

The first recorded activity pattern for the Sunda stink-badger *Mydaus javanensis* (Mammalia: Carnivora: Mephitidae) using camera traps

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Abstract. The Sunda stink-badger *Mydaus javanensis* is a small carnivore inhabiting the Southeast Asian islands of Borneo, Java, Sumatra, and the Natuna Archipelago. Documented sightings are relatively common, yet the species' behavioural ecology remains poorly understood. Whilst the species is reported to be broadly nocturnal, its detailed activity pattern has never been quantified. This study analysed photographic events from a large scale, long-term camera trapping study to assess times of activity for the Sunda stink-badger. The study took place within the lowland riparian forest corridor of the Lower Kinabatangan Wildlife Sanctuary (LKWS) in the Northeast Bornean state of Sabah. Through 2010–2015, 24,506 potential trap nights collected 2,268 Sunda stink-badger images across 470 unique events. Sunda stink-badger activity pattern was modelled using kernel density estimation, and indicated a highly nocturnal activity pattern with no detected activity during the diurnal hours, consistent with previous records. All photographs were taken between 1839 hours and 0627 hours, and modelling indicated two clear peaks in nocturnal activity, the first at 2100 hours and the second at 0500 hours. Overlap in activity patterns was found to be high ($\geq 80\%$) between wet and dry seasons, and also between moon phases, indicating a lack of seasonal or lunar effects on Sunda stink-badger activity. An encounter rate of 1.92 unique Sunda stink-badger events per 100 potential trap nights was recorded for the LKWS. This encounter rate was lower than those found in other regional studies with lower levels of anthropogenic disturbance, suggesting extensive anthropogenic disturbance may pose a potential negative impact to the species. Whilst activity patterns derived from camera trapping are restricted to movement through the environment, these results have established a baseline for Sunda stink-badger activity patterns within a fragmented habitat subjected to high levels of anthropogenic disturbance, and have improved the basic ecological understanding of the species.

Key words. camera trapping, Borneo, carnivore, animal behaviour, overlap

INTRODUCTION

The Bornean carnivore guild is a highly biodiverse and highly threatened guild of 25 species (Shepherd et al., 2011); despite increasing research efforts in the region, the behavioural ecology of these species remains poorly understood. Many of the Bornean carnivores reside in remote habitats or at low densities; however, it is their tendencies to display secretive behaviours and nocturnal activity patterns that present the most significant challenges to behavioural studies (Sunarto et al., 2013). Until recently, studies that did occur required long term, large scale, highly expensive or logistically demanding methodologies. To address these issues, camera

traps are now being widely utilised to study the guild and have been effective tools to counter some of the difficulties associated with researching tropical carnivores (Sunarto et al., 2013). Within the Bornean carnivore guild is the Sunda stink-badger *Mydaus javanensis* (Leschenault, in Desmarest) (Fig. A1, A3); a small, robust-bodied carnivore found across the Southeast Asian islands of Java, Sumatra, Borneo, and the Natuna Archipelago. The species is amongst the least-studied within the Bornean carnivore guild, yet is well known throughout the region for its “abominable odour” (Brehm, 1896). Whilst the species is not considered under immediate threat, it is this lack of studies which makes the Sunda stink-badger suitable for single-species targeted research.

The Sunda stink-badger is a nocturnal ground-dwelling skunk (Mephitidae) weighing 1.4–3.6 kg, with a head-body length of 375–510 mm (Hwang & Lariviere, 2003). As is the case with nearly all other carnivores in the region, there is a paucity of ecological data for the Sunda stink-badger. Comments on its habitat use have varied significantly, with some sources suggesting it is mainly found at high altitudes (Hwang & Lariviere, 2003); however, in some of its range the species has shown extensive use of lowland plains (e.g., Sabah; Payne et al., 1985; Samejima et al., 2016). Little is known of the threats facing the Sunda stink-badger, and it is currently listed as Least Concern by the IUCN Red List

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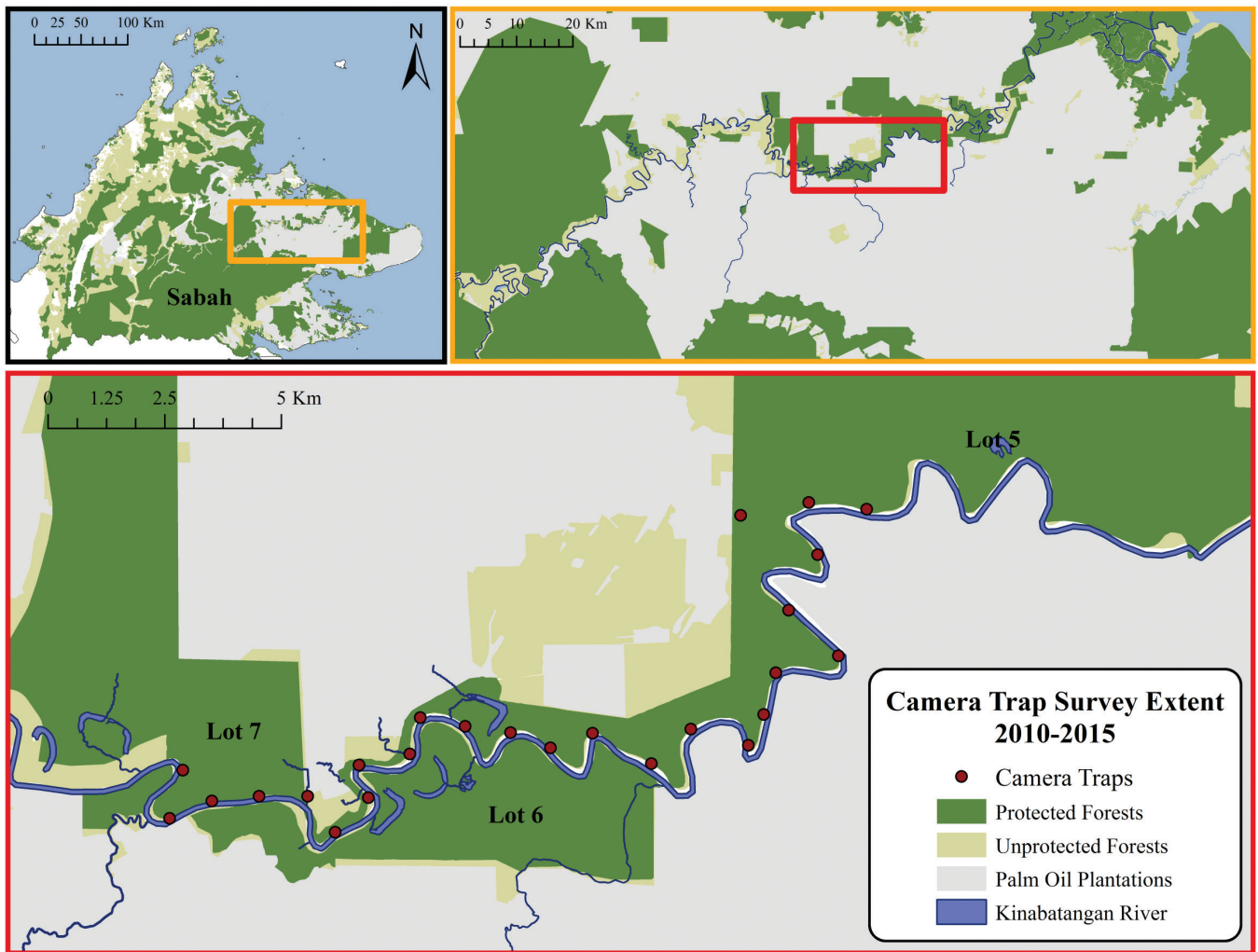


Fig. 1. Location of the camera trap stations in Lots 5 and 7 of the LKWS along the northern bank of the Kinabatangan River, Sabah, Borneo.

of Threatened Species (Wilting et al., 2015). This listing is based on the apparent ability of Sunda stink-badgers to withstand habitat degradation and fragmentation, paired with the lack of records in large-scale bushmeat hunting reports, in the context of its large (relative to Red List thresholds) geographical range and inferred large population (Samejima et al., 2016). There are indications of a historical reduction in the distribution of the Sunda stink-badger in parts of Borneo; however, these suspected declines are poorly understood and there is only speculation as to the causes (Samejima et al., 2016).

An aspect largely unstudied in the Sunda stink-badger is its circadian activity pattern. This is the 24-hour cyclical pattern describing when a species is active (i.e. not resting), something that is often variable between species, seasons of the year, and habitats. Historically, the frequency or proportion of species' detection records within sections of the diel have been widely used to report activity patterns (e.g., Cheyne et al., 2010); however, this outdated approach has been replaced by more accurate statistical modelling methodologies such as kernel density estimators (Ridout & Linkie, 2009; Linkie & Ridout, 2011). Currently, broadly nocturnal activity is universally reported for the Sunda stink-badger (Samejima et al., 2016); however, no more precise

pattern has been documented. Understanding the daily cyclical patterns of species activity is intrinsically valuable for furthering our understanding of a species and its niche, but it can also be utilised as an indicator of species' responses to ecological change. Analysis of long-term camera trapping data from the Lower Kinabatangan Wildlife Sanctuary was undertaken to develop the first detailed circadian activity pattern for the Sunda stink-badger. Activity here refers to movement along and around wildlife trails, as detectable by the study design. Any behaviours that may not occur on trails would thus not be detected. These baseline data will contribute to a greater understanding of this poorly known species in the lowland plains of Malaysian Borneo.

MATERIAL AND METHODS

Study area. The Lower Kinabatangan Wildlife Sanctuary (LKWS, 279.6 km², elevation 10–200 m) is situated in the Lower Kinabatangan floodplain of Eastern Sabah, Malaysian Borneo (5°10'–5°50'N, 117°40'–118°30'E). Running through the sanctuary is the 560 km long Kinabatangan River, which has an extensive floodplain with limestone ridge formations. The sanctuary consists of 10 protected lots with varying degrees of disturbance history and isolation from extensive native forest. Lots are comprised of a mixture of

semi-inundated, humid forest systems, along with regions of permanent swamp, grasslands, and eventually mangroves at the coast. The area is recovering from selective logging that occurred repeatedly over the past century (Brookfield & Byron, 1990) and is surrounded by large areas of agricultural oil palm (*Elaeis guineensis*) plantations. Temperature fluctuations are low with a mean monthly temperature range of 21°–34°C, and annual rainfall averages 3,000 mm (Ancrenaz et al., 2004).

Camera trapping. Biodiversity monitoring of the wildlife sanctuary was undertaken using camera traps from 12 November 2010 until 9 May 2015, and camera trap placements were designed to optimise the probability of recording Sunda clouded leopards *Neofelis diardi*. Cameras were active throughout the study period with the exception of a 7-month break in camera trapping between March and November of 2011. A total of 25 camera stations were utilised during the study effort; however, active stations varied in number. Each station consisted of two Reconyx HyperFire Professional Infrared (IR) passive camera traps (Model HC500 or PC800, Reconyx, Holmen, USA) placed in armour casing to protect from damage and theft. Cameras were set ~0.5 m above ground level on trees facing each other but were placed slightly off-set to avoid camera flash obstructing the opposing unit. Cameras were active throughout the diel, and when movement across the IR detection beam of an object with a different surface temperature from background objects occurred, a series of three photos at 1-second intervals were taken. At low light conditions, an IR flash illuminated the subject, as this allows for successful imaging of an animal subject with lower disturbance than with white light (Ancrenaz et al., 2012). Stations were selected on existing riverine wildlife trails and were cleared of ground foliage to improve picture quality and reduce false camera triggers. Stations were not baited during the study effort. Camera traps were situated within a strip of LKWS forest along the northern bank of the Kinabatangan River, which acts as a wildlife corridor between two larger forest blocks. This corridor is part of Lot 5 of the LKWS and is flanked by the Kinabatangan River and a large oil palm plantation (Fig. 1). Camera trap stations were spaced at least 1 km apart in order to minimise spatial autocorrelation.

Data entry and analysis. Prior to analysis, metadata were extracted from the images, including time, date, moon phase, image number, and a range of image quality specifics. Metadata extraction was completed using ExifTool 9.6.8.0. Images were individually examined and the species identified and logged. Each burst of three images was considered a single photo-capture. In order to reduce pseudoreplication, photo-captures were classed as unique and separate photographic events when an interval of > 30 minutes between photo-captures of the same species were recorded, per Yasuda & Tsuyuki (2012). Sunda stink-badger encounter rate was defined as the number of unique Sunda stink-badger photographic events recorded per 100 potential trap nights. Events were compiled and the timestamps of the first photo in each unique event were used to model the activity pattern. Group size was not taken into consideration for these analyses,

such that photo-captures containing multiple individuals were considered a single event. Day-night cycles remain nearly constant throughout the year in the study area, with sunrise and sunset occurring at approximately 0600 hours and 1800 hours local time (GMT +8), respectively. In this study, nocturnal activity was defined as photographic events between 1900–0459 hours, diurnal as 0700–1659 hours, and crepuscular as the periods of 0500–0659 hours and 1700–1859 hours, following the design set by other researchers within the region (Ross et al., 2013).

Sunda stink-badger activity pattern was modelled using kernel density estimators following the methodology of Ridout & Linkie (2009) and the package ‘overlap’ (Meredith & Ridout, 2014); with a bandwidth adjust value of 2 as per recommendations from Rowcliffe et al. (2014). To evaluate the effects of season and lunar phase on badger behaviour, activity patterns were generated for subsets of the data and an overlap analysis conducted between the two activity patterns. Analysis of overlap in activity patterns was completed utilising the Ridout & Linkie (2009) methodology and the package ‘overlap’ (Meredith & Ridout, 2014), with Dhat 4 estimator of overlap, 10,000 bootstrap replicates, and the basic0 output for bootstrap confidence intervals. The package ‘activity’ (Rowcliffe, 2015) was then used with 10,000 bootstrap replicates to statistically test the probability that the two sets of observations came from the same distribution. Analysis of overlap in activity patterns was completed between three pairings; the dry season (March–October) compared to the wet season (November–February), full moon nights compared to new moon nights (including two nights before and after the full and new moon nights), and ‘bright’ nights (full moon, waxing gibbous, and waning gibbous) compared to ‘dim’ nights (new moon, new crescent, and old crescent). Statistical analyses were conducted using the statistical software R (version 3.2.1, R Development Core Team, 2015).

RESULTS

Camera trapping overview. The camera trapping effort ran for 48 non-consecutive months and resulted in 24,506 total potential trap nights (sum of active calendar nights × number of active camera traps). Potential trap nights have been used as a metric of data collection effort as the precise timing of any camera malfunctions or battery death were not possible to ascertain. A total of 2,268 raw *M. javanensis* images (756 photo-captures) across 470 unique events were collected from 18 of the 25 camera stations. Single Sunda stink-badgers were recorded in the majority of events (98.7%), with groupings of two individuals imaged in six unique events and never larger groupings (Fig. A1), supporting the notion that the Sunda stink-badger is a solitary species (Samejima et al., 2016). In all six events in which a duo was imaged, individuals were travelling the same direction and route through the imaged area, were of similar size, and were assumed to be adults. All co-occurrence events took place between the months of March–July; however, there was no distinctive pattern in timing of these events in the diel. Whilst this could be an early indication of seasonal

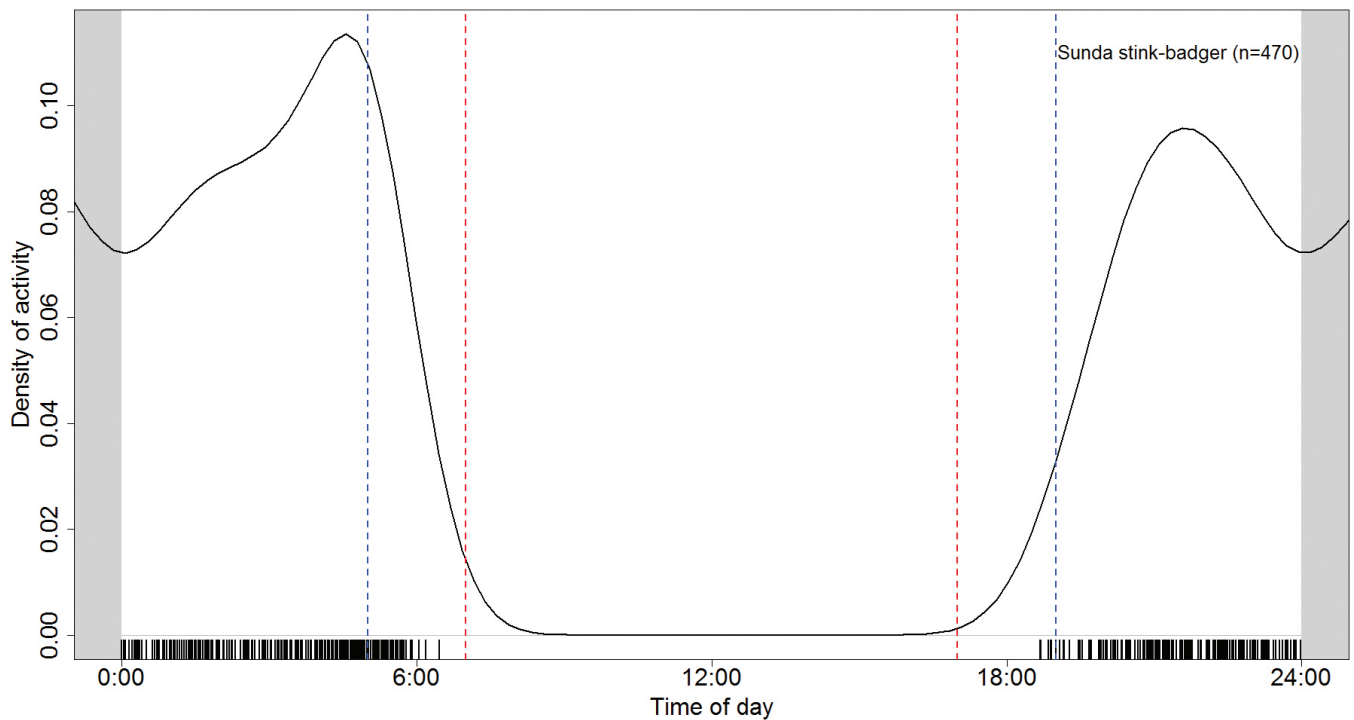


Fig. 2. Daily activity patterns of Sunda stink-badger within Lots 5 and 7 of the Lower Kinabatangan Wildlife Sanctuary, Sabah, Borneo. The grey areas represent an extension of the activity pattern to depict its circular nature, and ‘carpet’ marks along the x-axis represent individual photographic events. Vertical dashed red lines indicate either the end or beginning of the diurnal phase of the diel (0700–1659 hours). Vertical blue lines indicate either the end or beginning of the nocturnal phase of the diel (1900–0459 hours). Regions between red and blue lines represent the crepuscular regions of the diel (0500–0659 hours and 1700–1859 hours).

Table 1. Overlap coefficients for Sunda stink badger activity patterns across seasonal and lunar variation.

Activity pattern 1	Sample size (N) of unique Sunda stink-badger events	Activity Pattern 2	Sample size (N) of unique Sunda stink-badger events	Coefficient of overlap (Confidence interval)	P-value
Dry season (March–October)	339	Wet season (November–February)	131	0.90 (0.89–0.96)	0.69
Full moon	58	New moon	64	0.81 (0.71–0.93)	0.26
‘Bright’ nights (full moon, waxing gibbous, and waning gibbous)	165	‘Dim’ nights (new moon, new crescent, and old crescent)	183	0.90 (0.88–0.97)	0.72

mating or courtship, visual sexing was not possible, and as such, this assumption cannot be made. Overall, the camera trapping effort returned 1.92 unique Sunda stink-badger events every 100 potential trap nights.

Camera trap activity patterns. The activity pattern of the Sunda stink-badger was modelled using 470 photographic events (Fig. 2). Within the LKWS, the Sunda stink-badger displayed a highly nocturnal activity pattern, with no photographic events recorded within diurnal hours. The earliest time in the evening a stink-badger was recorded was 1839 hours, and the latest morning detection was 0627 hours. Activity began and rose sharply within the crepuscular time period of 1700–1859 hours and then continued throughout

nocturnal hours. Once the morning crepuscular hours (0500–0659 hours) began, stink-badger activity quickly fell. Sunda stink-badgers demonstrated two clear peaks in activity, the first occurred around 2100 hours, and the second around 0500 hours with a greater magnitude.

Seasonal and lunar effects. All tested overlaps of modelled activity patterns using subsets of Sunda stink-badger events were found to have high coefficients of overlap (≥ 0.8) (Table 1; Fig. A2). Statistical analysis found that none of the analysed overlaps were significantly different (Table 1), indicating that the activity pattern of the Sunda stink-badger does not significantly vary between seasons or moon phase.

DISCUSSION

These results provide the first detailed 24-hour daily activity pattern for the Sunda stink-badger, a metric currently only available for few of the Bornean carnivores, e.g., Sunda clouded leopard *Neofelis diardi* (Cuvier) (Ross et al., 2013) and sun bear *Helarctos Malayanus* (Raffles) (Wong et al., 2004). The Sunda stink-badger was found to be highly nocturnal, with activity primarily between the hours of 1800 hours and 0600 hours. Furthermore, activity was not uniform throughout this period and displayed two peaks at 2100 hours and 0500 hours. Whilst nocturnal activity between the hours of 1800 hours and 0600 hours has been previously reported (Samejima et al., 2016), this is the first study to show the intricacies of activity between these hours for this species. Over the five-year study period, the study collected 470 photographic events of the Sunda stink-badger, the largest reported collection of photographic events for this species in the wild at the time of publication. This extensive data set has enabled a high level of accuracy within the kernel density modelled activity pattern, avoiding accuracy issues associated with small sample sizes and seasonal biases that may occur with shorter camera trapping studies (Oliveira-Santos et al., 2008; Chen et al., 2009; Cheyne et al., 2010).

It is, however, important to note the potential bias within this study based on the trail-based positioning of camera stations. The Sunda stink-badger's activity pattern presented here should therefore be interpreted as its activity along wildlife trails. As an example, the lack of a single image containing visibly young stink-badgers within such an extensive dataset supports the belief that Sunda stink-badgers raise their young in secluded dens (Long & Killingley, 1983), a behaviour unlikely to be detected with trail-based camera traps. Furthermore, the paucity of apparent mating images similarly suggests this species may conduct reproductive courtship behaviours away from wildlife trails, and future targeted studies should seek to place camera traps throughout a variety of forest microhabitats. The deployment of technologies alternative to camera traps, such as radio telemetry, satellite tracking, or collar-based accelerometers could provide researchers with even more accurate insights into stink-badger activity patterns, especially for more fine-scale behaviours, those involving little movement through the habitat, or those occurring off-trail (Shepard et al., 2008; Nathan et al., 2012); however, these techniques do suffer from practical limitations of high costs and limited sample sizes compared with camera trapping efforts. The most informative picture of Sunda stink-badger ecology is therefore most likely to be generated from a mixture of research methodologies deployed simultaneously, when financially viable. Despite the limitations of camera trapping when deployed alone, the results of the activity pattern modelling have enhanced understanding of the behavioural ecology of the Sunda stink-badger, and will act as baseline for future ecological studies aiming to assess the species' activity pattern.

The analysis of a species' activity pattern can indicate how a species responds to environmental and biological pressures. Seasonal variations in activity patterns have been recorded for

many species (Patterson et al., 1999; Kauhala et al., 2006); however, no such variation was found for the Sunda stink-badger in this study. Additionally, many nocturnal species also vary their activity across the lunar cycle (Di Bitetti et al., 2006; Kauhala et al., 2006), yet no such behaviour was documented for the Sunda stink-badger. Activity patterns may also vary due to inter- and intra-specific competition, which often results in temporal niche partitioning (Lucherini et al., 2009), or predator-prey interactions, whereby species can shift activity patterns to either increase hunting success as predators or maximise survival as prey (Ross et al., 2013). Predation pressures on the Sunda stink-badger are expected to be limited due to the stink-badger's anal scent-gland secretions acting as a powerful deterrent to any potential predators. Although there are unsubstantiated reports of civets preying upon Sunda stink-badgers from popular science websites (Krauskopf, 2002), in four of our 470 photographic events (0.85%), a Sunda stink-badger was photographed co-occurring with a Malay civet (*Viverra zibethica*). In all co-occurrence events, there were no observed indications of physical contact or any behavioural interactions between the two species (Fig. A3). All instances of co-occurrence took place within areas with no obviously discernable presence of a concentrator of activity (e.g., salt lick), and are instances of photographic events where both species were imaged simultaneously in the same frame. This represents one of very few documented cases of Sunda stink-badger in close proximity to another species of carnivore.

Activity is, however, also heavily influenced by dietary demands in carnivores (Ross et al., 2013). Understanding of Sunda stink-badger diet is limited, although an omnivorous diet is reported (Payne et al., 1985) and the stomach contents of a dissected individual indicated a diet abundant in large earthworm species (Davis, 1961). Nocturnality in predators of earthworms is common, and is believed to be a result of nocturnal vertical migration to the soil surface by some earthworm species (Duriez et al., 2006). This may help explain the nocturnal activity pattern found in the Sunda stink-badger, perhaps even the two peaks in activity, as some earthworm species surface in the early evening and early morning (Lee, 1985).

Whilst dietary pressures are suspected to be the predominant generator of the broad activity pattern for Sunda stink-badgers in the LKWS, pressures may also be anthropogenic in nature. For example, the activity pattern of a species can vary in response to pressures such as hunting, habitat destruction, and other anthropogenic activities (Frederick, 2008; Presley et al., 2009; Marchand et al., 2014; Poudel et al., 2015). Close proximity to oil palm plantations, local road infrastructure, and the Kinabatangan River increases human accessibility into the LKWS, bringing tourism, fishermen, and illegal hunters, all of which heighten anthropogenic disturbances within the sanctuary. This anthropogenic disturbance is also exacerbated by the considerable historical habitat degradation that has occurred in the area through repeated selective logging during the 20th century. As such, the stink-badger's activity pattern presented here could be reflective of the highly disturbed environment within the LKWS.

Despite many records of Sunda stink-badger being available (Samejima et al., 2016), very few studies have obtained sizeable encounter datasets within a single area as presented here (Matsubayashi et al., 2007; Wilting et al., 2010; Bernard et al., 2014). Of those studies with many Sunda stink-badger records, all have occurred within the Malaysian state of Sabah; however, even within this limited scope, discernible differences in site ecology and disturbance regimes can allow for preliminary comparisons between studies. Within our LKWS camera trapping effort, 1.92 unique Sunda stink-badger events were recorded every 100 trap nights and the species was the second most commonly imaged carnivore in the survey (Evans et al., 2016). This encounter rate can be compared with other studies in an attempt to analyse the effect of site differences on local abundance. Whilst encounter rates (often naively but inappropriately termed Relative Abundance Indices) are increasingly considered a dated methodology for assessing abundances, particularly between species (Sollmann et al., 2013), with so few studies assessing Sunda stink-badger photographic rates (Matsubayashi et al., 2007; Wilting et al., 2010; Bernard et al., 2014), an encounter rate provides a comparative preliminary indicator of status for this under-studied species. Only three other studies have produced this measure or provided sufficient information for an encounter rate to be calculated for the Sunda stink-badger (Table A1), two of which were undertaken within the Deramakot Forest Reserve (DFR) situated further upstream on the Kinabatangan River. The third study was undertaken within Tabin Wildlife Reserve, Sabah; however, due to very low sample size, the results are not suitable for comparison here (Bernard et al., 2014). The two studies at DFR recorded 3.66 (Matsubayashi et al., 2007) and 3.60 (Wilting et al., 2010) unique Sunda stink-badger photographic events per 100 trap nights, which may be an indication that the species is comparatively less common in the LKWS than in DFR (Table A1). Given the higher amounts of habitat degradation and anthropogenic disturbance within the LKWS area compared to DFR (the LKWS is smaller, more fragmented, and more isolated from other native forest); these results may suggest that the Sunda stink-badger is more susceptible to anthropogenic disturbance than previously thought. However, caution must be advised with this interpretation due to differences in study methodologies and relatively small sample sizes; for example, whilst cameras were set on wildlife trails in both of the compared studies, localised features such as rivers and salt licks varied. This variation in relative encounter rate between study areas does, however, emphasise the importance of understanding how the behavioural ecology of this species may also vary across study sites.

Sunda stink-badgers have been observed in a wide variety of habitats including lowland forest, montane forests, forest mosaic, and non-forest at both protected and unprotected sites. Whilst presence may indicate human-modified habitats in the LKWS are used by the species, it does not necessarily indicate optimal habitat and gaining a greater understanding of Sunda stink-badger species' ecology remains pertinent. Particularly given the suggestion, above, that encounter rates (and thus perhaps population densities) might be lower in more degraded and fragmented habitats, further studies of

Sunda stink-badger behaviour are warranted to investigate to what extent habitat quality and human disturbance may be impacting the species. Whilst the persistence of Sunda stink-badger is not considered to be in immediate danger, improving knowledge of the species' ecology is nevertheless useful. Furthermore, the methodology utilised here is easily adopted and, due to the vast volume of camera trapping taking place within the region, can be applied to a plethora of other under-studied ground-dwelling species.

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APPENDIX



Fig. A1. A pair of Sunda stink-badgers *Mydaus javanensis* photo-captured in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysian Borneo on 09 March 2009.



Fig. A3. Co-occurrence of Sunda stink-badger *Mydaus javanensis* and Malay civet *Viverra zibetha* photo-captured in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysian Borneo on 13 June 2013.

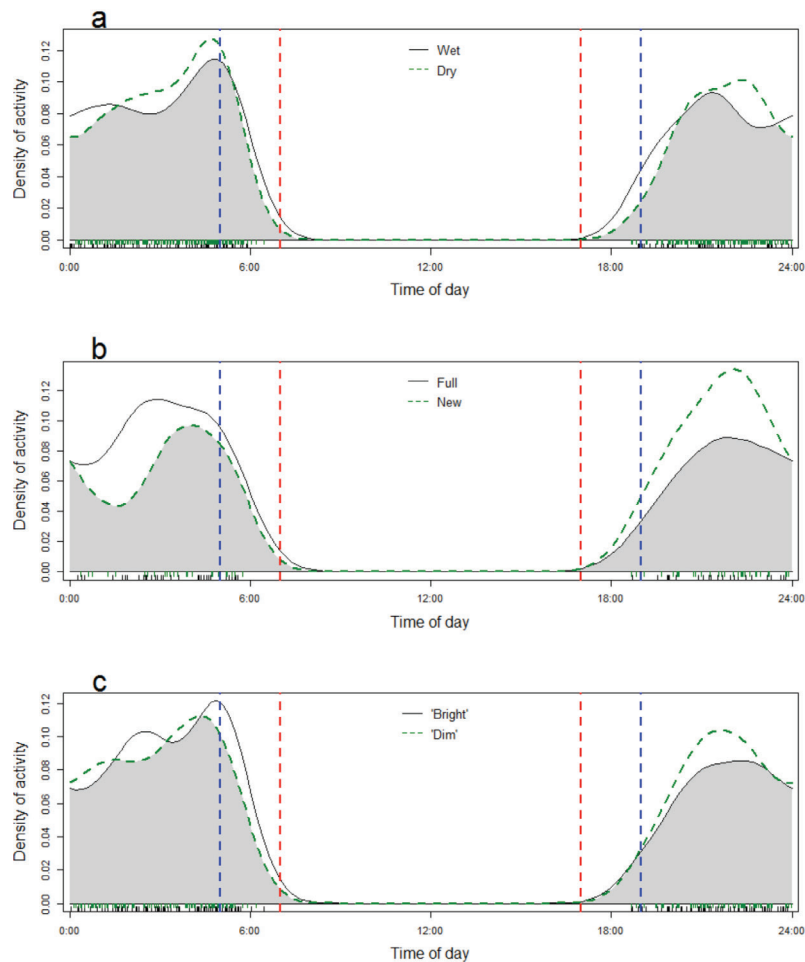


Fig. A2. Kernel density modelled activity patterns for the Sunda stink-badger during different periods; overlap between activity patterns is indicated by the shaded regions. Vertical dashed red lines indicate either the end or beginning of the diurnal phase of the diel (0700–1659h). Vertical blue lines indicate either the end or beginning of the nocturnal phase of the diel (1900–0459h). Regions between red and blue lines represent the crepuscular regions of the diel (0500–0659h and 1700–1859h). ‘Carpet’ marks along the x-axis represent individual photographic events, and are colour co-ordinated to their respective activity pattern. Top (a): Overlap in kernel density modelled activity pattern in the wet season (November–February) compared to the dry season (March–October). Middle (b): Overlap in kernel density modelled activity pattern on full moon nights compared to new moon nights. Bottom (c): Overlap in kernel density modelled activity pattern on ‘bright’ nights (full moon, waxing gibbous, and waning gibbous) compared to ‘dim’ nights (new moon, new crescent, and old crescent).

Table A1. Comparisons between remote camera trapping studies that have observed the Sunda stink-badger *Mydaus javanensis*.

Reference	Study site	Trap nights	Photographic Events	No. of unique photographic events per 100 potential trap nights	Notes	Study period
Matsubayashi et al., 2007	Deramakot Forest Reserve	981	36	3.66	Salt lick at 5 of 15 sites, area sustainably logged during study period.	June 2003–October 2005
Wilting et al., 2010	Deramakot Forest Reserve	1,916	69	3.60	Camera traps placed within large contiguous forest patch.	July 2008–January 2009
Bernard et al., 2013	Tabin Wildlife Reserve	307	2	0.65	Forest patch within oil palm plantation.	September 2009–December 2009 and May 2010–August 2010
Bernard et al., 2013	Tabin Wildlife Reserve	229	1	0.44	Forest patch within oil palm plantation.	September 2009–December 2009 and May 2010–August 2010
Current study	Lower Kinabatangan Wildlife Sanctuary	24,506	470	1.92	Highly fragmented riverine study site, with extensive areas of oil palm plantations.	November 2010–May 2015