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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.

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 (Kinnaird 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) 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.

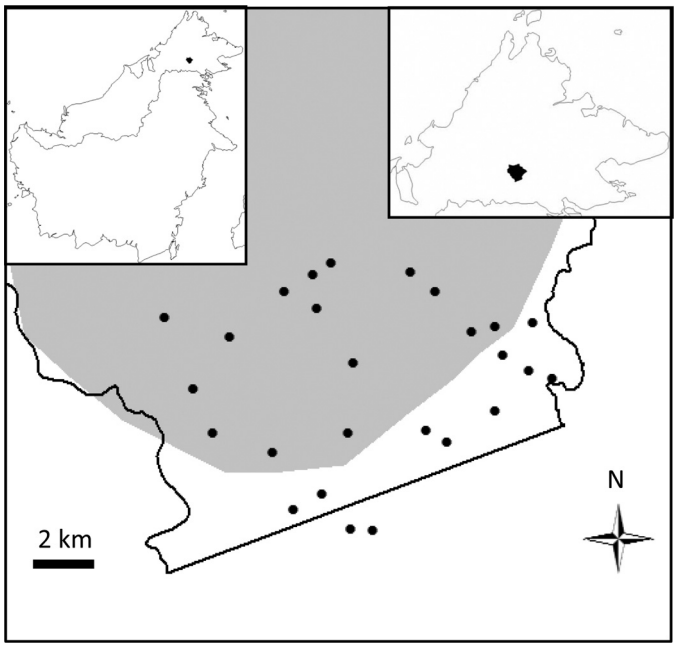

Fig. 1. Map of the study area in the southern portion of the Maliau Basin Conservation Area. Primary forest shown in gray, conservation area border as a black line, and camera trap locations as black circles. Insets show the location of the conservation area within Sabah (upper right) and within Borneo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

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^2; 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.