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Research Article

Temporal Partitioning of the Sympatric Large Terrestrial Mammals in Utilizing the Natural Saltlicks at a Commercial Forest Reserve of Northern Borneo

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ABSTRACT

A sign of temporal partitioning is detected between the Sambar Deer (*Rusa unicolor*), Bornean Orangutan (*Pongo pygmaeus morio*), Bearded Pig (*Sus barbatus*), and Banteng (*Bos javanicus*), when using the natural saltlicks at Segaliud-Lokan Forest Reserve in Sabah, Borneo, although the effects of habitat conditions and interspecific competition on the given matter remain uncertain for now. A camera trapping survey was conducted in this study, to examine the variability in both the diel activity patterns and visitation frequencies of the four sympatric species across four local saltlicks. The diel activity patterns of these four sympatric species were shaped by the habitat conditions, which resulted in a distinct temporal partitioning, unlike the interspecific competition that only contributed to a minor temporal partitioning, between certain two sympatric species using a specific saltlick. Their visitation frequencies were associated with their respective adopted diel activity patterns and levels of lick dependency for regular mineral intake, hence confirming their variation across different saltlicks and times of the day. Further research is required in the future to scientifically validate the given matter.

Keywords: Commercial Forest Reserve, Temporal Partitioning, Large Terrestrial Mammals, Natural Saltlick, Visitation Pattern

INTRODUCTION

The natural saltlicks that are presented in the inland tropical forest of Northern Borneo, which is known as Sabah of Malaysia, are visited mainly by large terrestrial mammals (Matsubayashi et al., 2011; Matsuda et al., 2015; and Lim & Mojiol, 2022). These large threatened species are known to have high daily requirements, especially for sodium minerals, which are available to these species in an insufficient amount in the local plants (Matsubayashi et al., 2007a; and Lim et al., 2020). Because of that, the large omnivores, frugivores, and herbivores resort to depend highly on the natural saltlicks for ascertaining, not only the sodium mineral, but also the other essential minerals and trace elements, in sufficient amounts and on a regular basis (Matsubayashi et al., 2011; Sim et al., 2020; Razali et al., 2022; and Tawa et al., 2022). Moreover, the presence of shrubs and grasses in the open environment of a saltlick can attract certain herd species to forage and conduct social activities in this area as well (Clayton & MacDonald, 1999; Chew et al., 2014; Lim & Mojiol, 2021; and Hiew et al., 2022). In a nutshell, the tropical saltlicks are used by the large Bornean terrestrial mammals for different reasons, which can cause these species to compete with one another for the usage of a particular saltlick, due to the similarity in their ecological niches (Hon & Shibata, 2013; Ikeda et al., 2016; Chen et al., 2019; Thinley et al., 2020; and Fox-Rosales & de Oliveira, 2023).

The principle of limiting similarity highlights that two species are unlikely to coexist with one another in the same ecological niche, thus certain species may partition their time, to avoid competing with the other sympatric species (MacArthur & Levin, 1967; and Frey et al., 2017). This phenomenon is referred to as temporal partitioning, which can trigger each sympatric species to adopt a particular pattern in utilizing a saltlick on a daily basis (Ikeda et al., 2016; Chen et al., 2019; and Thinley et al., 2020). The smaller-sized species tend to be intimidated by the larger-sized species, which can trigger them to modify their activity patterns, mainly to avoid overlapping with the activity patterns of the dominant species, and vice versa (Hon & Shibata, 2013; Hearn et al., 2018; Chen et al., 2019; and Thinley et al., 2020). Nonetheless, the diel activity pattern adopted by a species can be further altered by the anthropogenic disturbance and predation risk presented by a habitat (Matsubayashi et al., 2011; Matsuda et al., 2015; Ning, 2017; and Chen et al., 2019). The open environment of the tropical saltlick can increase the visual acuity of a predator in detecting its prey, hence attracting predator species to visit the tropical licks for prey-hunting (Lazarus et al., 2019; Razali et al., 2020; Griffiths et al., 2020; and Lazarus et al., 2021). Likewise, terrestrial mammals are more prone to being hunted or disturbed by humans, when using saltlicks with high accessibility to humans (Matsubayashi et al., 2011; Blake et al., 2013; Hon & Shibata, 2013; and Matsuda et al., 2015). Therefore, the existing habitat condition has a detrimental influence on the species composition of the mammalian community and, as a result, the

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temporal partitioning of different sympatric species in utilising the natural saltlick that is situated in a specific forest habitat (Frey et al., 2017; and Lim & Mojiol, 2021).

This phenomenon has occurred at the natural saltlicks in various permanent forest reserves of Sabah, including the Segaliud-Lokan Forest Reserve (SLFR) (Lim & Mojiol, 2022). The local forest was once severely degraded by the past unsustainable logging practices that started in the 1950s, but the implementation of reduce impact logging (RIL) practice in 1999 allowed the local degraded forest to slowly rehabilitate afterward (Wilting & Azlan, 2010). Presently, the secondary forest of SLFR is inhabited by different species of Bornean terrestrial mammals, and 14 species have been successfully detected at four local natural saltlicks (Wilting & Azlan, 2010; Kee et al., 2018; Bernard et al., 2019; and Lim et al., 2020). The large threatened species, particularly the Banteng (*Bos javanicus*), Bearded Pig (*Sus barbatus*), Sambar deer (*Rusa unicolor*), and Bornean Orangutan (*Pongo pygmaeus morio*), comprised the majority of the mammalian individuals detected at the given four licks, but they were sighted generally more frequently at different times on a daily basis (Bernard et al; and Lim & Mojiol, 2022). This indicates a sign of temporal partitioning between the given four sympatric species, when competing with each other for the usage of these four saltlicks (Ikeda et al., 2016; Hearn et al., 2017; Chen et al., 2019; and Thinley et al., 2020). Then, their visitation frequencies were varied across these four natural licks with different habitat conditions, thus suggesting an association between the habitat condition and mammalian activity pattern (Matsubayashi et al., 2011; Ning, 2017; Lazarus et al., 2019; Razali et al., 2020; and Lim & Mojiol, 2022), but this matter has yet to be validated by past researchers scientifically as well for the time being.

In other words, the effects of interspecific competition and habitat conditions on the temporal partitioning of four sympatric species using the natural saltlicks at SLFR remain poorly-understood at this moment. Henceforth, this study was conducted to fill up these research gaps by examining the variability in both the diel activity patterns and visitation frequencies of the given four species across the four natural saltlicks that were examined by the previous studies (Bernard et al., 2019; Lim et al., 2020; and Lim & Mojiol, 2022). The adopted activity patterns were hypothesized to be: 1) different between the sympatric species for a specific saltlick, and; 2) varied across the saltlicks with different habitat conditions only for particular large threatened species, based on the past findings reported by the relevant past studies (Matsubayashi et al., 2011; Blake et al, 2013; Hearn et al., 2018; and Lim & Mojiol, 2021). The findings of this research can provide a much comprehensive understanding of the importance of the existing conservation effort in determining the interactions between different biotic and abiotic factors presented in the secondary forest of this commercial forest reserve, and ultimately the shaping of the activity pattern adopted by a certain mammal species in using a local saltlick.

MATERIALS AND METHODS

Study Site

The 57,247 ha of inland tropical forest at SLFR is situated in the District of Sandakan, Sabah, and is divided into 70 forest compartments that are comprised of 10 Protection Area (PA: 6,447 ha), one Plantation Research Area (PRA: 777 ha), 17 Natural Forest Management (NFM: 12,603 ha), and 48 Industrial Tree Planting (ITP: 37,420 ha) compartments (Kee et al., 2018). The KTS Plantation Sdn. Bhd. manages the SLFR as a Class II Commercial Forest Reserve, and its steep undulating hills are currently dominated by regenerating lowland mixed dipterocarp forest (Lim et al., 2020). A total of four natural saltlicks that were assessed by previous research (e.g.: Bernard et al., 2019; Lim et al., 2020; and Lim & Mojiol, 2022) were selected as the sampling areas of this study. Two saltlicks were situated in the vicinity of the same timber plantation forest compartment (SL50_A & SL50_B), while the other two licks were located in the least-disturbed forest (SL56) and the partially-disturbed forest (SL59) respectively. These four saltlicks were still actively used by the local mammalian community and were easily accessible to humans, owing primarily to their proximity to the secondary (logging) road (<0.25 km). Then, they were at least 1.0 km apart from each other, indicating that the probability of double-counting an identical mammalian individual in a short time gap (<30 min) across different licks was minimized (Lim & Mojiol, 2022). Limited grasses, shrubs, and trees can be found alongside with small streams and a mineral-rich spring on the rocky and muddy surface of every lick, although the springs at both the SL50_A and SL56 may dry up temporarily during the dry season, whereas the springs at both the SL59 and SL50_B remain available year-round. Figure 1 displays the locations of the four natural saltlicks that are selected as the sampling areas of this study.

Data Collection

The SunTek HC-800M passive infrared motion-triggered game trail camera traps (Hong Kong Suntek International Co., Ltd.) were applied in surveying the activity patterns adopted by the Banteng, Sambar Deer, Bearded Pig, and Bornean Orangutan in visiting the four selected saltlicks at SLFR for eight months (July 2019 until February 2020) in this study. Each selected saltlick was installed with a unit of camera trap, using the settings and configurations suggested by Lim et al. (2020). No further alteration was made to the positions of the given deployed camera traps, and their performances were maintained at optimal levels by conducting maintenance work on them twice a month, throughout the 8-month sampling period of the present study (Lim & Mojiol, 2022). The maintenance work that was required to be done for the deployed camera traps included replacing the batteries, updating the time and date, removing the view-blocking obstacles, and transferring the camera trapping data, every time they were set to remain actively capturing the footage (photographs and videos) of the four sympatric species at the respective saltlicks throughout the day. The morphological attributes of each detected mammalian individual were used in identifying its species, by referring to the field guide of Phillipps and Phillipps (2018). The footages that failed to detect any of the four species were excluded, and a 30-min time gap was utilized to distinguish two independent sightings from the successive detection of a certain mammal species at a specific lick and at a specific time of day (Matsubayashi et al., 2007a; and Lim et al., 2020). Based on this assumption, the information related to the frequency and time of detection for each species at a particular saltlick was derived from the processed camera trapping data.

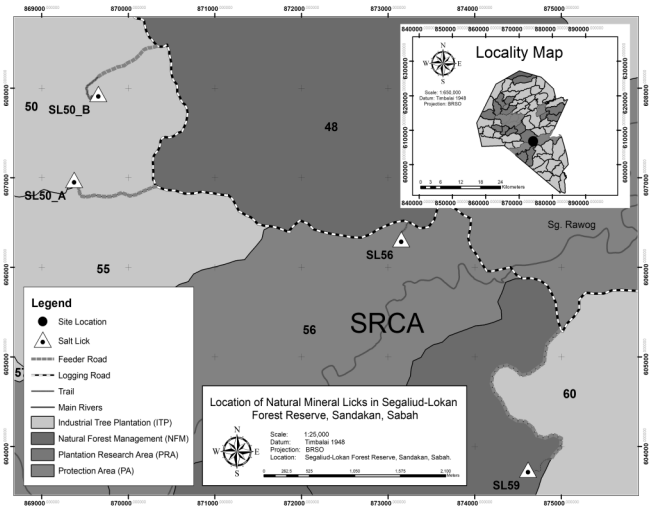

Figure 1. Locations of the four natural saltlicks that are selected as the sampling areas of this study

Data Analysis

The visitation frequency of a certain species to a given saltlick and at a particular time of the day was estimated as the relative abundance index (RAI), in the number of independent sighting per 100 trap nights ($100TN^{-1}$) in this research (Lim & Mojiol, 2021). After that, the time of sightings was classified either as twilight period (dawn: 0501 to 0700 hours; dusk: 1701 to 1900 hours), night-time (1901 to 0500 hours), or daytime (0701 to 1700 hours) (Hon & Shibata, 2013; Ikeda et al., 2016; and Hearn et al., 2018). The estimated mammalian RAI data was assessed and verified to not conform to the normal distribution (Shapiro-Wilk Test; $p<0.05$) and homogeneity of variance (Levene's test; $p<0.05$), even after the data transformation was applied to this dataset. Therefore, the non-parametric Kruskal-Wallis test was employed to obtain the variability in visitation frequency of each species to a certain saltlick between different times of the day, to validate if the given species adopted diurnality, crepuscularity, nocturnality, or cathemerality (using a saltlick similarly frequently from day till night), in visiting the given saltlick in this study (Ikeda et al., 2016). The Dunn-Bonferroni Test was utilized as the post-hoc analysis for the Kruskal-Wallis Test, which was derived from the "FSA" and "Stats" packages respectively in R (Ogle et al., 2019; and R Core Team, 2022).

The kernel density analysis was conducted to ascertain the diel (24 hours) activity patterns of the four large threatened mammal species using each natural saltlick evaluated in this research. Then, the coefficient of overlapping (Δ) was estimated to evaluate the similarity in diel activity patterns: 1) among the four selected licks visited by a certain species, and; 2) between the four sympatric species in utilizing a particular saltlick, at this forest reserve (Very high: $\Delta>0.75$; High: $0.50<\Delta<0.75$; Low: $0.25<\Delta<0.50$; Very Low:$\Delta<0.25$) (Hearn et al., 2018; and Thinley et al., 2020). Two equations were suggested for the estimation of the coefficient of overlapping, in which the formula $\Delta1$ was used when the sample size was smaller than 50, whereas the formula $\Delta4$ was applied when the sample size was larger than 75 (Ridout & Linkie, 2009). Both the kernel density analysis and analysis of overlapping were conducted using the "Overlap" package in R (Ridout & Linkie, 2009).

Moreover, the outcomes of the analysis of overlapping were supported by using the results obtained through both the Kruskal-Wallis test and the Dun-Bonferroni test in the present study.

The interactions between the four sympatric species visiting the four selected natural saltlicks at SLFR were predicted by utilizing the Poisson regression analysis that was derived from the "vegan" package (Oksanen et al., 2020). The hourly visitation frequency of a specific species to a saltlick was selected as the outcome variable, whereas the hourly visitation frequencies of other sympatric species to the given saltlick were applied as the predictor variables, to determine the influence of interspecific competition on the temporal partitioning of these four sympatric species visiting the given lick (Ikeda et al., 2016). The prediction models were selected through a both-direction stepwise-procedure, and then only the model determined with the lowest value of the Akaike Information Criterion (AIC) was highlighted in the present research. The ascertainment of a positive estimate value indicated a positive association between the activity patterns of two sympatric species in using a certain saltlick, whereas a negative estimate value signified otherwise (Hearn et al., 2018). All of the statistical analyses were conducted by employing the statistical software RStudio ver.1.2.5001 (R Core Team, 2022), in which the significance level of $p<0.05$ was considered significant in this research.

RESULTS

General Activity Patterns of the Four Sympatric Species

The activity patterns of the four species of large threatened mammals in using the four selected natural saltlicks at SLFR were determined, with the camera trapping effort amounted to a total of 345 nights (SL50_A=85 TN; SL50_B=94 TN; SL56=87 TN; SL59=79 TN) in this research. The Banteng was observed similarly frequent throughout the day and across the given four licks ($p>0.05$), but this species generally used the SL56 and SL59 more frequently at dawn (SL56: RAI=1.437 100 TN^{-1}) and dusk (SL59: RAI=1.266 100 TN^{-1}) respectively, whereas the SL50_A and SL50_B were visited more frequently at midday (SL50_A: RAI=0.353 100 TN^{-1}) and early morning (SL50_B: RAI=0.380 100 TN^{-1}) respectively. Henceforth, its diel activity patterns were highly similar between these four licks ($\Delta>0.50$), except between the SL50_B with SL50_A ($\Delta=0.4909$) and SL59 ($\Delta=0.4730$). Actually, its visitation frequency was determined to be generally higher at the SL56 and SL59 than at the SL50_A and SL50_B, revealing that the cathemeral Banteng preferred to visit the two saltlicks located in the disturbed natural forests over the two licks situated in the timber plantation forest at SLFR. Figure 2 illustrates the diel activity patterns adopted by the four sympatric species in visiting to the four natural saltlicks assessed in this study. Then, Table 1 displays the visitation frequencies of the four sympatric species to the given four saltlicks at various times of the day, while Table 2 shows the coefficients of overlapping that signify the similarity in diel activity patterns adopted by the given four species when using two specific licks. The overlaid diel activity patterns of each large threatened mammal species in using two specific saltlicks

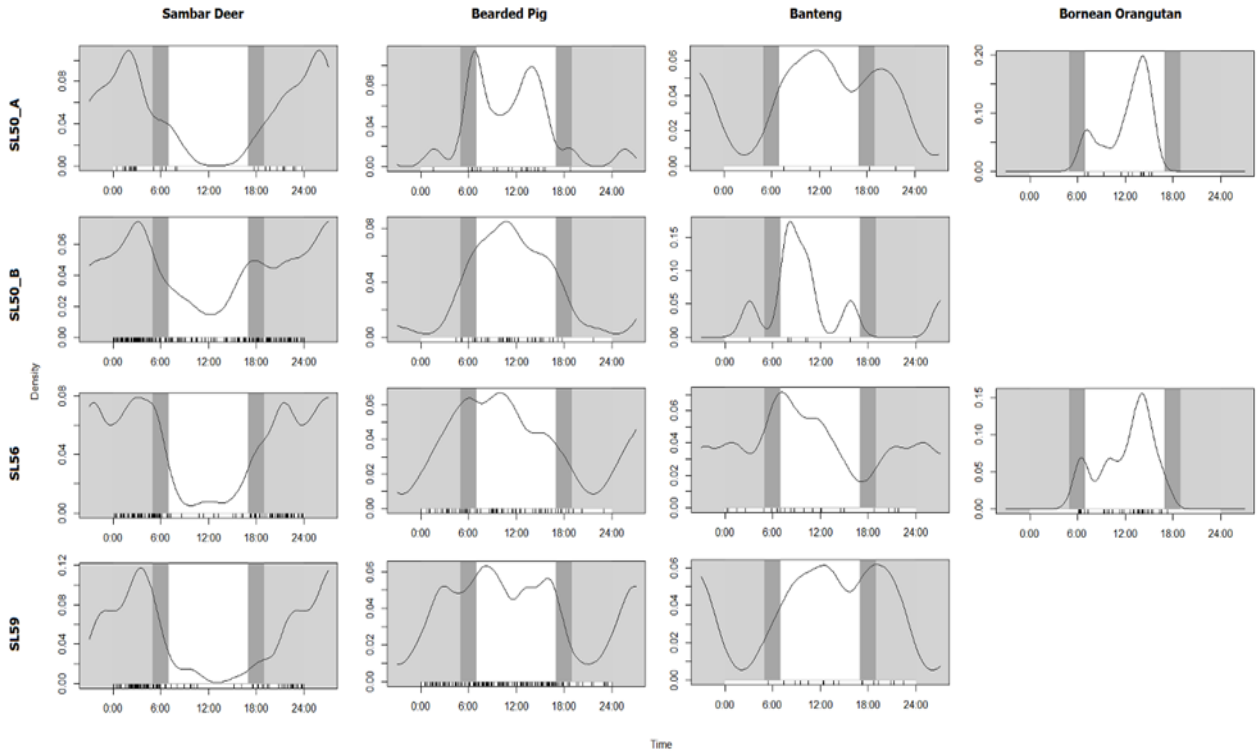

Figure 2. The diel activity patterns adopted by the four sympatric species in visiting to the four natural saltlicks investigated in this research

Table 1. Visitation frequencies of the four sympatric species to the four selected natural saltlicks at different times of the day in SLFR

Species	Mineral Licks	Relative Abundance Index ($100TN^{-1}$)			Statistic	
		Twilight	Daytime	Night-time	X^2_1	p
Banteng	SL50A	0.294 ± 0.294	0.353 ± 0.180	0.118 ± 0.118	1.211	0.546
	SL50B	-	0.380 ± 0.284	0.106 ± 0.106	4.07	0.131
	SL56	1.437 ± 0.723	1.149 ± 0.383	0.920 ± 0.287	0.386	0.825
	SL59	1.266 ± 0.517	1.013 ± 0.253	0.506 ± 0.207	3.067	0.216
Bearded Pig	SL50A	1.765 ± 1.019	1.647 ± 0.400	0.118 ± 0.118	8.96	*
	SL50B	2.660 ± 1.019	2.979 ± 0.382	0.213 ± 0.142	15.499	***
	SL56	5.172 ± 1.521	4.828 ± 0.887	2.184 ± 0.580	5.869	0.053
	SL59	8.861 ± 2.635	11.899 ± 1.135	6.203 ± 1.418	6.965	*
Bornean Orangutan	SL50A	0.294 ± 0.294	1.294 ± 0.370	-	10.776	**
	SL50B	-	-	-	-	-
	SL56	2.011 ± 1.651	3.678 ± 0.951	-	13.95	***
	SL59	-	0.253 ± 0.253	-	-	-
Sambar Deer	SL50A	1.765 ± 0.340	0.235 ± 0.157	2.942 ± 1.011	10.686	***
	SL50B	11.436 ± 1.647	5.957 ± 0.914	14.894 ± 1.327	16.024	***
	SL56	8.046 ± 1.817	1.379 ± 0.334	10.690 ± 1.000	17.519	***
	SL59	6.013 ± 1.890	1.139 ± 0.350	11.899 ± 2.043	14.999	***

***Note:** X^2=Chi-squared value; p=Level of significance (*p<0.05; **p<0.01; ***p<0.001).

Table 2. Coefficients of overlapping that signifies the similarity in diel activity patterns adopted by the four sympatric species in using two particular natural saltlicks examined in this study

Parameter	Sambar Deer	Bearded Pig	Bornean Orang-utan	Banteng
SL50_A vs SL50_B	**0.7802** (0.6644–0.8849)	**0.7827** (0.6150–0.1923)	-	0.4909 (0.1573–0.8158)
SL50_A vs SL56	**0.8339** (0.7085–0.9333)	**0.7341** (0.5726–0.8784)	**0.8301** (0.6276–0.9764)	**0.7504** (0.4586–1.0079)
SL50_A vs SL59	**0.8421** (0.7159–0.9430)	**0.7246** (0.5713–0.8623)	-	**0.9478** (0.6406–1.1902)
SL50_B vs SL56	**0.8465** (0.7731–0.9155)	**0.8163** (0.6917–0.9277)	-	**0.5466** (0.2836–0.7908)
SL50_B vs SL59	**0.7506** (0.6685–0.8319)	**0.8078** (0.6994–0.9045)	-	0.4730 (0.2140–0.7311)
SL56 vs SL59	**0.8286** (0.7340–0.9144)	**0.9075** (0.8207–0.9753)	-	**0.7329** (0.5261–0.9129)

***Note:** Coefficients of overlapping (Δ) are shown as the top values, whereas the range of confidence interval values are presented as the bottom values in brackets. The bolded values indicate high (0.50<Δ<0.75) and very high (Δ>0.75) similarity in the mammalian diel activity patterns.

The Sambar Deer visited the four selected natural saltlicks mainly at night ($p<0.001$), although its visitation frequency to the SL50_A was verified to be generally less frequent (RAI=2.942 100 TN^{-1}) than those recorded at the SL50_B (RAI=14.894 100 TN^{-1}), SL56 (RAI=10.69 100 TN^{-1}) and SL59 (RAI=11.899 100 TN^{-1}) in this research. Likewise, this species was observed more frequently at dawn and dusk than at daytime in the same manner, but the differences were determined as significant only for the SL50_A (Twilight: RAI=1.765 100 TN^{-1}; Day: RAI=0.235 100 TN^{-1}; Z=2.341, p=0.029) and the SL56 (Twilight: RAI=8.046 100 TN^{-1}; Day: RAI=1.379 100 TN^{-1}; Z=2.375, p=0.026). The given phenomenon resulted in a very high similarity in its diel activity patterns when using the given four licks (Δ> 0.75), despite the fact that this study was conducted at night. The given phenomena resulted in the very high similarity in its diel activity patterns in using the given four licks (Δ>0.75), while adopting nocturnality .

Next, the bearded pig was observed significantly less frequently during the night-time at the SL50_A (RAI=0.118 100 TN^{-1}; X^2_2=8.960, p=0.011), SL50_B (RAI=0.213 100 TN^{-1}; X^2_2=15.50, p< 0.001) and SL59 (RAI=6.203 100 TN^{-1}; X^2_2=6.965, p=0.031), except for SL56 (RAI=2.184 100 TN^{-1}; X^2_2=5.869, p=0.053). Its diurnal visitation frequency was significantly different with its crepuscular visitation frequency only at the SL50_B (Twilight: RAI=2.660 100 TN^{-1}; Day: RAI=2.979 100 TN^{-1}; Z=2.407, p=0.024), highlighting that the Bearded Pig only adopted diurnality in using this saltlick, especially at early morning. However, this species generally used the SL59 most frequently, followed by the SL56, SL50_B, and SL50_A. Although the Bearded Pig adopted cathemerality in utilizing the SL56, and also diurnality and crepuscularity in using the SL50_A and SL59, its diel activity patterns when using the given four licks were found to be highly similar (Δ>0.70) in this study. This indicated that the Bearded Pig mainly visited the local licks at daytime and twilight periods, especially at dawn for the SL50_B, and also at midday and dusk for both the SL50_A and SL59, in this research.

The Bornean Orangutan was not observed at the SL50_B, and it was detected only once at the SL59 (RAI=0.253 100TN^{-1}), during daytime in this study. Henceforth, its diel activity patterns were estimated only for both the SL50_A and SL56, which were very highly similar (Δ=0.8301), since this species only utilized these two licks during the crepuscular and diurnal hours (zero detection at night). However, this species was seen more frequently at the SL56 than at the SL50_A. Then, the difference in visitation frequency between daytime (SL50_A: RAI=1.294 100 TN^{-1}; SL56: RAI = 3.678 100 TN^{-1}) and twilight hours (SL50_A: RAI = 0.294 100 TN^{-1}; SL56: RAI = 2.011 100 TN^{-1}) for both saltlicks was confirmed to be not significant (SL50_A: Z=-1.699; p=0.134; SL56; Z=-1.254, p=0.21), although it was found visiting the given two licks mainly during the late afternoon (12.00 to 17.00 hours). This showed that the Bornean Orangutan adopted diurnality and crepuscularity in using both the SL50_A and SL56 at SLFR throughout the eight-month sampling period of the present research.

Interactions between the Four Sympatric Species

The interactions between the four sympatric species were examined in this study, in terms of the differences in both their diel activity patterns and visitation frequencies, between the four selected saltlicks at SLFR. In general, the diel activity patterns of certain species were determined to be highly similar (Δ> 0.50) across all four saltlicks, such as the Banteng with the Bearded Pig, and the Bornean Orangutan with these two species. These three large threatened species generally used the local licks more frequently at daytime and twilight periods than at night-time, but the Bearded Pig was detected most frequently, followed by the Bornean Orangutan, and lastly the Banteng, at both the SL50_A and SL56, mainly due to the absence and low detection rate of the Bornean Orangutan at the SL50_B and SL59 respectively in this study. Nonetheless, a significantly positive association was ascertained only between the activity patterns of the Bearded Pig and Bornean Orangutan at

the SL50_A ($p<0.05$), for they were both actively utilizing this saltlick at late afternoon (1200 to 1700 hours), emphasizing their competition with each other for the usage of this lick at this forest reserve. The Banteng, on the other hand, was validated to share no significant association with the other two species ($p>0.05$), indicating that its activity patterns in using the local four saltlicks were not dictated by the presence of both the diurnal Bearded Pig and Bornean Orangutan.

In a nutshell, the Banteng, Bearded Pig and Bornean Orangutan exhibited similar diel activity patterns in utilizing the four selected natural saltlicks, but at different visitation frequencies, at SLFR. Then, no distinct temporal partitioning was observed between these three species across all four licks, especially between the Bornean Orangutan and Bearded Pig that competed for the usages of SL50_A in this research. Table 3 reveals the results of the comparison in visitation frequency between the four sympatric species to each selected saltlick across different times of the day in SLFR. Then, Table 4 shows the coefficients of overlapping that signifies the similarity in diel activity patterns adopted by two sympatric species when visiting to a certain saltlick assessed in this research. Finally, Table 5 mentions the outcomes of the Poisson regression for predicting the impacts of the interactions between the four sympatric species on their respective adopted activity patterns for using the four selected natural saltlicks at SLFR.

Table 3. Results of the comparison in visitation frequency between the four sympatric species to each selected natural saltlick at different times of the day in SLFR

Mineral Licks	Times of Day	Relative Abundance Index ($100TN^{-1}$)				Statistic	
		Banteng	Bearded Pig	Bornean Orangutan	Sambar Deer	X^2_3	p
SL50A	Night-time	0.118 ± 0.118	0.118 ± 0.118	-	2.942 ± 1.011	22.645	***
	Daytime	0.353 ± 0.180	1.647 ± 0.400	1.294 ± 0.370	0.235 ± 0.157	11.485	**
	Twilight	0.294 ± 0.294	1.765 ± 1.019	0.294 ± 0.294	1.765 ± 0.340	7.264	0.064
SL50B	Night-time	0.106 ± 0.106	0.213 ± 0.142	-	14.894 ± 1.327	32.192	***
	Daytime	0.380 ± 0.284	2.979 ± 0.382	-	5.957 ± 0.914	31.524	***
	Twilight	-	2.660 ± 1.019	-	11.436 ± 1.647	13.202	**
SL56	Night-time	0.920 ± 0.287	2.184 ± 0.580	-	10.690 ± 1.000	30.449	***
	Daytime	1.149 ± 0.383	4.828 ± 0.887	3.678 ± 0.951	1.379 ± 0.334	15.073	**
	Twilight	1.437 ± 0.723	5.172 ± 1.521	2.011 ± 1.651	8.046 ± 1.817	7.92	*
SL59	Night-time	0.506 ± 0.207	6.203 ± 1.418	-	11.899 ± 2.043	31.542	***
	Daytime	1.013 ± 0.253	11.899 ± 1.135	0.253 ± 0.253	1.139 ± 0.350	26.827	***
	Twilight	1.266 ± 0.517	8.861 ± 2.635	-	6.013 ± 1.890	12.133	**

***Note:** X^2=Chi-squared value; p=Level of significance (*p<0.05; **p<0.01; ***p<0.001).

Table 4. Coefficients of overlapping that signifies the similarity in diel activity patterns adopted by two sympatric species in visiting to a specific natural saltlick evaluated in this research

Parameter	SL50_A	SL50_B	SL56	SL59
Bearded Pig vs Banteng	**0.6716** (0.3542–0.9473)	**0.6256** (0.3638–0.8621)	**0.8354** (0.6885–0.9542)	**0.7230** (0.5503–0.8749)
Sambar Deer vs Bearded Pig	0.2966 (0.1373–0.4726)	**0.5027** (0.3879–0.6176)	**0.5479** (0.4420–0.6545)	**0.5030** (0.4114–0.5979)
Sambar Deer vs Banteng	0.4768 (0.2134–0.7568)	0.4189 (0.1813–0.6559)	**0.6021** (0.4243–0.7659)	0.4069 (0.2423–0.5797)
Sambar Deer vs Bornean Orangutan	0.1513 (0.0291–0.2835)	-	0.2419 (0.1546–0.3319)	-
Bearded Pig vs Bornean Orangutan	**0.7080** (0.4604–0.9060)	-	**0.6514** (0.5135–0.7777)	-
Banteng vs Bornean Orangutan	**0.5485** (0.2252–0.8645)	-	**0.5628** (0.3870–0.7326)	-

***Note:** Coefficients of overlapping (Δ) are shown as the top values, whereas the range of confidence interval values are presented as the bottom values in brackets. The bolded values indicate high ($0.50<\Delta<0.75$) and very high ($\Delta>0.75$) similarity in the mammalian diel activity patterns.

When visiting the SL50_B (Δ=0.5027), SL56 (Δ=0.5479) and SL59 (Δ=0.5030), Sambar deer showed diel activity patterns that were highly similar to those of the Bearded Pig, but not the SL50_A (Δ=0.2966). Although both species were observed frequently at the twilight hours across all four licks, still the Sambar Deer was sighted significantly more frequent than the Bearded Pig at night-time, and vice versa during daytime ($p<0.05$), except for the SL59 at night-time ($Z=-1.051$, $p=0.352$). Actually, the difference was distinct at the SL50_A, but not for the other three licks at these times of the day, thus resulting in the dissimilarity in their diel activity patterns only at SL50_A in this study. However, negative associations were obtained between their activity patterns only at the SL50_B and SL59 ($p< 0.05$), highlighting that a distinct temporal partitioning happened between these species, only in using these two saltlicks, in response to this interspecific competition. This was because the activity patterns of Sambar Deer in using the SL50_A and SL56 were negatively associated with those of the Bornean Orangutan ($p<0.05$). The Sambar Deer avoided in using these two licks during the daytime, and also was detected majorly at night-time, and vice versa for the Bornean Orangutan, which caused the very high dissimilarity in their activity patterns for these two licks (SL50_A: Δ=0.1513; SL56: Δ=0.2419) recorded in this research. Henceforth, the Sambar Deer competed with the Bearded Pig and Bornean Orangutan, which ultimately resulted in the distinct temporal partitioning between the Sambar Deer and the Bearded Pig for using both the SL50_B and SL59, as well as with the Bornean Orangutan for the usage of both the SL50_A and SL56, at this forest reserve.

Moreover, the Sambar deer only shared a similar diel activity pattern with the Banteng, when using the SL56 (Δ=0.6821), in which they were detected similarly frequently during the daytime ($Z=-0.351$, $p=0.726$), as well as frequently during the night and twilight period in this study. However, the finding of Poisson regression analysis revealed that no significant association was obtained between these two species, thus signifying that this interspecific competition did not trigger a distinct temporal partitioning between these two ungulate species in using the SL56 in this study. Apart from that, they were verified to adopt highly dissimilar diel activity patterns in using the other three saltlicks ($\Delta<0.50$), and also their nocturnal and diurnal visitation frequencies were different significantly across all four saltlicks ($p<0.05$) and at the SL50_B ($Z=-3.974$, $p=0.002$) respectively. Nonetheless, only the activity pattern of Sambar Deer in utilizing the SL59 was found negatively associated with that of the Banteng ($p<0.001$), but not the other way around ($p>0.05$), and also not at both the SL50_A and SL50_B ($p> 0.05$). This revealed that the temporal partitioning observed between these two species was distinctive at SL56, but minor at both the SL50_A (Δ= 0.4768) and SL50_B (Δ=0.4189), in this forest reserve.

Table 5. Outcomes of the Poisson regression for predicting the influences of the interactions between the four sympatric species towards their respective adopted activity patterns for visiting to the natural saltlicks at SLFR

Species	Variables	Estimate	SE	Z	p	Estimate	SE	Z	p
SL50_A						**SL56**			
Sambar Deer	Intercept	0.743	0.196	3.791	***	2.165	0.165	13.121	***
	Bornean Orangutan	-2.135	0.813	-2.625	**	-0.376	0.069	-5.458	***
	Banteng	-0.380	0.384	-0.991	0.322	0.055	0.089	0.623	0.533
	Bearded Pig	0.462	0.256	1.794	0.073	0.001	0.034	0.041	0.967
Bearded Pig	Intercept	-0.812	0.455	-1.786	0.074	1.289	0.271	4.751	***
	Bornean Orangutan	0.664	0.187	3.540	***	0.067	0.048	1.397	0.162
	Sambar Deer	0.007	0.127	0.058	0.954	-0.015	0.029	-0.498	0.619
	Banteng	0.648	0.409	1.585	0.113	-0.017	0.102	-0.165	0.869
Banteng	Intercept	-1.217	0.660	-1.843	0.065	-0.383	0.597	-0.641	0.521
	Bornean Orangutan	-1.063	1.125	-0.945	0.345	0.128	0.082	1.555	0.120
	Sambar Deer	-0.225	0.316	-0.711	0.477	0.035	0.053	0.652	0.514
	Bearded Pig	0.536	0.440	1.219	0.223	-0.006	0.078	-0.072	0.943
Bornean Orangutan	Intercept	-1.318	0.663	-1.989	*	1.192	0.492	2.422	*
	Banteng	-0.923	0.662	-1.396	0.163	0.224	0.131	1.711	0.087
	Sambar Deer	-1.068	0.421	-2.534	*	-0.312	0.072	-4.351	***
	Bearded Pig	0.876	0.285	3.078	**	0.046	0.060	0.776	0.438
SL50_B						**SL59**			
Sambar Deer	Intercept	2.644	0.082	32.08	***	2.910	0.192	14.85	***
	Banteng	0.052	0.112	0.466	0.641	-0.762	0.128	-5.975	***
	Bearded Pig	-0.197	0.044	-4.536	***	-0.065	0.0185	-3.497	***
Bearded Pig	Intercept	1.508	0.338	4.463	***	2.483	0.138	17.95	***
	Sambar Deer	-0.114	0.035	-3.299	***	-0.024	0.012	-2.023	*
	Banteng	0.234	0.185	1.266	0.206	-0.166	0.095	-1.748	0.080
Banteng	Intercept	-2.490	1.348	-1.847	0.065	0.709	0.518	1.369	0.171
	Sambar Deer	0.025	0.083	0.301	0.764	-0.096	0.049	-1.955	0.051
	Bearded Pig	0.449	0.247	1.818	0.069	-0.046	0.046	-1.003	0.316

*Note: SE=Standard Error; Z=Z-Score, and; p=Level of significance (*p<0.05; **p<0.01; ***p< 0.001).
This table only displays the prediction models determined with the lowest values of AIC. The Bornean Orangutan is not included as a predictor variable for both the SL50_B and SL59, due to its small sample size (n<2) recorded at these two natural saltlicks in this study.

DISCUSSION

Relationship between the Saltlicks and Terrestrial Mammals

The Bearded Pig, Bornean Orangutan and Sambar Deer of SLFR were determined to generally adopt similar diel activity patterns, but different in their frequencies, in using the four natural saltlicks assessed in this research. Habitat disturbance caused by human activities (e.g.: illegal hunting, timber harvesting and forest plantation) can stimulate the Sambar Deer to adopt permanent nocturnality, just to avoid in contacting humans at daytime, when using the local lick (Matsubayashi et al., 2007b; Hon & Shibata, 2013; Ning, 2017; and Ota et al., 2019). The SL50_A is the closest lick to the secondary road, thus it is highly accessible by humans, which can subsequently trigger the Sambar Deer to avoid in using this saltlick frequently at this forest reserve. Likewise, the predation risk at a saltlick is higher in the disturbed natural forests than in the timber plantation forests, for the Bornean Clouded Leopard (*Neofelis diardi borneensis*), which is the natural predator for the juveniles of large Bornean terrestrial mammals, majorly inhabits the disturbed and undisturbed natural forests (Ross et al., 2013; Hearn et al., 2018; and Phillipps & Phillipps, 2018). Therefore, the Sambar Deer may prefer to use the SL50_B more frequently than both the SL56 and SL59, to avoid encountering its natural predator in this forest reserve (Wilting & Azlan, 2010; Kee et al., 2018; and Thinley et al., 2020).

Actually, this prey-predator relationship can explain the low visitation frequencies of Bearded Pig to the four selected natural saltlicks at SLFR at night-time, which is the main active period of the Bornean Clouded Leopard (Ross et al., 2013; and Hearn et al., 2018). The Bearded Pig is attracted to and frequently visits

Locations with high food or sodium availability (Matsubayashi et al., 2007a; and Phillipps & Phillipps, 2018). With a higher variation and abundance of invertebrates and understorey vegetation can be found at the post-selectively-logged natural forests with high canopy openness, thus further forest regeneration can reduce the local canopy gaps and ultimately the local food availability (Wearn et al., 2017). This can attract the Bearded Pig to travel to the partially-disturbed natural forests more frequently, which can subsequently result in its higher visitation frequency to the SL59, than to the SL56 surrounded by a least-disturbed forest, although further study should be conducted to verify this matter scientifically in future. The Bornean Orangutan, on the other hand, was detected only once at the SL59 and was absent from the SL50_B, mostly to avoid competing with the Sambar Deer and Bearded Pig respectively (MacArthur & Levin, 1967; Frey et al., 2017; and Lim & Mojiol, 2022). At the same time, not only that this primate species prefers to inhabit the least-disturbed and undisturbed natural forests with higher food and shelter availabilities, but also it prefers to utilize the licks that are hardly accessible by humans (Matsubayashi et al., 2011; Cheyne et al., 2016; and Seaman et al., 2019). Since the Bornean Orangutan is visual-dependent for movement and foraging, hence its activity level is positively associated with the solar illumination (Phillipps & Phillipps, 2018). These resulted in the Bornean Orangutan adopted both crepuscularity and diurnality in utilizing both the SL56 and SL50_A at different frequencies in this forest reserve.

The activity pattern of Banteng in visiting each of the four selected natural licks at SLFR was verified as cathemeral, which contrasted with the finding of Lim and Mojiol (2022), because this past study only assessed its diel activity pattern in using all four licks as a whole, which was different from this research. The Banteng is naturally a cathemeral species, but it is mainly active in visiting an open space for foraging and conducting social activities in the twilight period (Prosser et al., 2016). Hence, the abundance of food (shrubs and grasses) and minerals in the open environment of a natural saltlick can entice this ungulate species to visit the area, particularly at dawn and dusk (Clayton & MacDonald, 1999; and Chew et al., 2014). However, this phenomenon occurs mostly in the least-disturbed forests that are seldom disturbed by humans, which can explain its generally higher visitation frequencies to the SL56 and SL59 at dawn and dusk respectively in this research (Gardner et al., 2018; and Rahman et al., 2019). Moreover, the preferred habitat for Banteng is similar to that of the Bornean Orangutan, which can result in its low visitation frequencies to the SL50_A and SL50_B, where the surrounding timber plantation forests have low food availability (Wearn et al., 2017; and Rahman et al., 2019). In fact, the dissimilarities in its activity patterns between the SL50_B with the SL50_A and SL59 were caused by its zero-detection at the SL50_B during the twilight period, signifying its lower dependency on the given two licks than the other three sympatric species for replenishing body minerals regularly (Lim & Mojiol, 2021), although the given matter should be further validated in future.

Correlation between the Interspecific Competition and Temporal Partitioning

Among the four large threatened mammal species examined in this research, only two species were competing with one another for the use of certain natural saltlicks at SLFR, and also the temporal partitioning was confirmed to be distinct only between certain two sympatric species. The Banteng is larger than the other three sympatric species with similar body sizes, particularly of the same sex and age (Phillipps & Phillipps, 2018). Therefore, the smaller-sized species are intimidated by its presence, such as the nocturnal Sambar Deer that avoided in using the SL59 during the active visiting hours of the cathemeral Banteng (Hearn et al., 2018; Thinley et al., 2020; and Lim & Mojiol, 2021). However, their respective diel activity patterns in using each lick are majorly defined by other biotic and abiotic factors, which can consequently result in the high similarity in their diel activity patterns only in using the SL56, but not to the other three licks at SLFR (Wearn et al., 2017; Hearn et al., 2018; and Rahman et al., 2019). Actually, this phenomenon can also cause the Banteng, Bornean Orangutan and Bearded Pig to adopt similar diel activity patterns, as well as trigger the Sambar Deer to exhibit different diel activity patterns than the Bearded Pig and Bornean Orangutan, when using these four saltlicks.

The diel activity pattern adopted by a certain mammal species reflects its capability to survive at a habitat, under the local environmental conditions that are persisted in long-term (Kronfeld-Schor & Dayan, 2003; and Gerber et al., 2012). The anthropogenic disturbance can alter the existing forest structure and vegetation composition at a habitat, which can alter the local resource availability (food and shelter) and predation risk, and subsequently defining the survivality of the given species at this habitat (Ross et al., 2013; Wearn et al., 2017; and Gardner et al., 2018). The interspecific competition, on the contrary, only triggers two sympatric species to readjust their visitation frequencies to a certain area at a specific time period, thus the variability may only be minor, when compared to the changes caused by the other mentioned biotic and abiotic factors (Ikeda et al., 2016; Chen et al., 2019; Ota et al., 2019; and Rahman et al., 2019). Therefore, the temporal partitioning triggered by the interspecific competition can be minor, as long as the different species of terrestrial mammals can coexist with one another when sharing the usage of a certain area for survival, under a state of equilibrium (MacArthur & Levin, 1967; and Frey et al., 2017). The given matters can explain the observations recorded in this research, where the difference in diel activity patterns between two of the four sympatric species are most likely triggered by the existing habitat conditions, anthropogenic disturbance and predation risk, instead of the interspecific competition (Hon & Shibata, 2013; Chen et al., 2019; Ota et al., 2019; and Thinley et al., 2020), although it is essential to conduct further verification in future.

Regarding the variability in visitation frequencies of the four large threatened mammal species to the four natural saltlicks evaluated in this research, this phenomenon is expected to be triggered by the difference in their levels of lick dependency for regular mineral intake (Matsubayashi et al., 2007a; Lim et al., 2020; and Lim & Mojiol, 2022).

The visitation frequency of a species to a saltlick is closely related to the adopted diel activity pattern, thus the visitation frequencies can be further varied among different species at a specific time of the day (Matsubayashi et al., 2007b; Ikeda et al., 2016;

and Ning, 2017). Henceforth, the present findings indicated that the nocturnal Sambar Deer exhibited the highest level of lick dependency, because it used the licks at SLFR most frequently at night, followed by the diurnal Bearded Pig, diurnal Bornean Orangutan, and the cathemeral Banteng, which agreed with the findings of past research (Lim et al., 2020; and Lim & Mojiol, 2022). Likewise, the difference in diel activity patterns caused the lick-dependent Sambar Deer and Bearded Pig to dominate the usages of SL50_B and SL59 respectively, thus the avoidance of Bornean Orangutan in using these two saltlicks, and also its high visitation frequencies to the other two saltlicks, could be a sign of niche partitioning that is triggered by the interspecific competition between this primate species with the other ungulate species (MacArthur & Levin, 1967, Hon & Shibata, 2013; Frey et al., 2017; and Lim & Mojiol, 2021). Still, it is vital to conduct an in-depth research for examining this matter at these four licks in future.

CONCLUSION

Evidences are attained in this study to proof the competitive interactions only between two of the four large threatened mammal species for the usages of four natural saltlicks that are presented in SLFR. Nonetheless, the existing habitat conditions, anthropogenic disturbance and predation risk are likely to alter their respective diel activity patterns, which can ultimately result in a distinct temporal partitioning, only between the nocturnal Sambar Deer with both the diurnal Bearded Pig and Bornean Orangutan, in using the local licks. The impact of interspecific competition, on the contrary, can only cause a minor temporal partitioning between specific two sympatric species with similar diel activity patterns, such as the Banteng, Bearded Pig and Bornean Orangutan, in using a given saltlick at SLFR. The mammalian visitation frequency is dependent onto the adopted diel activity pattern, and also the level of lick dependency level for regular mineral intake, thus can result in the variability in visitation frequencies between the four sympatric species across different saltlicks and times of the day at SLFR.

The anthropogenic disturbance exhibits both direct and indirect negative impacts onto the diel activity pattern and ultimately the visitation frequency of a given mammal species to a certain saltlick (Blake et al., 2013; Matsuda et al., 2015; Ning, 2017; and Thinley et al., 2020). However, a permanent distinct alteration in the diel activity pattern will happen, only when the influence of anthropogenic disturbance is long-term and prominent to the local survivality of the given species (Kronfeld-Schor & Dayan, 2003; Gerber et al., 2012; Ikeda et al., 2016; and Ota et al., 2019). Henceforth, the species composition of mammalian community, as well as the interspecific interactions between the members of this community, are determined by the anthropogenic disturbance, which can be regulated through forest conservation and rehabilitation efforts (Hon & Shibata, 2013; Hearn et al., 2018; Lazarus et al., 2019; Razali et al., 2020; and Lim & Mojiol, 2021). In a nutshell, the present findings emphasize the importance of regulating the long-term influence of anthropogenic disturbance to the activity patterns of large threatened mammals in using the tropical saltlicks, especially at a commercial forest reserve with the timber harvesting and forest plantation operations persisted throughout the year.

However, the impacts of anthropogenic disturbance, existing habitat conditions and predation risk onto the activity patterns of the four sympatric species in utilizing a natural saltlick at SLFR are only based on the assumptions suggested by past findings (e.g.: Wearn et al., 2017; Hearn et al., 2018; Griffiths et al., 2020; and Lazarus et al., 2021). The Bornean Clouded Leopard was not sighted at the four assessed local saltlicks (Bernard et al., 2019; Lim et al., 2020; and Lim & Mojiol, 2022), and the effect of anthropogenic disturbance onto the shaping of local mammalian activity pattern in using the given four licks has yet been examined scientifically as well. Although the activity pattern of Bearded Pig in visiting a certain location is known to be influenced by the local resource availability (Hon & Shibata, 2013; Matsuda et al., 2015; and Phillipps & Phillipps, 2018), still the extent of influence of this relationship onto its activity pattern in using a certain saltlick remains uncertain, not only at SLFR, but also at the other forested areas of Sabah. Likewise, the avoidances of Bornean Orangutan in using the SL59 and SL50_B are assumed to be a sign of niche partitioning with the Bearded Pig and Sambar Deer respectively (MacArthur & Levin, 1967; and Frey et al., 2017), and then the low frequencies of Banteng in visiting both the SL50_A and SL50_B may indicate its low dependencies onto these two saltlicks (Lim & Mojiol, 2021). Nevertheless, there may be other biotic and abiotic variable that can potentially cause the occurrence of this situation in this forest reserve. Therefore, further research is required to be conducted onto these four large threatened species, not only at the given four licks, but also at the other natural licks in SLFR, to address these research gaps in future. In the end, the present findings are aligned with the proposed hypotheses, and then the research objective is achieved.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Mr. Lim Wing Shen plays an important role in conducting the camera trapping survey at the four selected natural saltlicks in SLFR, and also in processing and analysing the camera trap data. Dr. Andy Russel Mojiol, on the other hand, mainly writes up and proof-reads the manuscript of this study.

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