

Research Article

Links between bushmeat species occupancy and indigenous hunting: a pilot study from Royal Belum State Park, Peninsula Malaysia

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ABSTRACT

Indigenous communities have been hunting bushmeat species in the tropical forests of South East Asia for over 40,000 years. Today however, many bushmeat species are threatened by unsustainable hunting compounded by the pressures of decreasing forest area and growing human populations. This pilot study aimed to investigate the relationship between the Jahai, an indigenous hunter gatherer tribe and the mammal bushmeat species which they hunt in Royal Belum State Park (RBSP), peninsula Malaysia. A wildlife triggered camera survey was conducted between early May and late June 2018, from which data was used to calculate occupancy predictions for observed Jahai hunters and bushmeat species. Four mammal species occupancy were found to be associated with Jahai hunting pressure, all of which were preferred species among Jahai communities. Species richness of bushmeat species was also found to increase with Jahai occupancy while species diversity index declined, suggesting that Jahai hunting pressure was concentrated on a select few species, even when bushmeat species richness was high. Vegetation cover and the presence of saltlicks were significant drivers of species occupancy. Based on these findings, Jahai hunting pressure should not be disregarded as a threat to bushmeat species in RBSP.

Key words: bushmeat species, indigenous hunting, species occupancy, tropical forests

INTRODUCTION

Unsustainable hunting is a significant threat to mammal species of tropical forests globally (Ripple *et al.*, 2016). Approximately 301 mammal species are primarily threatened by human hunting, accounting for 26% of all threatened mammals listed under the International Union for Conservation of Nature (IUCN) (Ripple *et al.*, 2016). Compounded by the pressures of decreasing forest area and growing human populations, unsustainable hunting has already resulted in multiple mammal extinctions across the globe and will continue to do so if the rate of hunting persists (E. L. Bennett, 2002; Diamond, Ashmole, & Purves, 1989; Sodhi, Koh, Brook, & Ng, 2004).

Over 60 million people globally depend on the hunting of bushmeat species and the collection of forest resources (Errico, 2017). The vast majority of these people reside in South East Asia, where some indigenous communities have been hunting bushmeat for over 40,000 years (E. Bennett, J. Nyaoi, & Sompud, 2000; Corlett, 2007; Hutterer, 1988). For many South East Asian communities, bushmeat is still utilised as a primary source of protein (E. L. Bennett, 2002). However, the extension of market systems into rural forest areas has led to a significant shift in community utilisation of bushmeat towards trade and sale for cash incomes (E. Bennett *et al.*, 2000; Sunderlin *et al.*, 2005).

As reliance on bushmeat increases, there is a pressing need to evaluate the impact of hunting in remaining forest areas, as well as the consequences to human populations (E. L. Bennett, 2002). Robinson and Bennett (2000) estimated that one square kilometre of

tropical forest could sustainably support the protein needs of just one individual hunter. However, in South East Asia there is an estimated 522 people per square kilometre of remaining tropical forest (E. L. Bennett, 2002). Of that remaining forest approximately 2.7 million hectares is lost annually to expanding palm-oil, rubber and acacia plantations (FAO, 2005; Hughes, 2017).

The majority of South East Asia's most threatened bushmeat species exist only within the boundaries of protected forest reserves scattered throughout the region (Harrison, 2011). However, protected zones are not exempt from the impacts of unsustainable hunting (Corlett, 2007; Harrison, 2011). Improved infrastructure, forest degradation and rapid population growth have significantly increased the accessibility of many protected forests to commercial hunters and illegal wildlife markets (Corlett, 2007). However, a substantial threat to protected wildlife populations may already exist within reserve boundaries (Steinmetz, Chutipong, & Seuaturien, 2006).

Today, some wildlife reserves are co-inhabited by the last remaining hunter-gatherer tribes (Gomes, 2007; Nicholas, 2000; Sodhi *et al.*, 2006). Traditionally these tribes were entirely self-sufficient as they continually shifted and hunted across large areas of forest (E. Bennett *et al.*, 2000; Corlett, 2007; Nicholas, 2000). Now however, these tribes practice relatively sedentary lifestyles within increasingly smaller and fragmented reserves (Nicholas, 2000). Rapid population growth in these communities has led to a greater demand for food and income (E. Bennett *et al.*, 2000). Thus, the

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extraction rate of bushmeat has increased beyond the rate at which species are able to replenish their populations within reserves of limited carrying capacity, effectively driving many species to local extinction (Robinson & Bennett, 2000).

Now conservationists, sociologists and others are faced with the pressing need to protect the last of South East Asia's endangered mammal species whilst simultaneously addressing indigenous hunting and landuse rights (Abdullah, Ching, & Fadzol, 2011; Aziz, Clements, Rayan, & Sankar, 2013; E. L. Bennett, 2002). The impacts of indigenous hunting in South East Asia and the current status of the regions threatened species are still understudied in comparison to the multitude of studies which have arisen out of Africa and South America (Alvard, Robinson, Redford, & Kaplan, 1997; Koppert & Hladik, 1990; Nasi, Taber, & Van Vliet, 2011; Ojasti, 1996; Peres, 2000; Ripple *et al.*, 2016; Smith, 1976; Wilkie & Carpenter, 1999; Willcox & Nambu, 2007). This paper presents results from a pilot study of indigenous hunting within Royal Belum State Park, a wildlife and indigenous reserve in Peninsula Malaysia.

In 2007, the Royal Belum State Park (RBSP) was gazetted by the Perak State Government as a wildlife reserve within the greater Belum-Temengor Forest Complex (Azrina *et al.* 2011). The park is approximately 117, 000 hectares in size, of which most is relatively hilly terrain sitting at 300m above sea level (Schwabe *et al.*, 2014). Dipterocarp forests cover most of the landscape and host a rich diversity of wildlife (Clements *et al.*, 2010; Schwabe *et al.*, 2014). The only human inhabitants of the park are the Jahai, a small hunter gatherer

tribe, which constitute one of the 19 officially recognised indigenous tribes (*Orang asli*) of peninsula Malaysia (Endicott, 2016).

The Jahai are one of the last hunter gatherer tribes in Malaysia who still rely on forest resources for their subsistence (Nicholas, 2000). The Jahai hunt and utilise a wide range of mammal species from within the park (Abdullah *et al.*, 2011; Aziz *et al.*, 2013; Loke, Lim, & Campos-Arceiz, 2020). Legally however, under the sixth schedule of the 2010 Wildlife Conservation Act, the Jahai are only permitted to hunt ten species (Wild Pig, Sambar Deer, Lesser Mouse Deer, Pig-tailed Macaque, Silvered Leaf Monkey, Dusky Leaf Monkey, Malayan Porcupine, Brushtailed Porcupine, White-breasted Waterhen and Emerald Dove) for their individual consumption within RBSP.

This pilot study aimed to determine whether a significant relationship was evident between the occupancy of Jahai hunters and the bushmeat species which they target in RBSP. It was hypothesised that the occupancy of bushmeat species, particularly those considered preferable among the Jahai, would be significantly depressed in areas of higher hunting pressure.

MATERIALS AND METHODS

Study Species

The focus species of this study were mammals permitted for hunting under the 2010 Wildlife Conservation Act (Table 1). However, all mammal species recorded in this pilot study, which were known to be hunted by the Jahai, were included for analysis.

Table 1. The hunting and conservation status of the 19 species observed over the survey period. (Abdullah *et al.*, 2011; Aziz *et al.*, 2013; IUCN (International Union for Conservation of Nature), 2018)

Species Name Common (<i>Scientific</i>)	Hunted	Permitted For Hunting	IUCN Conservation Status	No. of Sites Observed	Species Occupancy Median [95% CI]
Barking Deer (<i>Muntiacus</i>)	Yes	No	Least Concern	23	0.90 [0.70, 0.90]
Sambar Deer (<i>Rusa unicolor</i>)	Yes	Yes	Vulnerable	9	0.19 [0.18, 0.49]
Lesser Mouse Deer (<i>Tragulus kanchil</i>)	Yes	Yes	Least Concern	2	0.24 [0.24, 0.43]
Wild Boar (<i>Sus scrofa</i>)	Yes	Yes	Least Concern	25	0.90 [0.81, 0.91]
Asian Palm Civet (<i>Paradoxurus hermaphroditus</i>)	Yes	No	Least Concern	2	0.49 [0.49, 0.71]*
Banded Palm Civet (<i>Hemigalus derbyanus</i>)	Yes	No	Near Threatened	1	0.49 [0.49, 0.71]*
Large Indian Civet (<i>Viverra zibetha</i>)	Yes	No	Near Threatened	1	0.49 [0.49, 0.71]*
Squirrel <i>sp.</i> (<i>Sciuridae</i>)	Yes	No	Least Concern	6	0.22 [0.20, 0.24]
Porcupine <i>sp.</i> (<i>Atherurus sp.</i>)	Yes	Yes	Least Concern	4	0.09 [0.07, 0.29]
White Thighed Surili (<i>Presbytis siamensis</i>)	Yes	No	Near Threatened	1	0.13 [0.07, 0.35]
Pig Tailed Macaque (<i>Macaca nemestrina</i>)	Yes	Yes	Vulnerable	10	0.38 [0.38, 0.43]
Sunda Pangolin (<i>Manis javanica</i>)	Yes	No	Critically Endangered	1	0.12 [0.12, 0.29]
Tapir (<i>Tapirus indicus</i>)	Yes	No	Endangered	2	0.62 [0.62, 0.68]
Asian Golden Cat (<i>Catopuma temminckii</i>)	No	No	Near Threatened	2	0.46 [0.44, 0.76]
Asian Elephant (<i>Elephas maximus</i>)	No	No	Endangered	5	0.55 [0.41, 0.85]
Seladang (<i>Bos gaurus</i>)	No	No	Vulnerable	3	0.02 [0.01, 0.04]
Sun Bear (<i>Helarctos malayanus</i>)	No	No	Vulnerable	1	0.35 [0.24, 0.37]
Tiger (<i>Panthera tigris jacksoni</i>)	No	No	Critically Endangered	1	0.46 [0.46, 0.61]

* Indicates median value for all three civet species combined.

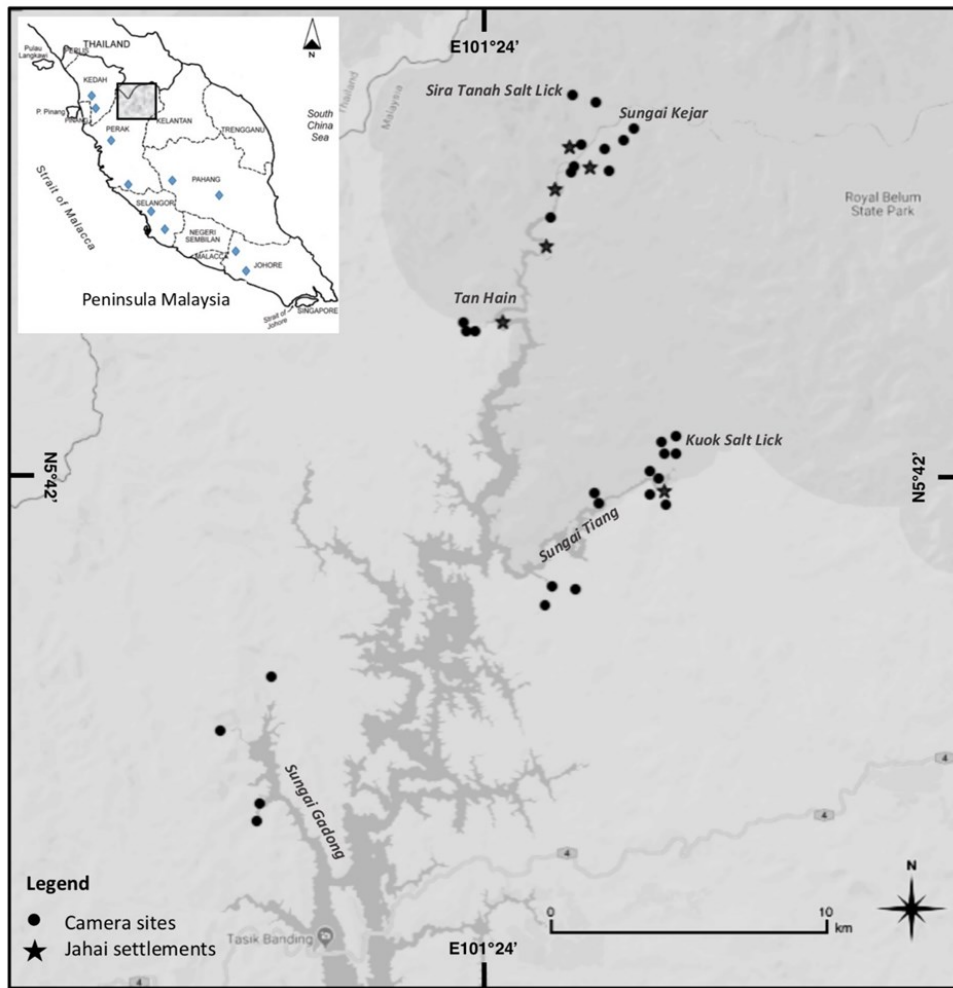


Figure 1. Map of the 30 camera sampling sites in Royal Belum State Park

Bushmeat Camera Survey

Surveying was conducted from May 3rd to June 24th 2018, using 38 Scout Guard SG550/SG530 motion triggered infrared cameras, set to detect species at a range of up to 15 meters. This six week period was considered as a long enough period to detect fauna, but short enough not to violate the assumption of a closed population for occupancy modelling (see below). Cameras were set to take three photos when triggered, immediately followed by a three-minute sleep interval. A total of 16 cameras were placed along pre-existing animal trails spanning 20km along the northern Kejar tributary running past five Jahai settlements. Another 10 cameras were placed along trails spanning 20km along the southern Tiang tributary which is occupied by only one Jahai settlement. Four cameras were also deployed around the head of the southern Gadong tributary where there are no Jahai settlements or known indigenous hunting. Two saltlicks, Sira Tanah and Kuok, were also sampled with four cameras in each (Figure 1).

Each camera was attached to a tree trunk approximately one meter above the forest floor and positioned facing down the animal trail capturing the forest floor and the trunks of neighbouring trees. This design optimised the probability of capturing both ground dwelling species, such as deer and porcupine, as well as species, such as macaque and squirrel, which were often seen moving up and down neighbouring tree trunks. Due to the density of the vegetation within the park and restricted access points into the vegetation from the river,

camera deployment sites were opportunistically selected within 500m of water access.

Site Surveys

Canopy cover at each site was estimated by holding a 30cm x 30cm frame directly above each camera and recording the percentage of the frame filled by the canopy vegetation. The percentage cover of understorey and ground vegetation was estimated within a 20m circumference of each camera. Ground cover was defined as vegetation up to 0.25m in height, while understorey cover was defined as vegetation between 0.25-2m in height. The straight-line distance to the nearest village from any given camera site was estimated using google earth and the co-ordinates taken by GPS at each camera and village site (Google Inc., 2018). However, straight line distance does not directly represent the exact distance travelled by hunters given that on foot, hunters must cross relatively hilly terrain and various geographical obstacles. The Jahai sometimes use small watercraft as transport, the use of waterways can increase the distance travelled but increase the ease of access.

Data Curation

The presence or absence of each mammal species was recorded for every 24 hour period for all individual cameras over the total six weeks, assigning a value of one (1) if the species was present or zero (0) if it was absent. All fauna observed were recorded to the species level, with the exception of squirrel (*Sciuridae sp.*) and

porcupine (*Atherurus sp.*) which were amalgamated at the genus level due to difficulty differentiating between species. Civet species were also amalgamated due to small sample sizes captured for each individual species.

Occupancy Modelling

A species is determined present when it is detected at a site, however non-detection of the species at the same site does not necessarily infer that the species is absent (MacKenzie, 2005). Rather than assigning a binary presence or absence to each species, occupancy models predict the probability of a species being present at a site, based on the detection history of the species at the given site (MacKenzie, 2005). Occupancy models are based on the assumptions that populations are closed, sites are independent and there is no unexplained heterogeneity in species occupancy and detectability across sites (MacKenzie, 2005). To accommodate the assumption of site independence for some cameras which were located within a short distance of one another, a spatial heterogeneity variable was built into the model to allow the measurement of any potential spatial dependence (Comer *et al.*, 2018). The model was run in WinBUGS (v14), as outlined by Comer *et al.* (2018).

Occupancy probabilities were produced for each species at each camera site. The occupancy of Jahai was also calculated for each site and used as a surrogate for hunting pressure. The use of occupancy as a surrogate for hunting pressure was not ideal as it assumes that the presence of Jahai is related to hunting, while it is possible that they were in transit to another area or gathering plant material. Therefore, estimates of hunting activity may be overestimated. Sites with Jahai occupancy greater than 0.5 were considered areas of high hunting pressure, while camera sites with Jahai occupancy lower than 0.5 were considered as areas of low hunting pressure.

Data Analysis

All species occupancy values were log transformed to conform to a normal distribution. Species richness, Shannon-Weiner diversity index (H) and community composition were calculated for each camera site using the statistical software package Primer 6 (Clarke & Gorley, 2006). Community composition was defined as the list of species present at each site. Species occupancy, richness, diversity index and community composition were then tested against vegetation cover and distance to the nearest Jahai village using linear regressions in the statistical package R and a permanova for community data in Primer 6 (R Development Core Team, 2008). Species variables and community composition were also tested for differences between tributaries, to account for possible inter-tributary variations in Jahai hunting practices (non-parametric Anosim).

Sites with and without saltlicks were also compared for differences in species occupancy, richness, diversity index, community composition, vegetation cover and Jahai occupancy (non-parametric Anosim and Wilcoxon-Rank Sum Test). Saltlicks are known to exaggerate the occupancy of certain species which are drawn to their mineral properties (Blake *et al.*, 2010). Hence, saltlick sites were removed for any species found to be significantly affected, so as to reduce the risk of masking any potential relationship between species occupancy and hunting pressure. After controlling for the effects of saltlicks, species occupancy, species richness, species

diversity index and community composition were tested for differences between sites of high and low hunting pressure (non-parametric Anosim).

RESULTS

Of the 38 cameras which were used in the bushmeat survey, four were lost on site most likely as a result of interference from Asian elephants and/or Jahai children. Additionally, another four cameras malfunctioned during the survey period possibly due to water logging. The remaining 30 cameras were used in the analysis. Of those cameras, 23 recorded data for the full 52 day survey period, while seven stopped recording prematurely between 15 and 38 days, for various reasons including interference from wildlife, waterlogging and battery failure. Data obtained before the cameras malfunctioned was still included in the analysis as the model was able to deal with null records.

Over the maximum six week survey period a total of 19 identifiable mammal species were recorded across the 30 camera sites, including 13 species which are hunted by the Jahai for subsistence purposes (Table 1). Small rodent, bat and bird species were also observed across multiple cameras, although, due to the relatively low resolution of the camera photos, species were unable to be accurately identified, therefore they were not included for analysis.

Wild boar and barking deer were the most common species observed in this survey, present at over 75% of camera sites. While a multitude of other less common species such as the banded palm civet (*Hemigalus derbyanus*) and the white-thighed surili (*Presbytis siamensis*) were observed less than five times across the survey period. Two near threatened species, which are permitted for hunting but were not detected in the survey include the dusky leaf monkey (*Trachypithecus obscurus*) and silvered leaf monkey (*Trachypithecus cristatus*). The black giant squirrel (*Ratufa bicolor*), one of the Jahai's most preferred bushmeat species (Aziz *et al.*, 2013; Loke *et al.*, 2020), was also not detected in the survey.

The straight-line distance between any given camera site and the nearest Jahai village, ranged from 287m to 18,883m (mean (SE) = 3,871(1,060)). Proximity of cameras to Jahai settlements did not significantly explain any variation in community composition ($p > 0.25$), species richness ($p > 0.81$, $R < 0.01$) or species diversity index ($p > 0.68$, $R = 0.05$). However, the occupancy of pig-tailed macaque did increase significantly with increasing distance from Jahai villages ($p < 0.03$, $R = 0.50$). Comparatively, the highest occupancy of squirrel *sp.*, civet *sp.* and lesser mouse deer were recorded less than 1500 meters from the Tiang settlement, the largest Jahai settlement in the park.

The percentage of vegetation cover at each camera site was a significant driver of species occupancy. Wild boar and lesser mouse deer both decreased in occupancy as the percentage of canopy cover increased across camera sites (wild boar, $p < 0.01$, $R = 0.25$; mouse deer, $p < 0.04$, $R = 0.15$). A similar negative relationship was also present in the occupancy of lesser mouse deer, monkey *sp.* and tapir with increasing understorey vegetation (mouse deer, $p < 0.03$, $R = 0.16$; monkey *sp.*, $p < 0.01$, $R = 0.20$; tapir, $p < 0.01$, $R = 0.20$). Only civet *sp.* appeared to be related to ground cover vegetation, with occupancy again decreasing with increasing ground cover ($p < 0.03$, $R = 0.15$).

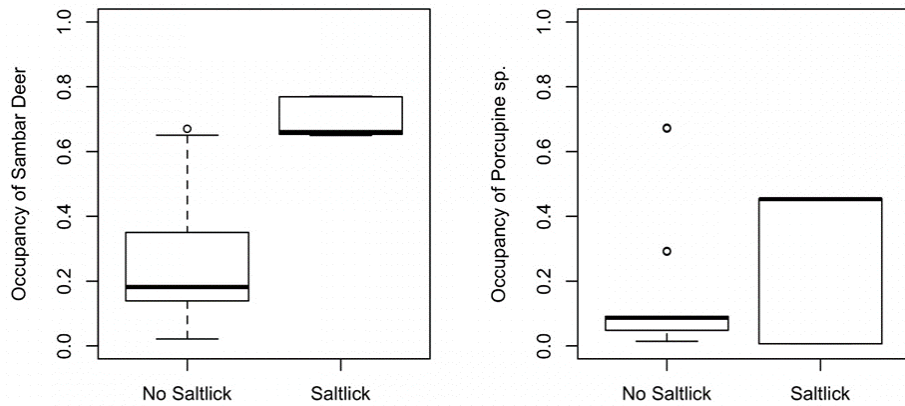


Figure 2. Species occupancy between sites with and without saltlicks.

The presence or absence of saltlicks also explained some of the variation in vegetation structure and species occupancy between survey sites. The six sites where saltlicks were present, had significantly reduced ground cover vegetation in comparison to the other 24 sites ($p < 0.04$). Sambar deer and porcupine *sp.* were also found in higher occupancies at sites containing saltlicks compared to sites without (Figure 2; sambar deer, $p < 0.04$; porcupine *sp.*, $p < 0.01$). However, saltlicks were not significantly related to community composition ($p > 0.43$), species richness ($p > 0.47$) or species diversity index ($p > 0.42$), nor was there a significant relationship with the occupancy of Jahai hunters ($p > 0.42$). All saltlick sites registered as areas of low hunting pressure, with Jahai occupancy remaining consistently below 0.5 (median [95% CI], 0.36 [0.04, 0.36]).

For select species, trends in occupancy clearly differed between tributaries, although, these differences were marginally non-significant. At sites along Sungai Kejar, the median [95% CI] occupancy of sambar deer (0.47 [0.18, 0.65]), pangolin (0.30 [0.08, 0.35]) and tapir (0.62 [0.01, 0.99]), were significantly higher compared to sites along Sungai Tiang (sambar, 0.18 [0.09, 0.65], $p > 0.17$; pangolin, 0.12 [0.10, 0.12], $p > 0.13$; tapir, 0.63 [0.62, 0.68], $p > 0.2$). The opposite trend was reflected for wild boar which had a considerably higher median occupancy along Sungai Tiang compared to Sungai Kejar (Tiang, 0.91 [0.81, 0.95]; Kejar, 0.71 [0.58, 0.91], $p > 0.46$).

Although the Jahai are known to hunt at 26 of the 30 survey sites, hunters were only observed at 10 of those sites (median [95% CI] occupancy 0.30 [0.23,

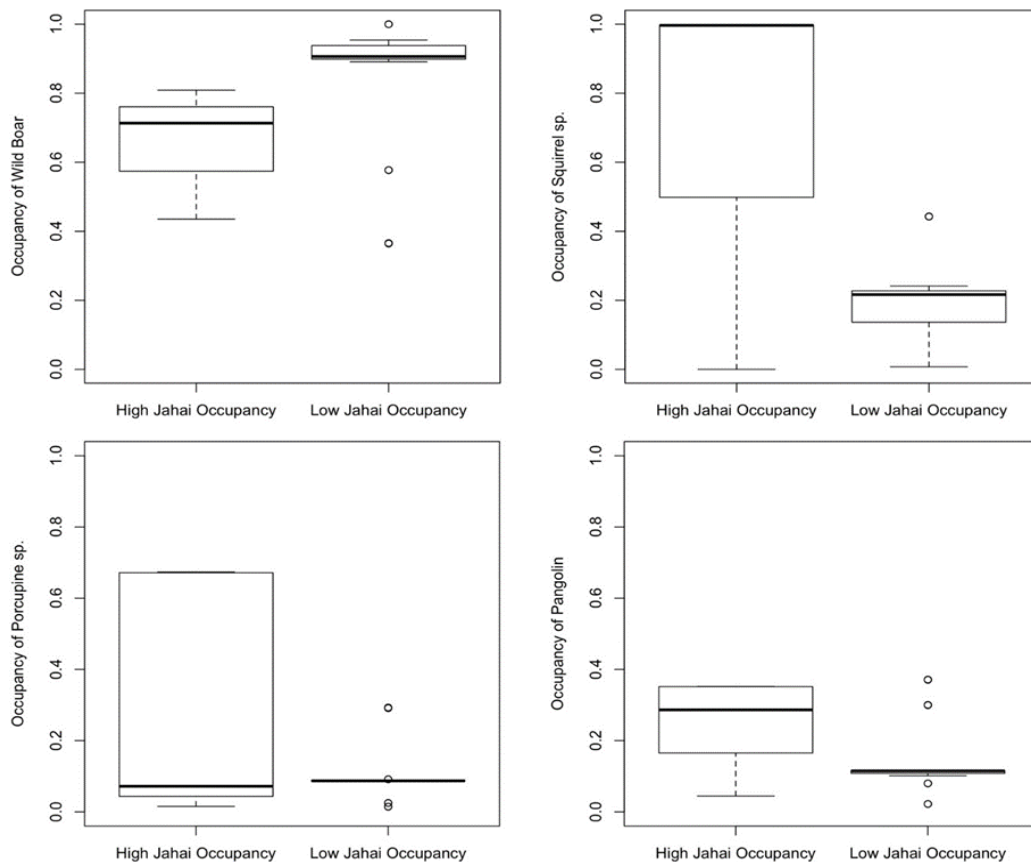


Figure 3. Species occupancy between sites of high and low Jahai occupancy.

0.48]). Jahai occupancy did not vary significantly with the presence or absence of saltlicks ($p > 0.42$) nor with proximity to Jahai villages ($p > 0.64$, $R = 0.01$), indicating that distance was not a good indicator of Jahai hunting pressure. However, the median Jahai occupancy was higher at sites along Sungai Tiang (0.36 [0.36, 0.64]) where the largest Jahai settlement in RBSP is located, in comparison to sites located along Sungai Kejar (0.23 [0.05, 0.47]), which is occupied by multiple small villages.

The median occupancy of boar was significantly lower at sites with high hunting pressure compared to sites of low pressure (Figure 3; $p < 0.01$). In contrast, squirrel *sp.* ($p < 0.001$), porcupine *sp.* ($p < 0.01$) and pangolin ($p < 0.01$) were all present in significantly higher occupancies at camera sites with high hunting pressure (Figure 3). Species richness was found to increase with Jahai occupancy ($p < 0.001$, $R = 0.32$), while species diversity (H) contrarily declined ($p < 0.001$, $R = 0.32$), indicating increasing dominance in terms of abundance of only a few species. A marginally non-significant result was also detected for civet *sp.* ($p > 0.08$), which again had a higher median [95% CI] occupancy at camera sites with high Jahai occupancy (0.88 [0.03, 0.89]) compared to sites with low Jahai occupancy (0.49 [0.49, 0.52]).

DISCUSSION

Despite the large range of mammal species detected in this study, only four were significantly related to Jahai occupancy (used as a surrogate for hunting pressure), all were preferred species among one or more Jahai villages. At the community level this relationship was reflected by an increase in species richness and contrasting decrease in diversity index with increasing Jahai occupancy. This suggests that even when species richness was high, Jahai hunters were only targeting select species. This kind of hunting behaviour would likely cause the occupancy of non-target and hunting tolerant species to increase, while the occupancy of target species would expectedly decrease, effectively lowering the evenness of species occupancy at the given site. These trends are consistent with numerous other studies which have shown that tropical forest hunters will consistently target a narrow range of preferred species, regardless of their local abundance or extinction probability (Bodmer, 1995; Fa & Peres, 2001; Hawkes, Hill, & O'Connell, 1982; Vickers, 1991).

The significant relationships detected in this study between species occupancy and Jahai occupancy may provide some indication as to which species are considered preferable among Jahai hunters and are consequently targeted. Squirrel *sp.*, porcupine *sp.* and pangolin all recorded a significantly higher occupancy at sites of high Jahai occupancy. This may indicate that Jahai hunters are selectively targeting sites known to have greater occupancies of these species which would align with findings from Abdullah *et al.* (2011) and Loke *et al.* (2020) in which Jahai hunters reported these species as three of the most preferable and highly targeted species in the park. Given the relatively small sample size collected for these species, specifically pangolin, the significance detected may be a result of low statistical power.

Assuming the significance detected does reflect a true effect, these findings may indicate that Jahai bushmeat preferences are skewed towards smaller

species. Preference for small species is uncommon among other tropical hunting communities where large mammals (>5kg) are typically preferred so as to obtain the greatest amount of meat per unit of hunting effort or time allocated (Bodmer, 1995; Jerzolimski & Peres, 2003). Larger species such as elephants, gaur, tiger and tapir are less frequently hunted than smaller species such as giant squirrel and deer (Loke *et al.*, 2020). Studies in other areas have found only upon the depletion of large mammals, have some hunting communities been found to allocate higher amounts of hunting effort to small species (Hames & Vickers, 1982; Jerzolimski & Peres, 2003; Smith, 1976; Suárez, Stallings, & Suárez, 1995). Jahai bushmeat preferences are unlikely to be a response to the depletion of larger mammals, given that both wild boar and barking deer were the most common species detected in this study.

Wild boar occupancy was significantly lower at sites of high Jahai occupancy. Boar is considered a highly preferable source of food among Jahai communities (Abdullah *et al.*, 2011). Compared to squirrel *sp.*, porcupine *sp.* and pangolin, the need for hunters to selectively target sites known to be occupied by boar is likely redundant, given the wide spread and relatively consistent occupancy of this species across the majority of survey sites. In contrast, the high level of variability in occupancy for other preferable species such as barking deer, may account for the lack of significant difference detected between sites of high and low Jahai occupancy. Alternatively, any significant relationship between Jahai occupancy and the occupancy of these species may have been masked by a number of uncontrolled sources of variation.

Vegetation cover was found to be negatively related to the occupancy of at least five observed bushmeat species, possibly indicating that as vegetation cover increased the detection probability of species decreased. Consequently, this relationship may have weakened the link between species occupancy and Jahai hunting pressure at sites where vegetation was dense. Salt licks which were included as known hunting sites, were also found to significantly bias the occupancy of porcupine *sp.* and sambar deer. While the effects of the two saltlicks recorded in this survey were controlled for, there were possibly other saltlicks in proximity to non-saltlick camera sites which were not accounted for. Klaus, Klaus-Hugi, and Schmid (1998) suggests that the presence of saltlicks can significantly influence the density and carrying capacity of herbivorous mammals in the surrounding forest area and these effects may vary seasonally with the availability of fruit. Hence multi-seasonal research is needed to determine the reach of saltlick effects in RBSP.

Given that at least two variables in this study were found to potentially confound the link between species occupancy and Jahai occupancy, in conjunction with the small sample sizes collected for some species, the lack of significance detected in species occupancy between sites of high and low Jahai occupancy should be interpreted with caution. Even small amounts of hunting pressure have been found to significantly deplete and endanger ungulate populations due to their slow reproductive rates (Bodmer, 1995; Bodmer, Fang, Moya, & Gill, 1994; Naranjo & Bodmer, 2007). Therefore, given that many species are already threatened, and the results of this study suggest that hunting pressure is linked to the occupancy of preferred species, hunting pressure should not be disregarded as a threat to

all species considered preferable by the Jahai without further long-term species-specific research.

Although differences in species occupancy between rivers were not statistically significant, most likely due to small sample sizes, the trends observed in this study do indicate the presence of inter-tributary variations which require further investigation. The majority of Jahai along Sungai Kejar practice a unique form of animism, encompassing a number of different food taboos (Bolton, 1972), which are not uncommon among other indigenous communities (Begossi, Hanazaki, & Ramos, 2004; Bolton, 1972; Luzar, Silvius, & Fragoso, 2012; Meyer-Rochow, 2009). These taboos often restrict select species from being hunted and eaten particularly by menstruating women and young children, providing an effective form of bushmeat regulation and conservation (Balée, 1985; Bolton, 1972). This may partially explain why sambar deer was relatively more abundant along Sungai Kejar, where it is considered a taboo species, compared to sites along Sungai Tiang (Mr Hassan 2018, pers.comm, May 11). In the Tiang settlement, many Jahai have converted to Islam which could potentially dissolve the traditional food taboos and consequently the protection of taboo species such as sambar deer (Nicholas, 2000). Islamic beliefs prohibit the consumption of wild boar, which possibly explains why the median boar occupancy was much higher for Sungai Tiang, compared to Sungai Kejar where boar is still widely eaten (Mr Hassan 2018, pers.comm, May 11).

It should not be assumed that the influence of other religions will certainly dissolve traditional food taboo's or culture as some authors have previously suggested (Redford & Robinson, 1987; Yost & Kelley, 1983). The implications of religion on wildlife populations and hunting practices are unstudied in RBSP. It is still unclear as to whether the Jahai consider the hunting or protection of some species a part of their culture or alternatively they may feel released from the observation of food taboos upon conversion to other religions. The latter could pose a serious threat to vulnerable species in the park which have previously been protected under animist food taboos. Luzar *et al.* (2012) found in his study of Amazonian indigenous communities, that food taboos were still perceived and observed as part of traditional culture even after communities had converted to evangelical Christianity. These contrasting findings in accordance with trends from this study, only highlight the need for a deeper understanding of the Jahai's perspective on culture and wildlife conservation.

Variations in bushmeat utilisation between Jahai communities could also be a possible driver of bushmeat occupancy in the park. In this study, commonly hunted trade species including pangolin, tapir and sambar deer were recorded in relatively lower occupancies at sites close to the Tiang settlement. Anecdotal evidence suggests that a higher proportion of men from this settlement hunt for trade purposes compared to those from settlements along Sungai Kejar where bushmeat is primarily hunted for personal consumption. However, this trend may also be the result of the confounding effects of population size and the number of active hunters in each settlement, which would align with the significantly higher median occupancy of Jahai hunters along Sungai Tiang. Alvard *et al.* (1997) suggests that the hunting of large mammals is not sustainable unless catchment size expands accordingly with the population size of the settlement. However, expansion is not necessarily possible in a relatively small park such

as RBSP and consequently large settlements such as Tiang may already be hunting and utilising more meat than is sustainable within their catchment area, hence the depressed occupancy of large mammals.

Pig-tailed macaque was the only bushmeat species which followed the expected trend of increased occupancy with distance from Jahai villages. While macaque is permitted for hunting, it is not considered a preferable food species among the majority of Jahai communities (Loke *et al.*, 2020), thus the detected gradient was unlikely a result of hunting activity. Jahai occupancy did not vary significantly with distance from villages, showing distance to be a poor predictor of Jahai hunting pressure. Any effect of distance if present was most likely masked by the effects of the flooding of the river valleys with the construction of the water resource dam and the consequent use of motorised boats, which are becoming common place among many hunting communities (E. Bennett *et al.*, 2000). The use of boats has allowed hunters to travel further within the park to previously unreachable forest areas where there are higher abundances of bushmeat (Jerozolinski & Peres, 2003). Such widespread hunting activity is sure to negatively affect source sink dynamics which may have previously repopulated consistently hunted areas (Novaro, Redford, & Bodmer, 2000).

The findings from this pilot study highlight the need to understand the relationships between fauna and indigenous hunting within the constrained boundaries of the park (and also the complex relationships with people, fauna and landuses outside the park). Simply removing species from a list of permitted species is not guaranteed to reduce hunting pressure on these species particularly if they are considered culturally significant, whilst adding preferred species to the list may result in even greater hunting pressure on species which are already heavily targeted.

Placing seasonal or area restrictions on some species rather than total bans could allow mammal populations time to regenerate. This solution could better encompass the wide variations in food taboo's and cultural practices between villages, allowing each community to utilise bushmeat species according to their village specific practices. Another potential solution may be to implement restrictions such as male directed hunting of ungulates, where only male deer are permitted for hunting. None of these potential restrictions are likely to be successful without greater involvement and assistance from Jahai village heads who would need to encourage these practices in their respective communities.

While restrictions may help to conserve wildlife populations in the park, they do not address the Jahai's growing demand for food as village populations continue to expand (Nicholas, 2000) or the impacts from outside the park (such as logging, poaching, landuse change (Schwabe *et al.*, 2014)). Extending RBSP's protected status to include the adjoining Temengor Forest complex to the south as well as the multiple forest corridors connecting RBSP to the sizable Taman Negara reserve, would be a significant step towards improving source sink dynamics in the region (Schwabe *et al.*, 2014). However large-scale changes are often financially and culturally complex and would require long-term coordination between the federal government and multiple state governments (Schwabe *et al.*, 2014).

In the meantime, long-term multifaceted modelling of RBSP's current source sink dynamics, taking into consideration the effects of saltlicks, population density, number of active hunters and catchment size is critical to developing more accurate estimates of hunting sustainability. Further research into village specific utilisation of bushmeat and the quantity of meat offtakes is also key to identifying which species are most at risk from indigenous hunting. In the past decade some Jahai communities have increasingly supplemented their diets with fish from the lake have also begun to rear captive bred animals such as chickens. This change in food source will reduce pressure on bushmeat species.

There is a need to protect the endangered mammal species of South East Asia, but it must also be recognised that indigenous hunting and landuse rights for sustainable income and security for indigenous communities is also a pressing need (Abdullah *et al.*, 2011; Aziz *et al.*, 2013; E. L. Bennett, 2002). While the need to address this conflict has been long recognised in Africa and South America (Alvard *et al.*, 1997; Koppert & Hladik, 1990; Nasi *et al.*, 2011; Ojasti, 1996; Peres, 2000; Ripple *et al.*, 2016; Smith, 1976; Wilkie & Carpenter, 1999; Willcox & Nambu, 2007), there is a pressing need to increase research on the issue in South East Asia as the lessons learned in these other areas may not be directly applicable.

Author Contributions

LP,PS,RK&NP all contributed to the design and planning of the project, LP,PS&RK conducted the fieldwork, LP,PS&NP conducted statistical analysis and LP,PS,RK&NP all contributed to the final paper.

Conflicts of interest

Authors declare no conflict of interest

Ethical Standards

As an observation study (using unbaited motion triggered cameras), this project was not required to submit a full University of Western Australia animal ethics committee application.

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