

# Occupancy patterns of ungulates and pig-tailed macaques across regenerating and anthropogenic forests on Borneo

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## Research Article

## Occupancy patterns of ungulates and pig-tailed macaques across regenerating and anthropogenic forests on Borneo

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### Abstract

Large seed dispersers play a key role in maintaining and restoring tree species diversity in tropical forests. These taxa may also represent important food sources for sympatric carnivores. Therefore, their occurrence and population status have implications for the health of the forest and conservation of predators. Here we examined patterns of occurrence of pig-tailed macaques (*Macaca nemestrina*), bearded pigs (*Sus barbatus*), muntjac deer (*Muntiacus* spp.), mouse deer (*Tragulus* spp.) and sambar deer (*Rusa unicolor*) across study areas on Indonesian Borneo characterised by different land use histories and forest changes. We expected that human activities, including logging and hunting, would have a negative effect on mean occupancy of these taxa. We also predicted that the relative abundance of Sunda clouded leopard (*Neofelis diardi*) would affect prey activity patterns. We conducted systematic camera trap surveys across six study areas on Indonesian Borneo and analysed data using occupancy modelling. Overall, mean occupancy probabilities for the clouded leopard's prey species within regenerating forests were comparable to those in pristine habitats, but severely decreased at a site with ongoing human disturbance (logging and hunting). Mouse deer and muntjac deer diurnal activity positively correlated with detection rates of clouded leopards across sites, whereas other prey taxa showed no significant relationship. Therefore, some taxa are able to recolonise regenerating forests relatively quickly, but their distribution is reduced when simultaneous logging and hunting occur. In addition, mouse deer and muntjac deer appear able to adjust their activity patterns in response to the risk of predation. Our results provide support for investing conservation efforts of regenerating forests on Indonesian Borneo, which benefits the conservation of important large seed dispersers including primates and ungulates. Maintaining populations of large prey taxa will be crucial for the long-term persistence of clouded leopards.

## Introduction

Forest regeneration in the tropics largely depends on interactions between plants and frugivorous animals that act as seed dispersers (Corlett, 1988; Jordano, 2000). Recent evidence showed that bird-mediated seed dispersal significantly increased plant species diversity and regeneration processes in degraded forests (Carlo and Morales, 2016). Among the terrestrial mammals, ungulates and primates represent important large-seed dispersers (Corlett, 1988). Similarly to the avifauna, mammals that are tolerant to habitat disturbance are believed to play a key role in forest regeneration due to their ability to disperse large seeds into degraded/disturbed areas (Calviño-Cancela, 2002). Therefore, their abundance in disturbed forests represent a good indicator of forest recovery potential (Lindsell et al., 2015).

Large seed dispersers also play a key ecological role in maintaining large carnivore diversity. On Borneo, seed dispersers such as pig-tailed macaques (*Macaca nemestrina*), bearded pigs (*Sus barbatus*), mouse deer (*Tragulus* spp.), muntjac deer (*Muntiacus* spp.) and sambar deer (*Rusa unicolor*), also represent the main medium/large-bodied species thought to be prey for Sunda clouded leopards (*Neofelis diardi*), the largest carnivore present on Borneo (Mohamed et al., 2009). Clouded leopards are listed as Vulnerable on the IUCN Red List of Threatened Species (Hearn et al., 2015). Habitat loss and fragmentation, as well as

poaching and disease risk are thought to be the main threats to clouded leopards (Cheyne et al., 2013; Hearn et al., 2015; Cheyne et al., 2016; Kaszta et al., 2019). Competition over prey food between carnivores and humans may also present a significant threat. Ungulates are often the main target species for hunters across Borneo (Corlett, 2007; Cheyne et al., 2016). Therefore, in addition to posing direct threats on the population of targeted species (Corlett, 2007), intensive hunting has important indirect implications on the capacity of carnivores to persist in the affected landscape.

Covering an area of 743330 km<sup>2</sup>, Borneo is the largest of the Sundaland islands. With over 190 species of mammals and 420 species of birds, Borneo is exceptionally rich in species endemism and diversity and is considered a major conservation hotspot (Myers et al., 2000; Curran et al., 2004; De Bruyn et al., 2014). However, between 1973 and 2010, logging, habitat conversion into agricultural plantations such as oil palm (*Elaeis guineensis*), and other anthropogenic activities caused the loss of 30.2% of forest cover, the majority of which occurred in the lowlands, including established protected areas (Gaveau et al., 2014). According to Gaveau and colleagues' (2014) models, nearly half of the remaining forested area on Borneo in 2010 were logged forests. In addition, re-occurring fires constitute further pressure to already vulnerable tropical forests. In 2002 alone, about 8000 km<sup>2</sup> of forest on Borneo was affected by fire (Langner et al., 2007) and these fires were repeated in 2015 with an estimated 26000 km<sup>2</sup> of forest lost (World Bank, 2015). Thus, biodiversity conservation on Borneo today heav-

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**Figure 1** – Location of study sites across Indonesian Borneo, showing one of the camera trap grid systems (Sungai Wain Protection Forest).

ily relies on managing the remaining regenerating forests, as well as the intact ones. Research that focuses on understanding the species' responses to habitat change in regenerating forests is relevant to formulating appropriate conservation interventions, for example to plan dispersal routes for enhancing species' resilience to predicted environmental changes (e.g. Struebig et al., 2015) and decrease hunting pressure.

Here we present the results of a Kalimantan-wide camera trap survey. Using occupancy modelling, we aimed to assess patterns of occurrence of the main prey species of the Sunda clouded leopard across study areas of different land use histories and forest changes. We predicted that occupancy probabilities would be lower in areas with higher human activities, based on the assumption that anthropogenic habitat change increases forest heterogeneity and reduces the availability of preferred habitat and important food sources (fruit), therefore negatively affecting the abundance and distribution of frugivorous taxa (e.g. Heydon and Bulloh, 1997). In addition, we sought to contribute to the growing literature on predator-prey spatiotemporal relationships (e.g. Ross et al., 2013) by testing the following hypothesis: due to clouded leopards on Borneo being mostly active at night (Cheyne and Macdonald, 2011; Hearn et al., 2018), prey taxa will maximise diurnal activity in response to predation risk. Thus, we predicted that diurnal activity patterns of prey species would positively correlate with density of clouded leopards, under the assumption that prey species adjust their temporal activity to minimise predation risks.

## Materials and methods

### Study sites

Our study took place across six study sites in Central and East Kalimantan (Fig. 1). The study sites comprised primary, secondary, fire-regenerating and disturbed or logged areas (Tab. 1). Bawan forest is

located c. 10 km from Bawan village, along the Kahayan River in Central Kalimantan. The forest comprises a 600 km<sup>2</sup> mosaic of lowland dipterocarp, heath and ombrogenous peat-swamp forests. Anthropogenic impacts include logging, burning and cultivations of rubber (*Hevea brasiliensis*). Hunting appears to be mainly focused on bearded pigs (Harrison et al., 2012). Globally significant species present in Bawan forest include the Bornean orangutan (*Pongo pygmaeus wurmbii*) and the Bornean agile gibbon (*Hylobates albibarbis*) (Harrison et al., 2012). Belantikan (Belantikan-Arut area, Central Kalimantan), is part of a 5000 km<sup>2</sup> hilly forest landscape that extends between West and Central Kalimantan. Approximately 6000 individuals of Bornean orangutans are believed to be present in Belantikan, representing the largest population of this species living outside protected areas (Wich et al., 2008). An iron ore mining site is present in Belantikan (outside our study grid). Although at the time of our study the site was not operational, local people complained about pollution in the river due to the mining. Other human activities in this area include selective logging and hunting. In Belantikan local people hunt for their own consumption and mainly target bearded pigs, muntjac and sambar deer. Kutai National Park is located 90 km north of Samarinda, East Kalimantan. It covers an area of 2000 km<sup>2</sup> and comprises a mosaic of pristine, secondary and fire-regenerating dipterocarp forests, coastal mangroves, heath and freshwater swamp forests. Hunting, encroachment, logging and repeated fires (incl. in 1982/83, 1997/98) have affected c. 70% of the National Park. Heavy hunting in Kutai National Park is believed to have driven the endemic Hose's langur (*Presbytis hosei canicrus*) to local extinction (Setiawan et al., 2009).

The Lesan Protection Forest, East Kalimantan, is a 110 km<sup>2</sup> large protected area connected to a larger secondary forest. Lesan comprises lowland dipterocarp and heath forests as well as hilly and montane forests. It was a logging concession until the second half of the 1990's and is now run as a conservation site by the Nature Conservancy. The Sebangau forest represents the largest contiguous lowland forest in Kalimantan, covering an area of 5600 km<sup>2</sup> (Cheyne, 2010). Comprising the Sebangau River, the habitat in Sebangau consists of a mosaic of mixed-peat-swamp, transitional swamp, low and tall interior forests. The Sungai Wain Protection Forest is a c. 100 km<sup>2</sup> lowland protected area located within the administrative area of Balikpapan, East Kalimantan. The core area is dominated by pristine dipterocarp vegetation and includes permanently and seasonally flooded swamp forests and alluvial forests along rivers. The forest surrounding the core area (60%) consists of forest regenerating from fires, the majority of which occurred in 1997/98 (Fredriksson, 2002). The average minimum linear distance between the six study sites was 203 km ±SD 104 (range 90–320 km).

### Data collection

For each study site we deployed camera traps following a systematic survey grid design (Fig. 1). Camera traps were placed along established trails, near fallen logs or man-made walkboards and, where possible, watering areas, located so as to maximise the success rate of photo-

**Table 1** – Characteristics of the six study sites.

Study site	Site code	Central		Indonesian protected status	Habitat type <sup>1</sup>	Logging status	Fires <sup>2</sup>	Hunting (% of days) <sup>3</sup>	N of clouded leopards <sup>4</sup>
		Latitude/Longitude							
Bawan	BAW	9821636 / 499986		Not protected	LD, PSF	Current	No	10	—
Belantikan	BEL	9834006 / 536542		Nature Reserve/Production Forest	LD	>20 years	No	9	1
Kutai	KUT	5457920 / 570690		National Park	LD	>10 years	Yes	3	1
Lesan	LES	1774120 / 527897		Nature Reserve	LM	>20 years	Yes	15	3
Sebangau	SAB	9739536 / 820452		National Park/Conservation Area	PSF, TP	>10 years	Yes	2	2
Sungai Wain	SW	9877564 / 480908		Nature Reserve	LD	>20 years	Yes	1	2

<sup>1</sup> Habitat types: LD=lowland dipterocarp forest; PSF=ombrogenous peat-swamp forest; LM=lowland montane forest; TP=tall pole forest.

<sup>2</sup> Fires occurred within the study areas >10 years prior to the survey period.

<sup>3</sup> Hunting was measured in % of days during which hunters were detected within the study grid (Cheyne et al., 2016). We considered as hunters all people that were detected by camera traps carrying guns, spears, dead animals or clearly carrying bags which are used for flying foxes.

<sup>4</sup> N of individual clouded leopards photographed on camera traps within each study grid (Cheyne et al., 2013, 2016).

graphic detections (Wilting et al., 2006; Gordon and Stewart, 2007; Cheyne et al., 2013). We used Cuddeback Capture IR®, set approximately 50 cm above the ground. Each sampling location had two cameras placed opposite each other, 7 to 10 m apart to create a paired station at each location with the aim of photographing each flank of the animal simultaneously. Sampling locations were placed at a minimum distance of 1 km from each other (Cheyne et al., 2016). The passive infrared sensors were set at about 50 cm height and used an infrared flash. All cameras were set to take 1 photograph followed by a 10 sec video and 5 sec intervals between triggers. We conducted camera trap surveys across the six study areas between May 2008 and June 2014 (Tab. 2). Data were collected over a long time period, and we recognize the potential biases of this relatively long time-span. Sites were selected based on having a limited presence of anthropogenic activity at the time of data collection, and based on areas likely used by clouded leopards (Cheyne et al., 2016).

We placed camera traps across different forest types, attempting to cover all the main habitat representatives of each study area. This study was part of the first survey covering Indonesian Borneo to gather data on clouded leopards (Struebig et al., 2015; Cheyne et al., 2017, 2013; Adul et al., 2015; Sastramidjaja et al., 2015; Cheyne et al., 2017). Therefore, the camera trap study design was based on the spatial ecology of clouded leopards, which have very large home ranges (Cheyne and Macdonald, 2011; Hearn et al., 2013; Cheyne et al., 2016). Grid sizes ranged from 50 to 140 km<sup>2</sup> and trap nights ranged from 3269 to 5548 (Cheyne et al., 2013, 2016).

### Data analysis

Camera trap data (Photo ID, Date, Time, Camera station, Habitat, Species, N of individuals, Sex and age) were entered in a customised Microsoft Access Database. Consecutive photographs at the same station were assumed to be an independent event if they occurred at least 0.5 hours from another photograph (O'Brien et al., 2003). Non-duplicate individuals within a single independent event were summed together as a single group. Because in several cases it was not possible to distinguish between lesser mouse deer (*Tragulus kanchil*) and greater mouse deer (*T. napu*) as well as between Bornean red muntjac (*Muntiacus muntjak*) and Bornean yellow muntjac (*M. atherodes*), we pooled independent events into mouse deer (*Tragulus* spp.) and muntjac deer (*Muntiacus* spp.).

To account for imperfect detection, we analysed data from the six study sites using occupancy models (MacKenzie et al., 2006). We used estimates of species occupancy ( $\Psi$ ) to infer patterns of occurrence at each study site and investigated the effects of habitats characterised by different types of human activities on occupancy and detection probabilities. We ran single-season occupancy models (MacKenzie et al., 2006) of each species (or species group, e.g. "mouse deer") separately for each site. This approach was previously used comparing species occupancy and mammal diversity across multiple tropical forest sites (Ahumada et al., 2011). We therefore built detection/non-detection matrices of each species at the six main study sites, where columns represented daily capture histories (1=detected, 0=not detected), and rows

represented each camera trap location. Let  $\left[ \Psi^{s_D} \prod_{t=1}^K p_t^{s_t} (1-p_t)^{s_D-s_t} \right]$  represent the probability of detection  $p$  based on the taxon's detection history  $h$  when it was detected at least once (e.g. 01001), and  $\left[ \Psi \prod_{t=1}^K (1-p_t) + (1-\Psi) \right]$  be the probability of detection when the taxon remained undetected across all sampling occasions; the single-season occupancy model likelihood is written in mathematical terms as:

$$L(\Psi, p|h_1, h_2, \dots, h_S) = \left[ \Psi^{s_D} \prod_{t=1}^K p_t^{s_t} (1-p_t)^{s_D-s_t} \right] \left[ \Psi \prod_{t=1}^K (1-p_t) + (1-\Psi) \right]^{s-s_D}$$

where  $k$  is the number of sampling occasions (or surveys)  $t$ ,  $s_D$  is the number of sites where the taxon was recorded at least once and  $s_t$  is the number of sites where the taxon was recorded during the  $t^{\text{th}}$  survey (MacKenzie et al., 2006). The single-season model is based on the assumption of population closure, i.e. a period during which the occupancy state of a species is unchanged (MacKenzie et al., 2006). In Sebangau, data was collected across multiple seasons, breaking the assumption of population closure. Therefore, for Sebangau we selected data from one single season (November 2011 – February 2012, 4410 trap nights) which corresponded to the sampling period with the highest number of camera locations deployed at the same time. We used a five-day resolution for each sampling occasion.

We fitted "habitat type" as a categorical covariate for both occupancy and detection probabilities. The number of habitat classes varied across sites (Sebangau N of habitat types=2: "mixed-swamp forest" and "tall pole forest"; Sungai Wain N=2: "primary" and "fire-regenerating"; Kutai N=2: "secondary" and "fire-regenerating"; Bawan N=3: "heath", "peat-swamp" and "disturbed"; Lesan N=3: "primary", "secondary" and "fire-regenerating"; and Belantikan N=4: "primary", "secondary", "plantation" and "disturbed"). We defined "fire-regenerating" and "secondary" forest locations those that burned or were logged more than 10 years prior this study, respectively. We defined forest locations as "disturbed" where they showed recent signs of anthropogenic use (e.g. cultivated plants, logging, burning).

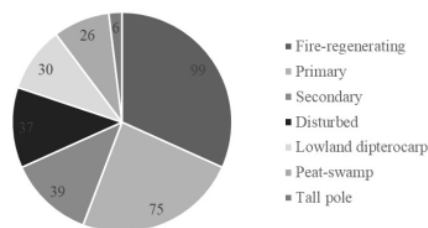
We fitted models to data using PRESENCE 7.3 software (<http://www.mbr-pwrc.usgs.gov/software/presence.html>). We ran species-specific models for each study site (see Supplemental material S1). We did not run models for sambar deer in Kutai and Sebangau due to low sample size (i.e. less than 5 events). We ranked models based on the Akaike Information Criterion (AIC) values: models with the lowest AIC values were identified as the best models (MacKenzie et al., 2006).

To investigate whether occupancy would be lower in areas with higher human activities and differed across forest ecosystem types, we compared mean occupancy estimates from the best models across sites and habitat types. For each of the six sites, we assigned an overall human disturbance classification (hunting and history of logging, Fig. 2). We considered hunting as "relatively frequent" at study sites where hunters were detected more frequently relative to the other study sites (in our case, 9–15% of the total sampling days in Bawan, Belantikan and Lesan). Logging history was considered "recent" where it occurred

**Table 2** – Details of camera trap survey period and sampling effort across the eight study sites.

Study site	Sampling dates	N of camera locations		Grid size (km <sup>2</sup> )
		Trap nights	Trap nights	
Bawan	9 Sept – 26 Nov 2012	63	4146	67
Belantikan	23 Feb – 28 Jun 2014	43	4583	140
Kutai	10 Jan – 23 Mar 2013	49	3269	124
Lesan	15 July 2013 – 29 Jan 2014	58	5548	110
Sebangau <sup>1</sup>	13 May 2008 – 4 Sep 2012	58*	25207*	50
		(21)	(4410)	
Sungai Wain	17 May – 1 Aug 2012	78	4729	100

<sup>1</sup> Sebangau: values in brackets represent the data included in the occupancy models.  
\* Sites excluded from occupancy modelling due to small number of camera locations.



**Figure 2** – Number of camera locations for each habitat type used as covariate at six study sites across Indonesian Borneo.

prior this study (in our case, 10–20 years before our surveys, in Sebangau and Kutai), and “ongoing” where it occurred during this study (Bawan). We also compared mean occupancy across forests types characterised by different types of disturbance (primary, secondary, fore-regenerating and disturbed). We averaged the mean occupancy of best models for habitat category. For example, if occupancy probability of the best model for species *i* at study site *i* was constant across “primary” and “fire-regenerating” habitat types (i.e. did not include habitat type covariate), we used the model’s mean occupancy value as data point for both habitat types. If at study site *ii* occupancy probability of species *i* differed between “primary” and “fire-regenerating” forests (i.e. occupancy was a function of habitat type in the best model), we took the mean occupancy estimates for each habitat and averaged with site *i* according to the habitat classification. The average occupancy for each species at each habitat type was then used as data point for group averages and standard deviations presented in text.

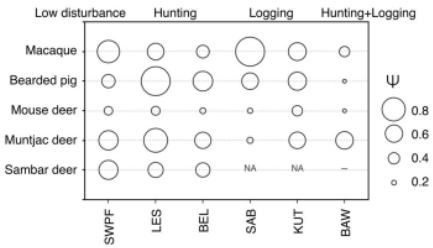
To test our hypothesis that prey taxa will maximise diurnal activity in response to predation risk by nocturnal clouded leopards, for each taxon we examined the relationships between clouded leopard detection rates with prey taxa relative amount of diurnal activities, measured as the proportion of diurnal independent events. We measured daily average of activity from camera trap detection time stamps, by calculating the percentage of total independent events for day and night periods. We defined day period as between 06:00 and 18:00. Clouded leopard detection rates were derived from the number of individuals detected within each grid / camera trap sampling points following Macdonald et al. (2018). We ran Pearson correlations using study sites as sampling units. We discarded sites with low sample sizes (N of independent events < 10), as less than ten events are unlikely to be representative of the species’ activity patterns.

**Results**

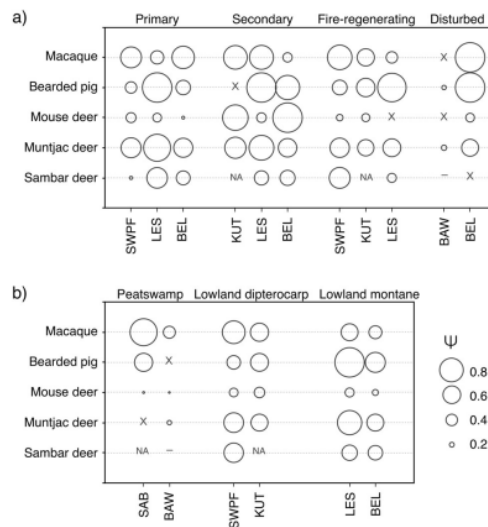
We recorded a total of 2915 camera trap events for pig-tailed macaques and ungulates across sites. From the occupancy models, habitat type was included as covariate in 16 of the 27 top models, influencing detection in twelve top models and occupancy probabilities in five models (Tab. 3). Overall, pig-tailed macaques were the species with highest mean occupancy probabilities (average  $\Psi$  across sites:  $0.64 \pm SD 0.22$ , N=6), followed by bearded pigs and muntjac deer (average  $\Psi$  across sites:  $0.59 \pm SD 0.27$ , N=6, and  $0.59 \pm SD 0.19$ , N=6, respectively). Detection probabilities of sambar deer were low, ranging from 0.004 to 0.08, but the average occupancy of this species across three sites was relatively high ( $0.57 \pm SD 0.09$ , N=3). Mouse deer had lowest occupancy probabilities compared to the other taxa (average  $\Psi$  across sites:  $0.27 \pm SD 0.08$ , N=6).

**Relationships between occupancy and anthropogenic influences**

We compared patterns of occupancy probabilities across sites characterised by different levels and types of anthropogenic activities (Fig. 3). Discarding sambar deer to allow direct comparisons, we found that hunting and history of logging (>10 years old) had little effect on occupancy probabilities (average  $\Psi$  of N=4 species at each site: Sungai Wain= $0.59 \pm SD 0.18$ , Lesan= $0.66 \pm SD 0.26$ , Belantikan= $0.49 \pm SD 0.17$ , Sebangau= $0.51 \pm SD 0.37$ , Kutai= $0.56 \pm SD 0.12$ ), but when hunting and logging were simultaneously ongoing, overall occupancy decreased (Bawan= $0.33 \pm SD 0.22$ ). At Bawan, sambar deer were not detected, and mean occupancy of bearded pigs was between 3 and 6 times lower compared to other sites. Occupancy probabilities in forest regenerating from fire (average of N=4 species:  $0.53 \pm SD 0.25$ ) were comparable to those in primary ( $0.56 \pm SD 0.26$ ) and secondary ( $0.66 \pm SD 0.29$ , ) forests (Fig. 4a). In contrast, in habitats with ongoing disturbance (i.e. logging/fragmented areas in Bawan and, to a lesser extent, Belantikan), occupancy and species richness showed a tendency to decrease ( $0.33 \pm SD 0.40$ , Fig. 4a). Number of species and occupancy were lower in peat swamp forests compared to other habitat types (Fig. 4b).



**Figure 3** – Comparison of average occupancy probabilities across study sites characterised by different human land use: low disturbance, frequent hunting, recent logging (10–20 years prior to this study) and a combination of ongoing logging and frequent hunting. NA=the species was detected, but occupancy models could not be computed due to low sample size, -= he species was not detected at the site.



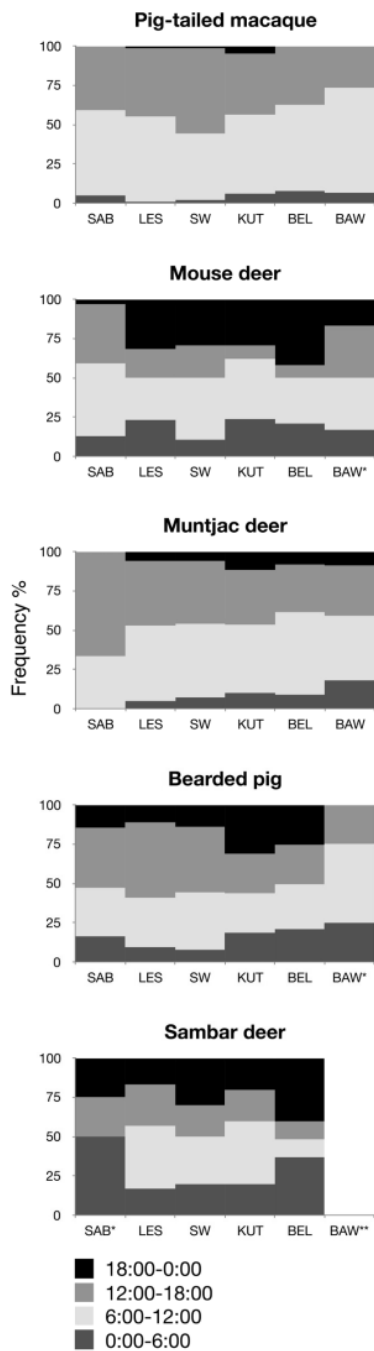
**Figure 4** – Comparison of occupancy probabilities across sites characterised by (a) different forest stages and (b) different forest habitats. NA=the species was detected, but occupancy models could not be computed due to low sample size, x=the species was not detected within habitat (despite being present at the site), -= he species was not detected at the site. Although muntjac deer was not detected in Sebangau’s peat-swamp forest during the season used for occupancy models, they were detected there at very low frequencies during previous and subsequent years.

**Relationships between clouded leopard densities and prey taxa activity patterns**

Daily activity patterns differed across taxa (Fig. 5). Overall, pig-tailed macaques, muntjac deer and bearded pigs were more diurnal (94, 85 and 68% of the total independent events were recorded during day time hours, respectively), whereas mouse deer and sambar deer activity was more or less equal between day and night (57 and 45% of total detections were recorded in the day, respectively). Across sites, relative amounts of diurnal activity of mouse deer and muntjac deer positively correlated with detection rates of clouded leopards (Mouse deer:  $r=0.94$ , N=5,  $p=0.02$ ; muntjac deer:  $r=0.83$ , N=6,  $p=0.04$ ). Under the assumption that increased nocturnal activity might be partially driven by human disturbance (e.g. Matsubayashi et al., 2003; Wahyudi and Stuebing, 2013) and not by the absence of clouded leopards alone, we discarded Bawan for the muntjac deer analysis (mouse deer already excluded Bawan due to low sample size). Without Bawan, the correlation between muntjac diurnal activity and clouded leopard detection rates was not significant ( $r=0.81$ , N=5,  $p=0.10$ ). Diurnal activity of the pig-tailed macaques and bearded pigs showed no statistically significant correlation with clouded leopard detection rates (pig-tailed macaques:  $r=0.28$ , N=6,  $p=0.59$ ; bearded pig:  $r=0.33$ , N=5,  $p=0.59$ ).

**Table 3** – Top models of pig-tailed macaque and ungulates across six sites on Borneo. K=number of parameters, w=Akaike's weight. Models were ranked using the Akaike's Information Criterion (see Supplemental material S1).

Taxon/site	Model	K	w	Habitat	$\Psi(\pm SE)$	$p(\pm SE)$
<b>Pig-tailed macaque</b>						
Sebangau	$\Psi(\cdot), p(\text{habitat})$	3	0.71	Tall pole	1.00 (0.00)	0.16 (0.03)
				Mixed swamp	1.00 (0.00)	0.05 (0.00)
SWPF	$\Psi(\cdot), p(\cdot)$	2	0.46	Primary+burned	0.78 (0.05)	0.23 (0.02)
Kutai	$\Psi(\cdot), p(\cdot)$	2	0.45	Secondary+burned	0.63 (0.08)	0.18 (0.02)
Bawan	$\Psi(\cdot), p(\cdot)$	2	0.40	Peatswamp+heath	0.38 (0.14)	0.07 (0.03)
Lesan	$\Psi(\text{habitat}), p(\cdot)$	4	0.50	Burned	0.41 (0.15)	0.10 (0.01)
				Primary	0.47 (0.11)	0.10 (0.01)
				Secondary	0.82 (0.09)	0.10 (0.01)
Belantikan	$\Psi(\text{habitat}), p(\text{habitat})$	8	0.84	Disturbed/patch	1.00 (0.00)	0.02 (0.01)
				Plantation	0.13 (0.12)	0.36 (0.15)
				Primary	0.77 (0.16)	0.11 (0.03)
				Secondary	0.34 (0.14)	0.22 (0.05)
<b>Bearded pig</b>						
Sebangau	$\Psi(\cdot), p(\text{habitat})$	3	0.47	Tall pole	0.59 (0.12)	0.15 (0.05)
				Mixed swamp	0.59 (0.12)	0.07 (0.02)
SWPF	$\Psi(\cdot), p(\cdot)$	2	0.45	Primary+burned	0.48 (0.07)	0.16 (0.02)
Kutai	$\Psi(\cdot), p(\cdot)$	2	NA	Burned	0.64 (0.17)	0.07 (0.02)
Bawan	$\Psi(\cdot), p(\cdot)$	2	0.50	Heath+disturbed/patch	0.16 (0.15)	0.04 (0.04)
Lesan	$\Psi(\cdot), p(\cdot)$	2	0.61	All	1.00 (0.00)	0.03 (0.01)
Belantikan	$\Psi(\cdot), p(\text{habitat})$	5	0.70	Disturbed/patch	0.69 (0.09)	0.02 (0.02)
				Plantation	0.69 (0.09)	0.14 (0.05)
				Primary	0.69 (0.09)	0.18 (0.03)
				Secondary	0.69 (0.09)	0.10 (0.03)
<b>Mouse deer</b>						
Sebangau	$\Psi(\text{habitat}), p(\cdot)$	3	0.43	Tall pole	0.63 (0.44)	0.04 (0.03)
				Mixed swamp	0.10 (0.10)	0.04 (0.03)
SWPF	$\Psi(\cdot), p(\text{habitat})$	3	0.64	Primary	0.32 (0.07)	0.26 (0.04)
				Burned	0.32 (0.07)	0.08 (0.03)
Kutai	$\Psi(\text{habitat}), p(\cdot)$	3	0.62	Secondary	0.87 (0.23)	0.11 (0.03)
				Burned	0.30 (0.09)	0.11 (0.03)
Bawan	$\Psi(\cdot), p(\text{habitat})$	3	0.35	Peatswamp	0.16 (0.10)	0.20 (0.12)
				Heath	0.16 (0.10)	0.04 (0.03)
Lesan	$\Psi(\cdot), p(\cdot)$	2	0.53	All	0.33 (0.07)	0.19 (0.02)
Belantikan	$\Psi(\cdot), p(\text{habitat})$	5	0.85	Disturbed/patch	0.23 (0.08)	0.14 (0.06)
				Plantation	0.23 (0.08)	0.52 (0.10)
				Primary	0.23 (0.08)	0.16 (0.07)
				Secondary	0.23 (0.08)	0.03 (0.03)
<b>Muntjac deer</b>						
Sebangau	$\Psi(\cdot), p(\cdot)$	2	NA	Tall pole+mixed swamp	0.24 (0.12)	0.05 (0.03)
SWPF	$\Psi(\cdot), p(\text{habitat})$	3	0.46	Primary	0.68 (0.06)	0.26 (0.03)
				Burned	0.68 (0.06)	0.20 (0.02)
Kutai	$\Psi(\cdot), p(\text{habitat})$	3	0.36	Secondary	0.59 (0.07)	0.33 (0.06)
				Burned	0.59 (0.07)	0.23 (0.03)
Bawan	$\Psi(\cdot), p(\text{habitat})$	4	0.59	Peatswamp	0.62 (0.22)	0.01 (0.01)
				Heath	0.62 (0.22)	0.06 (0.02)
				Disturbed/patch	0.62 (0.22)	0.01 (0.01)
Lesan	$\Psi(\text{habitat}), p(\cdot)$	4	0.51	Burned	0.62 (0.14)	0.24 (0.01)
				Primary	0.92 (0.05)	0.24 (0.01)
				Secondary	0.85 (0.08)	0.24 (0.01)
Belantikan	$\Psi(\cdot), p(\text{habitat})$	5	0.84	Disturbed/patch	0.58 (0.08)	0.16 (0.05)
				Plantation	0.58 (0.08)	0.37 (0.08)
				Primary	0.58 (0.08)	0.11 (0.03)
				Secondary	0.58 (0.08)	0.13 (0.03)
<b>Sambar deer</b>						
SWPF	$\Psi(\cdot), p(\text{habitat})$	3	0.38	Primary	0.67 (0.62)	0.004 (0.01)
				Burned	0.67 (0.62)	0.02 (0.02)
Lesan	$\Psi(\cdot), p(\cdot)$	2	0.46	All	0.54 (0.20)	0.02 (0.01)
Belantikan	$\Psi(\cdot), p(\cdot)$	2	0.73	All	0.51 (0.13)	0.08 (0.02)



**Figure 5** – Activity pattern of pig-tailed macaques and ungulates comparison across sites on Borneo. Sites are in decreasing order of clouded leopard density. \* indicates less than 5 events (>5), \*\* indicates 0 events.

## Discussion

### Relationships between occupancy and forest types: management implications

We found that overall, occupancy patterns of ungulates and pig-tailed macaque in regenerating forests were similar to those in pristine habitats, whereas in areas of ongoing, widespread hunting and habitat disturbance occupancy probabilities of all taxa except for muntjac deer

were either zero or considerably lower. Our findings also indicate that ground-dwelling seed dispersers such as ungulates and macaques might be able to respond rapidly to environmental change. While in heavily disturbed habitats their occupancy decreased, once forests were allowed to regenerate these species re-established their original occupancy, thus contributing to secondary forest succession. These are encouraging results considering that half of the remaining Bornean forests have suffered some degree of habitat degradation in the recent past (Gaveau et al., 2014). A previous camera trap study across sites on Malaysian Borneo (Sabah and Sarawak provinces) found similar patterns: among other species, bearded pig, pig-tailed macaque and sambar deer showed a substantial increase in occupancy in >10 years old logged forests compared to newly logged ones (Brodie et al., 2015). Along with previous research (e.g. Berry et al., 2010; Brodie et al., 2015; Granados et al., 2016), our study provides evidence that regenerating forests constitute a crucial part of biodiversity conservation on Borneo.

Human activities might show different effects on wildlife distribution or abundance when comparing at the island, regional or global scales. The type and intensity of human activities may generally be more similar within-island or country compared to the wider scale, depending on conservation policies and interventions as well as local traditions and beliefs, which may impact hunting preferences and agricultural systems. Data from the first cross-continental camera trap study showed that in general, the effects of habitat fragmentation varied across vertebrate functional guilds, with omnivores showing increased sensitivity (measured as a reduction in occupancy and richness) compared to herbivores (Ahumada et al., 2011). On Indonesian Borneo we showed that in general, intensive human activities had similar negative effects on the occupancy of two herbivores (mouse deer and sambar deer) and two omnivores (pig-tailed macaque and bearded pig). While in our study muntjac deer were the least affected taxa, Ahumada et al. (2011) estimated a lower occupancy of *M. muntjac* in a highly fragmented site in Lao PDR (0.03) compared to a less disturbed area on Sumatra (0.23). Cheyne et al. (2016) used data from the same study sites across Borneo and found that although hunting pressure was generally low, it was related to a lower number of mammalian species overall, with deer (muntjac, mouse and sambar) and bearded pigs being the most targeted species. Our results showed that pig-tailed macaque occupancy was low in Bawan. This could have been a consequence of hunting pressure, or perhaps the monkeys were detected in smaller parts of the survey grid because the cameras were not placed specifically within their territory. Pig-tailed macaques are thought to have home ranges of 0.6-8.2 km<sup>2</sup> and to travel in large groups (Sponsel et al., 2002) thus it is possible that pig-tailed macaques were not in the vicinity of the camera traps during the study. Hunting pressure is likely to have reduced the distribution of bearded pigs and mouse deer in Bawan. Muntjac deer smaller occupancy in Sabandau may reflect habitat preferences, with much lower densities in peat-swamp forest compared to tall pole forest. The low detection rates of sambar deer detection in Sabangau, Kutai and Bawan may be associated with logging. In Belantikan even though the iron ore mining site was outside our survey grid and not operational during the study, it could have had a significant impact on the distribution of some species due to forest clearance, habitat degradation, pollution and increased hunting. While this was beyond the scope of our study, we recommend future research focusing on the effects of mining on biodiversity in this region.

Predators use various strategies to hunt successfully (e.g. Petrunenko et al., 2013), for example, the arboreal hunting strategy of clouded leopards could provide an advantage to surprise prey. Where predators are present, prey species are known modify their behaviour when exposed to high risks of predation. These behavioural responses may consist of changes in ranging patterns (i.e. spatial avoidance, e.g. Valeix et al., 2009), changes in temporal activity (Fenn and Macdonald, 1995; Ross et al., 2013) and/or changes in response behaviour during encounters with predators (e.g. Croes et al., 2007). Ungulates are relatively flexible in their circadian rhythms. For example, muntjac deer were reported to be mainly diurnal at some sites (Kawanishi and Sunquist, 2004; Ross et al., 2013), and cathemeral at others (Kamler et

al., 2012). In the absence of tigers (*Panthera tigris*), Sunda clouded leopards are mainly, although not exclusively, nocturnal (Cheyne et al., 2013; Adul et al., 2015). Across our study sites, pig-tailed macaques and muntjac deer were predominantly diurnal, bearded pigs were twice more active during the day compared to night and the activity of mouse deer and sambar deer was more or less equal between day and night. Bearded pigs and sambar deer are the largest of the possible prey species across our sites. The amount of diurnal activity of bearded pigs was not associated with detection rates of clouded leopards, and that for sambar deer remains unknown. Ross et al. (2013) found that bearded pigs were significantly more nocturnal at sites where clouded leopards were absent compared to sites where clouded leopards were present. For bearded pigs we could not include Bawan due to low sample sizes, therefore, it is unclear whether the same is occurring at our sites. We found a positive relationship between mouse deer and muntjac deer diurnal activity and clouded leopards detection rates, which may suggest that these preys respond to the risk of predation by maximising their activity when predators are less active. However, in Sumatra van Schaik and Griffiths (1996) reported muntjac deer to be mostly nocturnal even though clouded leopards were present. When we excluded Bawan from our analysis, the correlation between muntjac deer diurnal activity and clouded leopard detections was no longer significant. It is therefore also possible that at least for muntjac deer, the occurrence of human activities such as hunting and logging may influence an increase in nocturnal activity. We also acknowledge the possible implications of using an index of abundance (in our case, detection rates of clouded leopards) that do not account for imperfect detection, which can potentially lead to biased inferences.

Given the range of habitats, threat levels and protected status we have highlighted that some species are more adaptable and resilient than others on Borneo. The cumulative effects of logging and hunting at Bawan may have contributed to the reduction of available suitable space for pig-tailed macaques and ungulates, possibly causing the decrease in their abundance. Our results provide support for investing conservation efforts of regenerating forests on Indonesian Borneo. Maintaining a healthy population of large seed dispersers including primates and ungulates in human-impacted habitats on Borneo will be crucial for promoting forest recovery and the long-term persistence of clouded leopards. 🌿

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Supplemental material S1** Occupancy models for pig-tailed macaques and ungulates across sites.

# Occupancy patterns of ungulates and pig-tailed macaques across regenerating and anthropogenic forests on Borneo

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