



## Original Investigation

## Differential responses of large mammals to logging and edge effects

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## ABSTRACT

Selective logging is one of the most widespread disturbances to tropical forests worldwide, yet its impacts on large mammals remain poorly understood. We used camera trapping and hierarchical models to compare local abundance of a variety of terrestrial mammal species in Borneo between selectively logged and unlogged forest, and to assess the impacts of edge effects. Our methods circumvent confounding factors that have plagued previous assessments of logging impacts by explicitly accounting for differential detection probability among habitats, separating the effects of hunting from those of logging-induced habitat disturbance, and explicitly measuring the distances over which edge effects occur. We found that mammalian carnivore species were either largely or completely confined to primary forest, although habitat use for the Sunda clouded leopard (*Neofelis diardi*) increased toward the ecotone. Several large ungulates, however, were either completely (elephant *Elephas maximus* and banteng *Bos javanicus*) or mostly (sambar *Rusa unicolor*) found in logged forest. This suggests that, in the absence of hunting, disturbed habitats can be important for the conservation of certain endangered and vulnerable species. Sambar and muntjac (*Muntiacus* spp.) both strongly avoided habitat edge in logged forest and primary forest, respectively. Lower habitat use by these species persisted 2–4 km from the habitat boundary – farther than has been observed for the infiltration of other edge effects such as canopy desiccation. Such avoidance of ecotones implies that 20–40% of the intact primary forest habitat in our study area is actually degraded “edge habitat” from the point of view of primary forest specialists. Our results suggest that, while selectively logged forests retain conservation value for certain large mammal species, it is critical that thresholds in logging intensity be identified so as to avoid declines in habitat use by taxa, such as carnivores, which appear intolerant of intensive logging pressure.

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## Introduction

Tropical rainforests harbor most of the Earth's terrestrial biodiversity (Dirzo and Raven, 2003; Kier et al., 2009) and yet are under increasing threat from habitat alteration and destruction. In particular, selective logging is one of the most widespread and important anthropogenic disturbances to tropical forests (Asner et al., 2005; Curran et al., 2004). Altered abiotic habitat conditions resulting from logging can affect the demography and abundance of taxa such as understory plants (Costa and Magnusson, 2002; Vieira et al., 2007), amphibians (Ernst et al., 2007; Fredericksen and Fredericksen, 2004), birds (Barlow et al., 2006; Datta, 1998;

Eyre et al., 2009; Gray et al., 2007), butterflies (Dumbrell and Hill, 2005; Lewis, 2001), rodents (Lambert et al., 2005; Ochoa, 2000), and bats (Clarke et al., 2005; Peters et al., 2006).

Our understanding of the impacts of selective logging on larger terrestrial mammals, however, is much more limited (Vetter et al., 2011). These species are often of high conservation concern due to their generally greater vulnerability to human activities than many smaller-bodied taxa (Chapin et al., 2000; IUCN, 2009). This increased vulnerability arises, in part, because larger-bodied taxa often occur at naturally low densities and many face direct exploitation from humans (Brodie et al., 2009; Milner-Gulland et al., 2003).

In addition to altering the habitat in areas where trees are actually removed, logging impacts can permeate into adjacent intact forest through the creation of an “edge” boundary, or ecotone, which can have different abiotic conditions than areas farther removed from the disturbance (Laurance et al., 2011). This is a very widespread and serious issue. For example, over 70,000 km of new

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edge habitat were generated per year in the Brazilian Amazon from 1999 to 2002 (Broadbent et al., 2008). Canopy desiccation can penetrate up to 2.5 km from these forest edges (Briant et al., 2010) and the proportion of forested areas within 2 km of an edge in the Amazon has increased by 4% per year, mostly as a result of selective logging activities (Broadbent et al., 2008). Edge effects at a protected area in Sumatra were found to extend 2–3 km for large mammals such as elephants and rhinoceros (Kinnaid et al., 2003), though this could have been confounded by differences in human population density along the park edge (O'Brien et al., 2003). In general, while edge effects are known to be among the strongest factors affecting microclimates and tree communities in tropical forests (Laurance et al., 2011; Santos et al., 2010), we have a poorer understanding of their impacts on large vertebrates (Lacerda et al., 2009; Norris et al., 2008).

The impacts of selective logging and edge effects vary considerably among mammals (Gerber et al., 2010; Meijaard and Sheil, 2008). Yet our ability to predict which species will be more susceptible, and under what conditions, remains rudimentary for several reasons. First, many larger mammals in tropical systems are cryptic, elusive, or naturally occur at low densities, making them logistically difficult to study (cf. Linkie et al., 2008). Second, the probability of detecting a species in a given area, even if it is there, can vary across habitats, making it critical to account for differential “detectability” when directly comparing abundance estimates or habitat use among sites (MacKenzie et al., 2005). In studies that do not explicitly incorporate detection probability, it is difficult to ascertain whether apparent responses of mammals to selective logging represent real ecological differences or merely differences in detectability (cf. Datta and Goyal, 2008; Duff et al., 1984; Nummelin, 1990). Third, increased access to the forest accorded by the construction of logging roads means that selective logging enhances hunting pressure from local human communities (Milner-Gulland et al., 2003; Robinson et al., 1999; Sampaio et al., 2010). This means that it can be difficult to separate the direct effects of logging (i.e., tree removal and the microhabitat changes that accompany it) from the joint effects of logging and hunting (Poulsen et al., 2011). Yet the need to discriminate between these impacts is essential, because each demand different solutions from protected area managers and government officials. Impacts of logging alone, for example, could be addressed by revising guidelines dictating the intensity and frequency of logging permissible for a given region. The adverse effects of hunting could be mitigated through road closures, restricting the supply of ammunition, or stronger enforcement of hunting laws or regulations among local communities and urban markets (Milner-Gulland et al., 2003).

Here we assess the impacts of selective logging and its associated edge effects on rainforest mammals in Malaysian Borneo. Borneo, Earth's third largest island, is a hotspot of biodiversity and endemism (Myers et al., 2000), yet suffers from one of the highest deforestation rates in the world (Langer et al., 2007). Previous attempts to investigate the responses of Bornean mammals to selective logging have employed a variety of techniques, some of which accounted for detectability while others did not. Few, however, have attempted to distinguish the impacts of hunting from those of the ecological changes directly resulting from logging. Selective logging has been shown to negatively impact mouse deer (*Tragulus* spp.) (Heydon and Bulloh, 1997) and several species of civet (Viverridae) (Colon, 2002; Heydon and Bulloh, 1996). Both sambar (Heydon, 1994) and red muntjac (*Muntiacus muntjak*) (Duff et al., 1984) populations responded positively to certain logging intensities, though another study has found no effect of logging on two muntjac species combined (Heydon, 1994). Practically nothing is known about logging's impacts on other Bornean ungulates such as the vulnerable bearded pig (*Sus barbatus*) or endangered banteng (Meijaard and Sheil, 2008). Finally, Meijaard et al. (2008)

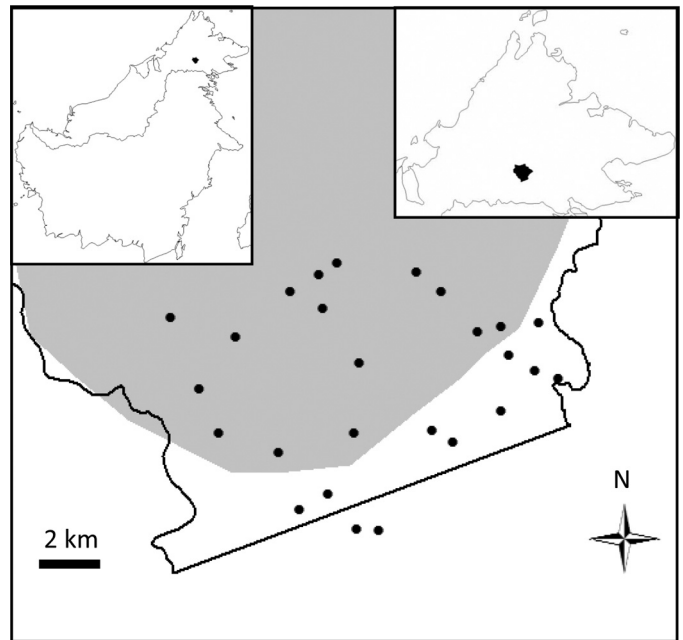


Fig. 1. Map of the study area in the southern portion of the Maliau Basin Conservation Area. Primary forest shown in gray, conservation area border as a black line, and camera trap locations as black circles. Insets show the location of the conservation area within Sabah (upper right) and within Borneo (upper left).

showed that banded linsang (*Prionodon linsang*), moonrat (*Echinosorex gymnura*), and long-tailed porcupine (*Trichys fasciculata*) responded negatively to selective logging, suggesting that perhaps taxonomic lineages of older evolutionary origin might be more susceptible to its effects.

We build on previous efforts to assess logging impacts on Bornean mammals in four ways. First, due to its remoteness and general inaccessibility, little documented hunting has occurred at our study site (and we detected none during our study), allowing us to assess the direct effects of habitat disturbance alone without the accompanying influence of intense hunting. Second, we employ a standardized sampling (camera trapping) and analysis framework (local abundance models) for all species. Third, we use an occupancy modeling based approach (cf. Royle and Nichols, 2003) that allows us to assess the relative habitat use of different species in adjacent logged and primary forest while explicitly accounting for potentially different detection probabilities between the two habitats. Finally, we specifically test for edge effects for all species. Our goals are to generate robust and unbiased (i.e., accounting for detectability) estimates of (1) relative habitat use in both selectively logged and primary rainforest for a variety of medium and large terrestrial mammal species, and (2) the effects of habitat edge for species that appear to use one habitat more than the other.

## Methods

### Study site

The Maliau Basin Conservation Area (MBCA; 588 km<sup>2</sup>; 4° 49' N, 116° 54' E; Fig. 1) harbors undisturbed primary rainforest, including mixed dipterocarp, tropical heath, and *Casuarina*-dominated formations, as well as adjacent mixed dipterocarp forest that was logged in the early- to mid-1990s. Logging consisted of the selective removal of 10–15 trees above 60 cm diameter per hectare. Reduced impact logging techniques were practiced, which consisted of increased effort to avoid damage to the trees that were not harvested, and also lower removal rates on steep slopes.

The geology of the area is mostly sedimentary (Hazebroek et al., 2004) and elevation ranges from a few hundred meters to ~1700 m above sea level. On average, the area receives ~3800 mm of rainfall annually (Mykura, 1989). Due to its relative remoteness, the Maliau Basin may have been historically unoccupied by humans and remains little-used today except for conservation area staff and a relatively small but growing number of tourists (Hazebroek et al., 2004). Except for occasional reports of banteng poaching by hunters in the southern portion of the conservation area, hunting is extremely limited in the area.

#### Data collection

We set up 26 camera trap stations the MBCA, 15 in primary forest and 11 in logged forest, and deployed two cameras per station from January to May 2010. Cameras in each station were affixed to tree trunks and faced the intended movement path from opposite sides. Stations were established along potential mammal travel routes such as ridge top game trails, human hiking paths, abandoned logging roads, and stream corridors. We used Reconyx™ RM45 camera traps, which were active 24 h a day and took time- and date-stamped photos of all species that triggered the infrared motion detector. Trigger speed was estimated at 0.1 s (manufacturer specifications) and trigger sensitivity was set to high; cameras were programmed to take three images in rapid-fire succession once triggered. Photos for which conclusive identifications were not possible or where it was unclear as to what triggered the camera were excluded from the overall analysis. We restricted our analysis to medium and large ( $\geq 1.5$  kg) mammals, as smaller taxa are difficult to identify to species. We also focus on terrestrial (i.e. non-aquatic and non-arboreal) species as they are amenable to detection with camera traps.

#### Analysis

We employed the Royle–Nichols modeling framework (Royle and Nichols, 2003) in program PRESENCE to assess habitat use and edge effects for different large mammal species while accounting for differential detectability. These models estimate two parameters: detectability ( $r$ ) and local abundance ( $\lambda$ ), or the number of individuals using each camera trap location.

To estimate local abundance in logged versus unlogged forests, we built eight models for each species representing all possible combinations of  $r$ , which was either constant or varied with forest type and/or the number of cameras operating at each station on any given day (i.e. where one camera failed before the other), and  $\lambda$ , which was constant or varied with forest type. We ranked the models with AIC (Akaike Information Criteria) and used model-averaged  $\lambda$  coefficients as our metrics of relative habitat use.

We assessed edge effects for those species that demonstrated higher local abundance in either logged or primary forest. For species where it was clear that local abundance was higher in one habitat than the other, we incorporated “distance to habitat edge” (i.e., the distance from within either logged or unlogged forest to the boundary between these habitat types) as a covariate and built four models representing all possible combinations of  $r$ , which was constant or varied with the number of cameras operating at each station on any given day, and  $\lambda$  which was constant or varied with distance to the habitat edge. Distance to the habitat edge was measured in a geographic information system (ESRI 2011; ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) where primary and logged forest were distinguished by the presence of logging roads in the latter habitat (clearly visible in Google Earth™). While this method may imprecisely identify ecotones on small spatial scales, we were interested in edge effects operating over scales of thousands of meters and we

felt that our delineation of habitat boundaries from aerial imagery provided a straightforward index well-suited to this task. We also used the “buffer” function in ArcGIS 10 to estimate the area occupied by edge habitats. Again we ranked the models with AIC and used model-averaging to assess the effects of distance from the ecotone boundary on relative habitat use.

#### Results

We recorded 1996 photographic sequences of 26 medium-large mammal species over 1747 camera trap station-days (one station day = cameras operating for 24 h at a given station) in primary forest and 1168 station-days in logged forest (Table 1). One station in primary forest failed completely after both cameras were destroyed by flooding. Batteries in many of the logged forest sites failed sooner than in most primary forest sites. This may be because higher wind velocities or taller ground vegetation in the former habitat caused numerous false triggers. Regardless, all stations operated for a minimum of 81 days (average = 116.6 days, range = 81–128).

We obtained 435 photographic sequences of human groups in the MBCA, with an average of 5.8 individuals per group. All but two of the individuals appeared to be tourists or known conservation area staff. No individuals with firearms or other hunting implements were observed in any photograph.

For native mammal species with an average observed group size  $>1$  that were present in both logged and primary forest habitats, we assessed whether average group size differed between habitats. No significant differences in group size between primary and logged forest was observed for bearded pig (two-tailed  $t_{422} = -0.526$ ,  $P = 0.599$ ; Latin names for all species given in Table 1), pig-tailed macaque ( $t_{107} = -0.718$ ,  $P = 0.474$ ), Malay porcupine ( $t_{96} = 0.030$ ,  $P = 0.976$ ), sambar ( $t_{455} = -1.066$ ,  $P = 0.287$ ), muntjac ( $t_{401} = 0.701$ ,  $P = 0.484$ ), or mousedeer ( $t_{133} = 0.741$ ,  $P = 0.460$ ).

Model selection revealed strong differences in local abundance between logged and primary forest habitat for some species but not others (Table 2). Elephant, banteng, binturong, long-tailed macaque, and common palm civet were only detected in logged forest. But of these, only elephant and banteng were detected more than six times. Local abundance of sambar was higher in logged forest than in primary forest by a factor of 2.8 (Fig. 2). Malay civet, leopard cat, masked palm civet, flat-headed cat, tufted ground squirrel, and yellow-throated marten were only detected in primary forest; but of these, only Malay civets and leopard cats were detected more than twice. Muntjac and clouded leopard had higher local abundance in primary forest than in logged forest by factors of 2.0 and 1.8, respectively (Fig. 2). Abundance of pig-tailed macaques, bearded pigs, banded civets, Malay porcupines, sun bears, and mousedeer did not appear higher in one habitat than the other.

Edge effects also varied substantially among the species that exhibited differential local abundance between logged and unlogged forests. Cervids, in particular, exhibited the strongest responses. Local abundance of sambar groups (see Table 1 for group size) was higher in logged forest as distance from the ecotone increased (Fig. 3 and Table 3). Compared to local abundance at 0.5 km from the habitat edge, sambar local abundance doubled at ~1.2 km from the edge. Muntjac local abundance increased with increasing distance from the habitat edge; their local abundance in primary forest at 0.5 km from the edge was half that at ~5.3 km. Clouded leopard local abundance was higher in primary forest than in secondary forest and their local abundance within primary forest increased toward the ecotone; however, the effect was weak. Leopard cats in primary forest and elephants in logged forest may exhibit edge effects, though the apparent dramatic increase in local abundance with increasing distance from the ecotone may be an artifact of small sample sizes for these species, as evidenced by the rapidly

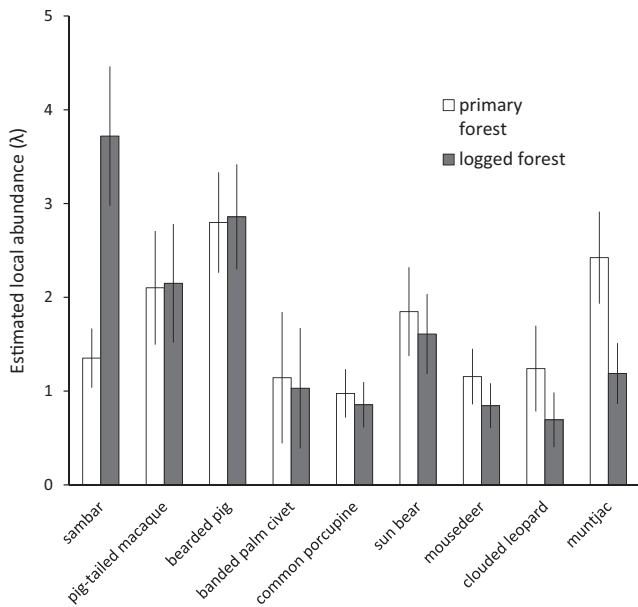
**Table 1**  
Information on mammal species detected.

Species	English name	Conservation status <sup>a</sup>	Number of stations with $\geq 1$ detection	Mean (SE) number of detections per station <sup>b</sup>	Mean (SE) observed group size
<i>Sus barbatus</i>	Bearded pig	Vulnerable	25	17.76 (4.55)	1.81 (0.08)
<i>Macaca nemestrina</i>	Pig-tailed macaque	Vulnerable	22	5.36 (1.17)	1.24 (0.08)
<i>Muntiacus muntjak</i> and <i>M. atherodes</i>	Muntjac	Least concern	19	21.95 (6.32)	1.06 (0.01)
<i>Helarctos malayanus</i>	Sun bear	Vulnerable	17	4.47 (1.86)	1.01 (0.01)
<i>Rusa unicolor</i>	Sambar	Vulnerable	16	31.38 (13.46)	1.12 (0.02)
<i>Tragulus kanchil</i> and <i>T. napu</i>	Mousedeer	Least concern	13	10.38 (3.43)	1.01 (0.01)
<i>Hystrix brachyura</i>	Malay porcupine	Least concern	13	7.92 (2.16)	1.15 (0.04)
<i>Viverra zangalunga</i>	Malay civet	Least concern	10	5.00 (1.51)	1.00 (0.00)
<i>Neofelis diardi</i>	Clouded leopard	Vulnerable	10	4.40 (1.38)	1.00 (0.00)
<i>Hemigalus derbyanus</i>	Banded civet	Vulnerable	10	1.80 (0.47)	1.00 (0.00)
<i>Herpestes brachyurus</i> and <i>H. semitorquatus</i>	Mongoose	Least concern and data deficient, respectively	7	1.29 (0.29)	1.00 (0.00)
<i>Prionailurus bengalensis</i>	Leopard cat	Least concern	5	4.00 (2.00)	1.00 (0.00)
<i>Elephas maximus</i>	Asian elephant	Endangered	4	4.25 (0.48)	2.25 (0.50)
<i>Bos javanicus</i>	Banteng	Endangered	4	3.25 (1.03)	3.75 (0.91)
<i>Macaca fascicularis</i>	Long-tailed macaque	Least concern	3	2.00 (0.58)	1.00 (0.00)
<i>Pardofelis marmorata</i>	Marbled cat	Vulnerable	3	1.00 (0.00)	1.00 (0.00)
<i>Trichys fasciculata</i>	Long-tailed porcupine	Least concern	2	2.00 (0.00)	1.00 (0.00)
<i>Prionodon linsang</i>	Banded linsang	Least concern	2	1.50 (0.50)	1.00 (0.00)
<i>Hystrix crassispinis</i>	Thick-spined porcupine	Least concern	3	1.33 (0.58)	1.25 (0.25)
<i>Arctictis binturong</i>	Binturong	Vulnerable	2	1.00 (0.00)	2.00 (1.00)
<i>Paguma larvata</i>	Masked palm civet	Least concern	2	1.00 (0.00)	1.00 (0.00)
<i>Diplogale hosei</i>	Hose's civet	Vulnerable	1	3.00 (0.00)	1.00 (0.00)
<i>Prionailurus planiceps</i>	Flat-headed cat	Endangered	1	1.00 (0.00)	1.00 (0.00)
<i>Rheithrosciurus macrotis</i>	Tufted ground squirrel	Vulnerable	1	1.00 (0.00)	1.00 (0.00)
<i>Martes flavigula</i>	Yellow-throated marten	Least concern	1	1.00 (0.00)	1.00 (0.00)
<i>Paradoxurus hermaphroditus</i>	Common palm civet	Least concern	1	1.00 (0.00)	1.00 (0.00)

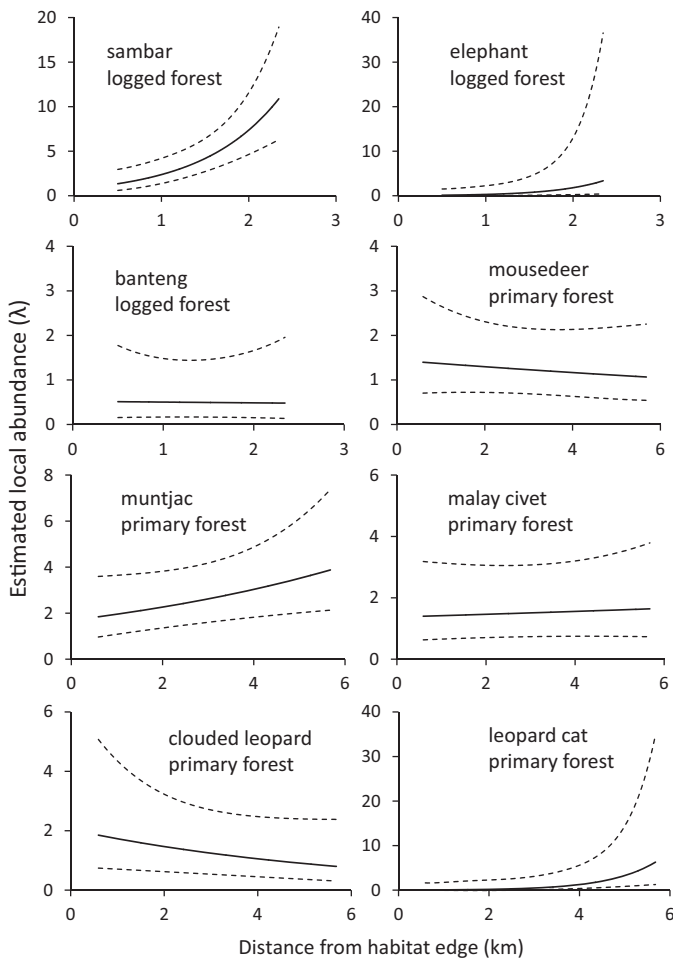
<sup>a</sup> IUCN (2009).<sup>b</sup> For stations with  $\geq 1$  detection.**Table 2**  
Model selection results assessing differences in estimated local abundance ( $\hat{N}_{local}$ ) between logged and primary forest using two abundance models for each species: an intercept-only model ("constant"), and a model including habitat differences ("logging"). Detection probability in all models was structured by time (i.e., Julian day), the number of camera hours operating per day at each station, and whether or not the camera station was on a trail.

Model	Coefficient (SE)	$\Delta$ AIC	AIC weight	Model-averaged $\hat{N}_{local}$ (SE)	
				Primary forest	Logged forest
<b>Banded civet</b>					
Constant	NA	0.00	0.56	3.14 (3.97)	2.29 (2.71)
Logging	-0.65 (0.54)	0.50	0.44		
<b>Bearded pig</b>					
Constant	NA	19.13	0.00	15.89 (1.74)	26.34 (2.97)
Logging	0.51 (0.11)	0.00	1.00		
<b>Clouded leopard</b>					
Constant	NA	13.12	0.00	3.62 (3.59)	0.26 (0.31)
Logging	-2.62 (1.12)	0.00	1.00		
<b>Malay porcupine</b>					
Constant	NA	0.00	0.63	5.46 (1.58)	6.14 (2.08)
Logging	0.30 (0.30)	1.05	0.37		
<b>Mousedeer</b>					
Constant	NA	7.27	0.03	4.26 (0.80)	1.35 (0.58)
Logging	-1.20 (0.42)	0.00	0.97		
<b>Muntjac</b>					
Constant	NA	5.00	0.08	5.85 (1.24)	2.95 (1.08)
Logging	-0.75 (0.32)	0.00	0.92		
<b>Pig-tailed macaque</b>					
Constant	NA	36.21	0.00	30.70 (4.06)	32.34 (4.88)
Logging	0.05 (0.14)	0.00	1.00		
<b>Sambar</b>					
Constant	NA	60.48	0.00	0.57 (0.20)	10.45 (1.89)
Logging	2.91 (0.39)	0.00	1.00		
<b>Sun bear</b>					
Constant	NA	7.65	0.02	3.32 (0.94)	0.96 (0.42)
Logging	-1.27 (0.45)	0.00	0.98		





**Fig. 2.** Estimated local abundance (i.e., number of individuals occurring at each camera station) in logged and unlogged habitats. Error bars show 95% confidence intervals.



**Fig. 3.** Edge effects on model-averaged local abundance (with 95% confidence intervals) of mammal species in primary and logged forest. The sampling units are animal groups (see Table 1 for number of individuals per group).

**Table 3**

Model selection results assessing edge effects on mammal species with higher local abundance in either logged or primary forest (from data in Table 2). Detection probability ( $r$ ) can be constant (“.”) or structured by the number of cameras active on any given day of sampling (“cameras”). The local abundance ( $\lambda$ ) function can be constant or structured by the distance from the edge of the habitat. The sampling units are animal groups (see Table 1 for number of individuals per group).

Model	$\Delta$ AIC	AIC weight
<b>Malay civet-primary forest</b>		
$r(.), \lambda(.)$	0.00	0.357
$r(\text{cameras}), \lambda(.)$	0.17	0.328
$r(.), \lambda(\text{edge})$	1.42	0.176
$r(\text{cameras}), \lambda(\text{edge})$	1.88	0.139
<b>Clouded leopard-primary forest</b>		
$r(\text{cameras}), \lambda(\text{edge})$	0.00	0.428
$r(\text{cameras}), \lambda(.)$	0.98	0.262
$r(.), \lambda(\text{edge})$	2.00	0.158
$r(.), \lambda(.)$	2.08	0.151
<b>Leopard cat-primary forest</b>		
$r(.), \lambda(\text{edge})$	0.00	0.595
$r(\text{cameras}), \lambda(\text{edge})$	0.81	0.397
$r(\text{cameras}), \lambda(.)$	9.71	0.005
$r(.), \lambda(.)$	10.25	0.004
<b>Mousedeer-primary forest</b>		
$r(\text{cameras}), \lambda(.)$	0.00	0.598
$r(\text{cameras}), \lambda(\text{edge})$	1.08	0.348
$r(.), \lambda(.)$	5.53	0.038
$r(.), \lambda(\text{edge})$	7.25	0.016
<b>Muntjac-primary forest</b>		
$r(\text{cameras}), \lambda(\text{edge})$	0.00	0.721
$r(\text{cameras}), \lambda(.)$	1.91	0.277
$r(.), \lambda(\text{edge})$	11.81	0.002
$r(.), \lambda(.)$	16.43	0.000
<b>Banteng-logged forest</b>		
$r(.), \lambda(.)$	0.00	0.532
$r(.), \lambda(\text{edge})$	1.98	0.198
$r(\text{cameras}), \lambda(.)$	1.99	0.197
$r(\text{cameras}), \lambda(\text{edge})$	3.96	0.073
<b>Elephant-logged forest</b>		
$r(.), \lambda(\text{edge})$	0.00	0.596
$r(\text{cameras}), \lambda(\text{edge})$	1.94	0.226
$r(.), \lambda(.)$	3.05	0.130
$r(\text{cameras}), \lambda(.)$	5.02	0.048
<b>Sambar-logged forest</b>		
$r(.), \lambda(\text{edge})$	0.00	0.573
$r(\text{cameras}), \lambda(\text{edge})$	0.59	0.426
$r(.), \lambda(.)$	14.31	0.000
$r(\text{cameras}), \lambda(.)$	14.81	0.000

expanding width of the confidence intervals as distance from the ecotone increased. Banteng, mousedeer, and Malay civets did not appear to exhibit edge effects, as there were no differences in local abundance for these species as functions of proximity to the habitat boundary.

Incorporating edge effects decreased the amount of primary forest habitat in the MBCA. Excluding areas within two and four km of the habitat edge reduced the amount of “non-edge primary forest” within the MBCA by 20.3% and 43.1%, respectively.

**Discussion**

Selective logging is one of the most important anthropogenic disturbances of tropical forests worldwide, yet our understanding of its impacts on medium and large terrestrial mammal species remains limited. Our results suggest that carnivores on Borneo, with clouded leopard, Malay civet and leopard cat all appearing to use primary forest substantially more than logged areas. Although Malay civets (Colon, 2002; Heydon and Bulloh, 1996), leopard cats

(Azlan and Sharma, 2006; Lim, 1999), and clouded leopards (A. Hearn and J. Ross, *personal communication*) are known to use disturbed forests in other areas, it is possible that logging intensity in the MBCA could have been higher than at other sites. Likewise, heavy selective logging reduced the density of primates in tropical Africa, while lower-intensity logging had no effect (Chapman et al., 2000). Additional work is needed in Borneo and other tropical areas to detect thresholds in logging intensity beyond which density or habitat use of carnivores (or other susceptible taxa) declines.

Our observed responses among ungulates confirm the findings of some but not all previous studies in Borneo. We show, as did Heydon (1994), that sambar use disturbed forests more than primary forest. In contrast to Heydon and Bulloh (1997), however, we show little response of mousedeer to selective logging. We also show strong negative responses to logging of both species of muntjac (combined), whereas Heydon (1994) showed no response for these same two species. Prior assessments of banteng or bearded pig responses to logging had not been made (Meijaard and Sheil, 2008).

Relatively few studies have explicitly examined edge effects associated with logging on medium and large rainforest mammals in a tropical forest. While most of the species in the MBCA that were more abundant in one habitat than the other did not exhibit edge effects, several species, particularly sambar and muntjac, did avoid habitat boundaries. Reduced habitat use by these species permeated 2–4 km from the habitat edge itself, similar to results observed by Kinnaid et al. (2003) for elephants and rhinoceros in Sumatra, and on par with or even farther than the infiltration of canopy desiccation (~2.5 km from the habitat edge in heavily fragmented Amazonian landscapes; Briant et al., 2010). Edge effects were already known to be among the strongest factors influencing the dynamics of tree and small animal communities, as well as microclimatic conditions, in tropical forests (Laurance et al., 2011). Our results demonstrate that they can importantly affect certain large mammals as well. The importance of assessing edge effects in planning for large mammal conservation is highlighted by our finding that 20–40% of the intact primary forest in the MBCA is actually degraded “edge habitat” from the standpoint of species, such as muntjac, that avoid ecotones.

In contrast to sambar and muntjac, clouded leopards increased their relative habitat use near the ecotone. This has been observed in other predators and may be related to increased abundance of small prey near habitat edges (Salek et al., 2010). Higher use of edge habitat by the clouded leopard could potentially explain the avoidance of edges by sambar and muntjac (medium-sized ungulates), but not elephants or banteng which are too large to be susceptible to clouded leopard predation (cf. Owen-Smith, 1992). However, given the low densities at which clouded leopards occur in the Maliau Basin (Brodie and Giordano, 2012), it is unclear how much of a role these carnivores play in influencing cervid habitat use.

Our study site is one of the few in Borneo subjected to, at most, very limited hunting pressure. Despite extensive camera-trapping in two habitats and over 400 photographic records of humans in the conservation area, we observed no activities indicative of hunting during our study. Although hunting may very well have accompanied logging operations during the 1990s, as it often does elsewhere in tropical forests (Milner-Gulland et al., 2003; Robinson et al., 1999), we feel that it is unlikely that such hunting, if it did exist in the past, can explain the relative lower use of logged forest by the medium-sized muntjac, yet greater use of this habitat by the larger-bodied sambar, banteng, and elephant.

Finally, our results have several management implications. First, selectively logged forests can provide valuable habitat for some endangered and vulnerable species. The three largest ungulates at our site were either completely (elephant and banteng) or mostly (sambar) found in logged areas over primary forests. Future

research is needed to quantify the availability of graminoids and other ungulate forage plants in logged versus unlogged forests. Second, the control of hunting in tropical forests, particularly in selectively-logged forests where roads increase accessibility, is critical for successful conservation of these species. Asian elephants, banteng, and sambar are all likely declining in abundance due to a combination of direct exploitation and habitat destruction (IUCN, 2009). Our results suggest, however, that carefully-planned selective logging, in the absence of hunting, might actually benefit these species, probably by increasing the abundance of graminoid forage. This implies that the declines of these large mammals across Southeast Asia are likely driven mostly by overexploitation. Third, in contrast to many of the large herbivorous mammals, past logging intensity at Maliau may have been too intense for several mammalian carnivore species. It is therefore imperative that we identify thresholds in logging intensity that preclude or negatively impact carnivore habitat use. This will allow logging guidelines to be revised so as to avoid compromising the regional persistence of these and other primary forest mammals.

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