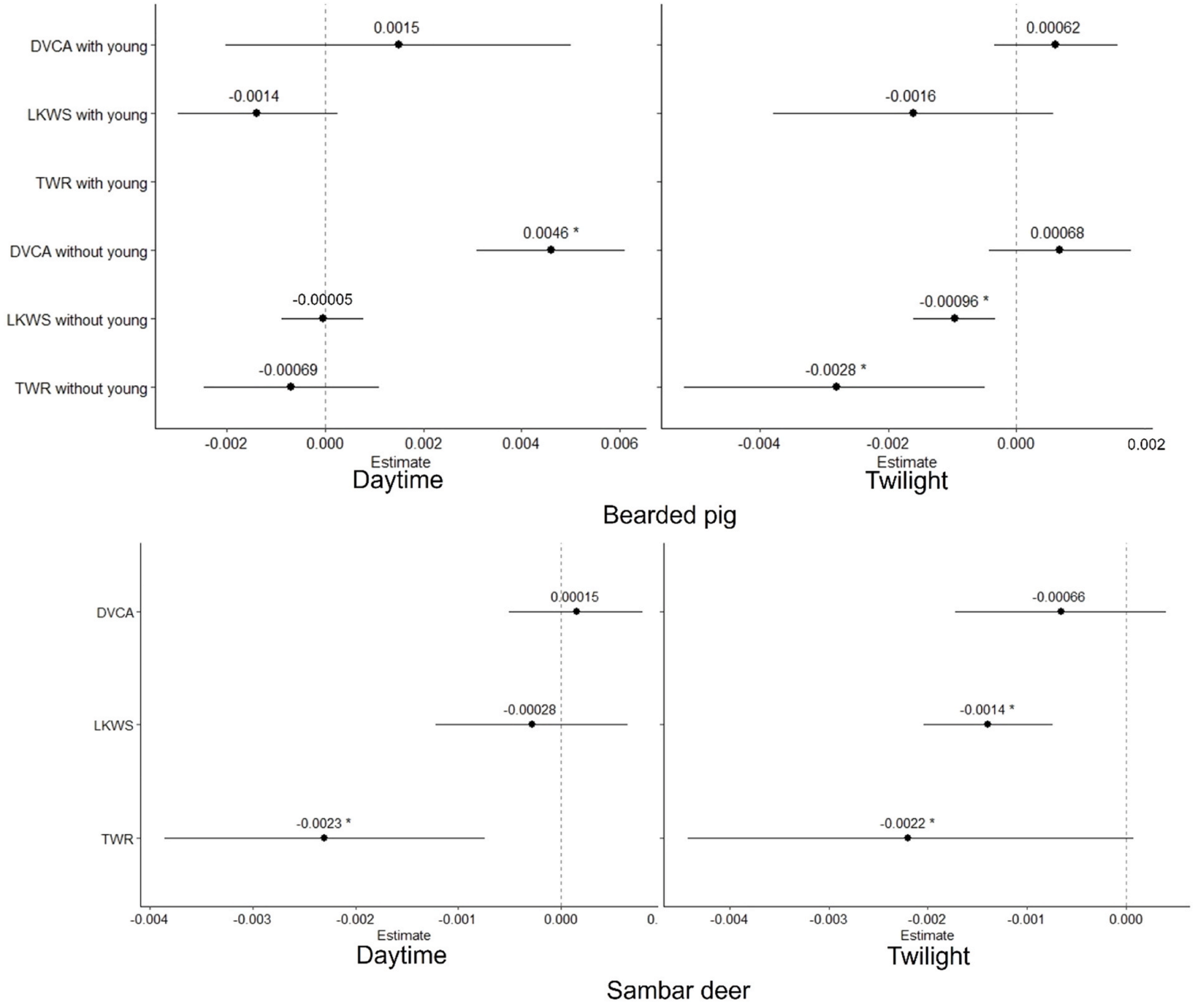


Fig. 5. Plots of the coefficients (distance from the gravel road in DVCA or oil palm plantations in LKWS and TWR) and 95 % confidence intervals of the GLMMs for the effects of anthropogenic disturbance on activities of bearded pigs and sambar deer during twilight and daytime periods. Values with asterisks indicate statistical significance.

workers or be hunted than during the day- or nighttime.

4.1.2. *Spatiotemporal activity pattern and anthropogenic disturbance*

Our analysis also revealed a tendency for human avoidance in bearded pigs. In particular, there are oil palm plantations in the vicinity of both LKWS and TWR, and the response of bearded pigs to the oil palm plantations was similar at each site. As the detections were greater closer to the plantations, individuals without young became more active during the twilight periods. This was presumably to forage for oil palm fruits (Luskin et al., 2014; Kurz et al., 2021; Love et al., 2017) when there were fewer people around. In short, they avoid encounters with humans but take advantage of human-modified environments, especially those they can use for feeding as reported for some ungulates benefitted from artificial land covers such as agroforestry for Palaeotropical cervids (Costa et al., 2021) and urban green areas for wild boar (Castillo-Contreras et al., 2018).

In this area, where there are no oil palm plantations within at least a 5 km perimeter, the population without young tends to avoid engaging in activity near the gravel road. In DVCA, where interactions with humans are generally less likely, bearded pigs may be more sensitive to the presence of human activity and more vigilant in response to anthropogenic stimuli. A study used camera traps indicates that abundance of bearded pigs declines with increase of distance from artificial environments such as roads and villages (Brodie and Giordano, 2013). It remains unclear if there are differences in behavioral responses to the artificial land covers depending on the frequency of human encounters. Empirical studies with tracking their actual movement are needed to validate these speculations.

4.1.3. *Effects of lunar illumination and anthropogenic disturbance on nocturnal activity*

In LKWS, nocturnal activity patterns of bearded pigs were notably affected by the degree of lunar illumination; they were more

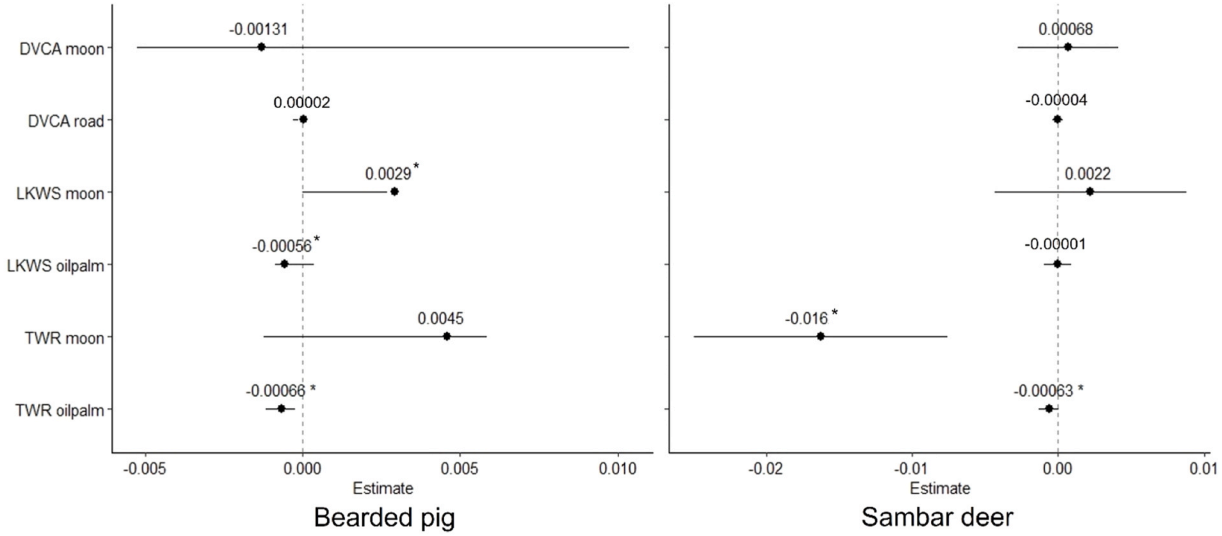


Fig. 6. Plots of the coefficients and 95 % confidence intervals of the GLMMs for the effects of lunar illumination and anthropogenic disturbance on nocturnal activity of bearded pigs and sambar deer. Values with asterisks indicate statistical significance.

active when the moonlight was brighter, while this tendency was not observed in DVCA and TWR. Considering the poor nocturnal vision of closely related wild boar (Ollivier et al., 2004), a plausible explanation for the spatial activity patterns observed in LKWS would be that they rely on moonlight for foraging and predator detection when Sunda clouded leopards tend to be active (Ampeng et al., 2018). It should be noted, however, that bearded pigs in LKWS are typically diurnal (Fig. SI1, Table SI4). Therefore, in this context, these are complementary foraging behaviors that benefit from a specific nocturnal environment, which may increase predator and poacher detectability under the moonlight and enhance foraging efficiency by sight (Prugh and Golden 2014), as well as provide the advantage of avoiding contact with workers in the vicinity of the plantation.

On the other hand, individuals without young in TWR that approached the plantation at night did not exhibit a similar tendency to that seen in LKWS, suggesting that lunar luminosity is not an essential factor for their nocturnal activity in TWR as reported in other wild boar species by Gordigiani et al. (2021). The poaching pressure on bearded pigs in TWR is greater compared with LKWS (Hearn et al., 2017; Kurz et al., 2021), and hunters using guns in Sabah tend to hunt during brightly moonlit nights (Saikim FH unpublished data). Hence, it is possible that the effects of lunar illumination in TWR were not as influential as in LKWS. Nighttime foraging in plantations may thus provide some benefits for bearded pigs in TWR, despite the risks associated with nocturnal activity. It should be noted, however, that there are limitations to analyzing the impact of lunar illumination on activity patterns, because the actual level of brightness on the ground must be assessed, taking into account the cloud cover (Krieg, 2021). With respect to the 36–41 % lower level of daytime activity among individuals without young in TWR compared with DVCA and LKWS (Table SI5), daytime activity, especially foraging behaviors, may be constrained by several factors such as human activity and predation pressure. Although the individuals in TWR showed crepuscular activity pattern, their twilight activity level was lower than those of DVCA and LKWS (Fig. 4, Table SI4). The nighttime activity level of individuals in TWR was also lower than that of DVCA where they exhibited avoidance of nocturnal activity (Fig. 4, SI4). These results indicate shortage of overall active times for individuals in TWR. As discussed earlier, a plausible factor for the reduction in time spent being active during the day in bearded pigs in TWR, which reduces their interactions with plantation workers, may contribute to their limited hours spent foraging during the daytime, considering that Suidae species typically spend most of their time foraging during daily activity (Meijaard et al., 2011). Hence, they may approach plantations where they can more efficiently acquire highly nutrient-rich oil palm fruits, despite increased poaching and predation pressure during the night. Furthermore, the percentage of time bearded pigs without young were active in TWR was never less than 2 % (Table SI5), supporting the possibility that they maintain a certain amount of activity throughout the day to find food that meets their nutritional requirements.

4.2. Sambar deer

4.2.1. Temporal activity levels

Temporal activity levels did not differ among sites, except for daytime activity levels between LKWS and TWR; sambar deer in TWR were higher than that in LKWS (Fig. 4). Since they are heavily poached in LKWS (Matsuda et al., 2015), they might avoid encountering humans when they are most active. However, temporal activity patterns indicate that they are crepuscular across sites (Figure SI1, Table SI4). Individuals in TWR were less active at night, while those in DVCA were less active during the day (Table SI4). Given the considerable overlap of the activity patterns of clouded leopards with sambar deer characterized by lower daytime activity levels (Ross et al., 2013), predation by clouded leopards may shape the activity patterns of sambar deer in TWR. One of the other explanations for their temporal activity may be human disturbance. In TWR, where poaching for both bearded pigs and sambar deer has been reported

(Hearn et al., 2017), sambar deer may reduce nighttime activities to avoid encounters with poachers because this species typically avoids human disturbed areas (O'Brien et al., 2003, Kushwaha et al., 2004, Srivastava et al., 2020). However, sambar deer in Sarawak, Sabah's neighboring state, are equally active day and night, irrespective of predation or poaching pressure (Bersacola et al., 2019). In contrast, smaller, closely related taxa, such as barking deer (*Muntiacus* spp.) and mouse deer (*Tragulus* spp.), flexibly adjust their activity patterns depending on the degree of logging and hunting in their environment (Bersacola et al., 2019). The larger sambar deer may be less sensitive to environmental changes but may respond to relatively high poaching pressure in protected areas as found in TWR (Hearn et al., 2017). These differences based on the previous studies and our results indicate that sambar deer can flexibly change their temporal activity patterns and activity levels at small regional scale. Future work should quantify and compare these pressures across different sites and examine human influence on sambar deer activity patterns to evaluate whether this species shows a response in activity patterns to anthropogenic disturbance.

4.2.2. Spatiotemporal activity pattern and anthropogenic disturbance

The effect of oil palm plantations and the gravel road on sambar deer temporal activity patterns showed differences between study sites. During the daytime, deer in TWR were frequently photographed near the plantation (Fig. 5). Although this species is shy and elusive (Leslie, 2011), individuals in TWR approached plantations during the daytime and twilight, when plantation workers were active. The higher diurnal activity levels of the individuals in TWR compared to those in LKWS (Fig. 4) corroborates this result. If the interactions are non-lethal, such as continuous noise and human disturbance, sambar deer may adjust to these stimuli (e.g., Stankowich, 2008) and subsequently invest more in feeding than in avoiding humans.

4.2.3. Effects of lunar illumination and anthropogenic disturbance on nocturnal activity

The nocturnal behavior of sambar deer in TWR was affected by the oil palm plantation. In TWR, they showed a similar tendency to bearded pigs, being active near the plantation at night. Herbicides are commonly used in oil palm plantations (Dilipkumar et al., 2020), reducing food resources for typical herbivores such as sambar deer (Leslie, 2011). Sambar deer often feed on understory foliage in logged forests and at forest edges (Davies et al., 2001). In the TWR study area, both a gravel road and the oil palm plantation are located on the forest edge (Fig. 2c). In Borneo, the roadside understory includes grass, herbs, and shrubs (Padmanaba and Sheil, 2014), which serve as food resources for sambar deer. These deer are often observed near the road in TWR at night (Nakabayashi et al., 2014), suggesting that sambar deer in TWR approach the road and plantation to feed. This may be their foraging strategy to avoid times when humans are active in the plantation, although there may be an increased risk of poaching near the road and plantation at night because poachers in TWR typically use vehicles along the gravel road or along the border of the plantation (Hearn et al., 2017). Conversely, in LKWS, sambar deer may feed on the riparian understory in riverine environments, reducing the need to approach the plantation. The balance between the conflicting factors of poaching risk and the need to forage may cause sambar deer to adjust their activity patterns in human-modified environments at night.

Our results showed that sambar deer were typically active during twilight periods (Figure SI1, Table SI4) but also active at night. Additionally, in TWR they were often photographed when lunar illumination was low. Considering their good nocturnal vision (VerCauteren and Pipas, 2003), they can exploit darkness to avoid predation by Sunda clouded leopards and poaching, which tend to be active during brightly moonlit nights (Ampeng et al., 2018; Saikim FH unpublished data). A night without moonlight may be unsuitable for both predation and poaching, but suitable for sambar deer to actively forage.

5. Conclusions

The spatiotemporal activity patterns of bearded pigs and sambar deer indicated elements of human avoidance; bearded pigs approached plantations during times of low human presence, presumably to forage, especially in study sites where poaching occurs. In areas where poaching was rare, they exhibited spatiotemporal activity patterns that avoided human contact, staying away from the road. Notably, our results suggest reduced active times for both species in TWR, potentially leading to decreased foraging times and fitness and increased energy expenditure (Kiffner et al., 2014). If human activity is non-lethal and regulated, ungulates in Peninsular Malaysia do not change their diel activity patterns in response to human (Ota et al., 2019). Thus, human activities may negatively affect the activity patterns of these two ungulate species. The impact of human activity, especially on diel activity in both ungulate species, may increase intra- and interspecific resource competition (Scoyoc et al., 2023), and reduce the predation success of their natural predators, such as Sunda clouded leopards, which may consequently affect the ecological balance by altering predator–prey densities (Scoyoc et al., 2023).

These ungulate species, however, also exhibit some behavioral plasticity to anthropogenic disturbance, which could potentially positively affect their feeding. Artificial environments such as oil palm plantations and roads provide food, allowing the two ungulate species to efficiently compensate for reduced feeding times by utilizing such food resources. The different movement patterns in sambar deer between LKWS and TWR where they approached the plantation when it was dark at night in TWR but not in LKWS, may also reflect their behavioral plasticity, despite exposure to poaching pressure at both sites. A previous study suggested they can persist in disturbed habitats (Granados et al., 2016). Local people in Sabah observed that bearded pigs become highly sensitive to the presence of humans in hunting areas (Kurz et al., 2021), suggesting clear avoidance of humans where hunting or poaching risk is high. Our results show that they can adapt to human-modified environments, with some individuals of both species in DVCA habituated and often observed near tourist accommodations. According to the meta-analysis of several ungulate species, when regulated seasonal hunting is permitted, some ungulates that regularly experience non-lethal human activities do not exhibit a fear response to humans (Stankowich, 2008). In our study sites, poaching is irregular and ecotourism operates year-round. These factors might reduce the fear response to humans, enabling these ungulate species to use resources in plantations and the surrounding areas. At the same time, however, the use of artificial environments, such as plantations, may alter their resource use and cause physiological changes related to metabolism and hormones necessary for survival, growth, and reproduction (Seebacher, 2022, Mirante et al., 2025). We need to assess the impact of utilizing artificial environments on their survivorship, distribution, population size, and fitness.

This study focused on only three sites with different poaching pressures, but there may be other differences such as vegetation among the three sites, which could affect activity patterns. Although vegetation does not change throughout the day, human activities such as poaching may vary greatly by time of day. More efforts are needed to clarify whether human activity has a stronger impact on wildlife activity patterns than vegetation by increasing the sample size. This study was conducted within protected areas where, although sporadic poaching occurs, the two ungulate species were relatively common (i.e. the largest total photo number among carnivorans was 410 for Malay civets recorded at the same period and in the same study sites; Nakabayashi et al., 2021). The negative impact of poaching is small but not negligible. Hunting/poaching pressure outside protected areas especially within oil palm plantations for bearded pigs is likely much higher than in protected areas in Sabah (Kurz et al., 2021, 2023). In such areas, local wildlife populations would suffer greatly without appropriate hunting regulations especially from commercial hunting (Corlett, 2007, Harrison et al., 2016). One of the limitations of this study is that we did not directly measure the level of human disturbance, such as human activity level and poaching pressure, and therefore measurements of these factors would improve the accuracy of the study.

Both bearded pigs and sambar deer are ecologically important species, serving roles as prey (Ross et al., 2013), grazers, and browsers (Haleem and Ilyas, 2022), and contributors to seed dispersal (Sridhara et al., 2016) and seed predation (Caldecott, 1991; Curran and Leighton, 2000; Sridhara et al., 2016) in their ecosystems. Additionally, they hold socio-cultural significance, having interacted with indigenous communities for over 35,000 years as sources of animal protein (Medway 1964; Bennett et al., 2000) and cultural customs (Kurz et al., 2021) in Borneo. Our methods and data on temporal activity patterns of ungulates can be used to assess the degree of hunting or poaching and to examine the adequacy of conservation management in a given area along with the evaluation of hunting/poaching pressure. We recommend urgent evaluations of current wildlife management plans and long-term monitoring of wildlife population dynamics, including studying behavioral and physiological responses that directly measure animals' stress, especially in Southeast Asia.

Ethics statement

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03580.

Data availability

Data will be made available on request.

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