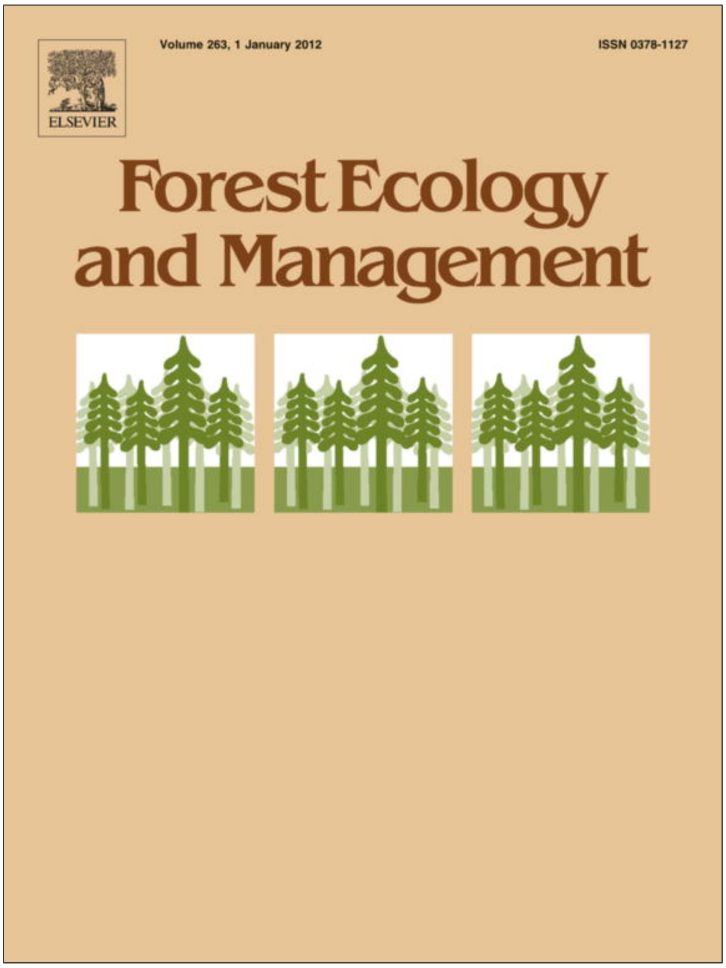
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# Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management

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ABSTRACT

To evaluate the effectiveness of sustainable forest management (SFM) for wildlife conservation, we investigated the abundances of medium to large ground-dwelling vertebrates in a forest management unit in Borneo by camera trapping. The forest management unit (FMU), Deramakot Forest Reserve (55,083 ha), has applied SFM for the past 15 years. We established 15 plots in preharvested areas and five plots in postharvested areas over the FMU. Plots in the postharvested areas had been subject to reduced-impact logging from 2 to 13 years ago. We obtained photos of ground-dwelling vertebrates with infrared sensor cameras set at 12 random points in each plot. Based on the numbers of photos taken over 770 camera days in each plot, we calculated the mean trapping rate (MTR) of each species for each plot. Over the 20 plots, we obtained 5444 photos of 39 medium-to-large vertebrates (i.e., mammals, birds, and monitor lizards); these included many elusive and endangered species. Among the 39 species, no species showed a significant difference in MTR between the pre- and postharvested areas. Furthermore, species composition was not significantly different between the pre- and postharvested areas. Our results support the idea that implementation of SFM can be an effective investment in wildlife conservation in tropical rainforests.



## 1. Introduction

Although tropical rainforests have a high biodiversity (Richards, 1952; Whitmore, 1998), most of the area in the Southeast Asian is used for timber production (Johns, 1997; Dennis et al., 2008). The direct and indirect impacts of logging activity on biodiversity have been widely noted (Burgess, 1971; Heydon and Bulloh, 1996; Whitman et al., 1998; Willott et al., 2000; Fimbel et al., 2001; Costa et al., 2002; St-Laurent et al., 2007; Dennis et al., 2008; Corlett, 2009). To reduce the negative impacts of logging, mitigating measures in logging practices have been recommended (Marcot et al., 2001; Mason and Putz, 2001; Meijaard et al., 2006; IUCN, 2007).

Sustainable forest management (SFM) aims to balance sustainable timber production and environmental soundness (Cerutti et al., 2006; Dennis et al., 2008). Minimizing the impacts of logging on biodiversity is one of the important targets of SFM. SFM includes the allocation of exclusively protected areas where logging is not allowed, the adoption of reduced-impact logging techniques (RIL) to minimize the impacts of timber harvesting, the regulation of annual allowable cutting volume (AAC) and the establishment of a long cutting cycle to maintain the total standing stock. Since the 1990s, several forest certification schemes, such as that provided by the Forest Stewardship Council (FSC), have been formulated to promote SFM (Vogt et al., 1999). These schemes define the criteria and standards of SFM of forest management units (FMU) (Hanlon et al., 1989; Forest Stewardship Council, 1996). Some of the criteria and standards require management efforts to reduce the impacts on biodiversity and to monitor the achievements (Forest Stewardship Council, 1996).

Several studies have assessed the effect of RIL, a component of SFM, on biodiversity conservation (Davis, 2000; Azevedo-Ramos et al., 2006; Wunderle et al., 2006; Castro-Arellano et al., 2007; Presley et al., 2008; Dias et al., 2009; Bicknell and Peres, 2010). However, the other measures of SFM, including limitation of AAC and controls on hunting, can also contribute to maintaining biodiversity conservation and thus should be evaluated.

Mammals are a good indicator taxon for the evaluation of the effects of forestry activities on biodiversity for two reasons. First, the impacts of logging on mammals have been well studied and reviewed (Azevedo-Ramos et al., 2006; Davies et al., 2001), especially in Borneo (WWF Malaysia, 1982; Johns, 1988; Heydon

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and Bulloh, 1996; Meijaard et al., 2005; Wells, 2005; Wells et al., 2007). Species groups that are sensitive to logging activity in general have already been indicated (Meijaard et al., 2005). Bennett and Gumal (2001) found that the species richness of mammals in Borneo is not significantly affected by logging, but rather that species composition can be changed. The abundances of insectivorous and frugivorous species often decrease after logging (Heydon and Bulloh, 1996; Meijaard et al., 2005), while the abundances of ungulates species often increase after logging, perhaps because the increase in canopy openness promotes herbaceous growth on the forest floor (Davies et al., 2001; Meijaard et al., 2005). Therefore, the performance of improved forestry practices can be evaluated by testing these changes. Second, unlike other taxa, such as trees and most insects, medium-to-large mammals have an indicator character in their large area requirements and high vagility (Barlow et al., 2007; O'Brien et al., 2010). Animals with large area requirements are sensitive to landscape changes, such as habitat fragmentation (O'Brien et al., 2010), but conversely, local extirpation in small patches can be easily compensated for by immigration from surrounding habitats. Their presence/absence or abundance at a specific site may be determined not only by the local conditions at the site, which can be maintained by RIL, but also by the location of the site in the broader landscape, which is affected by the layout of the conservation area, the cutting sequence of compartments in the FMU, and the length of the cutting cycle. Due to the high heterogeneity of tropical rainforests (Ancrenaz et al., 2010), the abundances of animals that depend on small areas can be highly variable over a small spatial scale, but the abundances of medium-to-large mammals can represent the averaged habitat quality across a large spatial scale, thus providing a proper index for forest management.

In Borneo, the orangutan is the only species whose population status has been evaluated over the spatial scale of an entire FMU. Ancrenaz et al. (2004) developed a formula to estimate orangutan population abundance from nest density, which can be counted by aerial census. Using this method, they estimated the orangutan populations in all FMUs in Sabah (Ancrenaz et al., 2005). They found that 60% of the orangutan population in Sabah lives outside protected areas, such as national parks, and they indicated the importance of the timber concessions for their conservation (Ancrenaz et al., 2005). However, they also found that the orangutan is a disturbance-tolerant species, inhabiting even highly degraded forest (Ancrenaz et al., 2010). This indicates that the orangutan is not a sensitive indicator species.

The Deramakot Forest Reserve, Sabah, Malaysia, is directly managed by the Sabah Forestry Department under SFM principles as a "model forest" to improve forest management in that state. Deramakot has one of the longest histories of the implementation of SFM in tropical regions; the conventional logging system was stopped in 1987, and RIL has been conducted since 1995. As a result of various efforts of SFM, Deramakot has been certified as "well managed" under the FSC scheme since 1997. As part of the monitoring of impacts on biodiversity, the density of orangutans in Deramakot has been monitored annually by aerial census since 1999, and no obvious population decline has been detected over the past 10 years (Sabah Forestry Department, 2009). Several other studies conducted in Deramakot have commented on the effects of SFM on biodiversity conservation (Eltz et al., 2003; Akutsu et al., 2007), but no assessment of the net performance of SFM on taxa other than orangutans has yet been conducted.

In this study, we tested the performance of SFM for conserving various medium-to-large ground-dwelling vertebrates in Deramakot. While we have already demonstrated that conventional logging has significantly reduced the abundance of several vertebrate species in the forest reserve located adjacent to Deramakot (Imai et al., 2009), this study focused on areas within Deramakot, in particular on the differences between before and after harvesting by RIL. We assumed that the abundances of each species and species richness and composition would not be significantly different between the pre- and postharvested areas when RIL started in 1995 because the original forest conditions and logging histories of these two types of areas were similar until that time. Thus, we assumed that any differences in the species abundances and composition at this study period (in 2008 and 2009) were caused by the impacts of RIL.

## 2. Materials and methods

### 2.1. Study site

We conducted our field work in the Deramakot Forest Reserve over a period of 19 months from February 2008 to September 2009. Deramakot is located in the interior of Sabah, Malaysia (5°13–28′N, 117°19–35′E). The area of the reserve is 55,083 ha, and the altitude is 30–330 m above sea level. The annual rainfall is approximately 4000 mm with no clear seasonality (Sabah Forestry Department, 2005). Most of the area is covered by lowland mixed dipterocarp forest.

Deramakot is legally classified as a production forest and has been managed primarily for timber production (Sabah Forestry Department, 2005). Logging activity in Deramakot started in 1956, and almost all areas were conventionally logged up to 1987 (Sabah Forestry Department, 2005). During 1959–1968, timber, with a mean volume of 109 $m^3\ ha^{-1}$, was harvested from the area (Sabah Forestry Department, 2005). Logging activity in Deramakot was halted in 1988 and then recommenced in 1995 under the SFM scheme. Under the current management, Deramakot is divided into 135 compartments (Fig. 1). Seventeen compartments (3473 ha or 6.3% of the area) are allocated to conservation, and the other 118 compartments (93.7% of the total area) are allocated to timber production (Lagan et al., 2007). However, parts of the production compartments are protected based on the steepness of the terrain or low density of harvestable trees. Hence, in total, 21% of the area of Deramakot is fully protected (Sabah Forestry Department, 2005). An inventory of the standing stock in all production compartments was conducted in 2002–2003 (Sabah Forestry Department, 2005). The results showed that the mean density of trees >60 cm diameter breast height (DBH) was 10.3 trees $ha^{-1}$ (ranging from 0.2 to 26.4 trees $ha^{-1}$ in each compartment), and the mean standing volume of trees >60 cm DBH in these production compartments was 50.8 $m^3\ ha^{-1}$ (1.0–121.8 $m^3\ ha^{-1}$). To ensure long-term sustainability, the annual allowable cut (AAC) for Deramakot was set at approximately 20,000 $m^3$. Based on this AAC, one to three compartments have been harvested using RIL every year; a total of 20 production compartments (105,800 ha) was harvested from 1995 to 2006. The mean standing volume of trees >60 cm DBH in these postharvested compartments prior to harvesting was estimated to be 83.3 $m^3\ ha^{-1}$, while the mean standing volume of the other production compartments was estimated to be 43.2 $m^3\ ha^{-1}$.

Based on RIL, all harvestable trees were measured before harvesting and located on a detailed map and appropriate routes for skidders were designed to minimize the damage to non-target trees. The trees harvested were limited to those in the range of 60–120 cm DBH, and trees that were near streams, on steep terrain, with hollows, or of fruiting species for wildlife were excluded from harvesting. Tangling vines were cut before harvesting and targeted trees were harvested with a directional felling technique. Felled trees were partly carried out by a cable crane, but mostly carried out by ground skidding. Between 1995 and 2006, a total

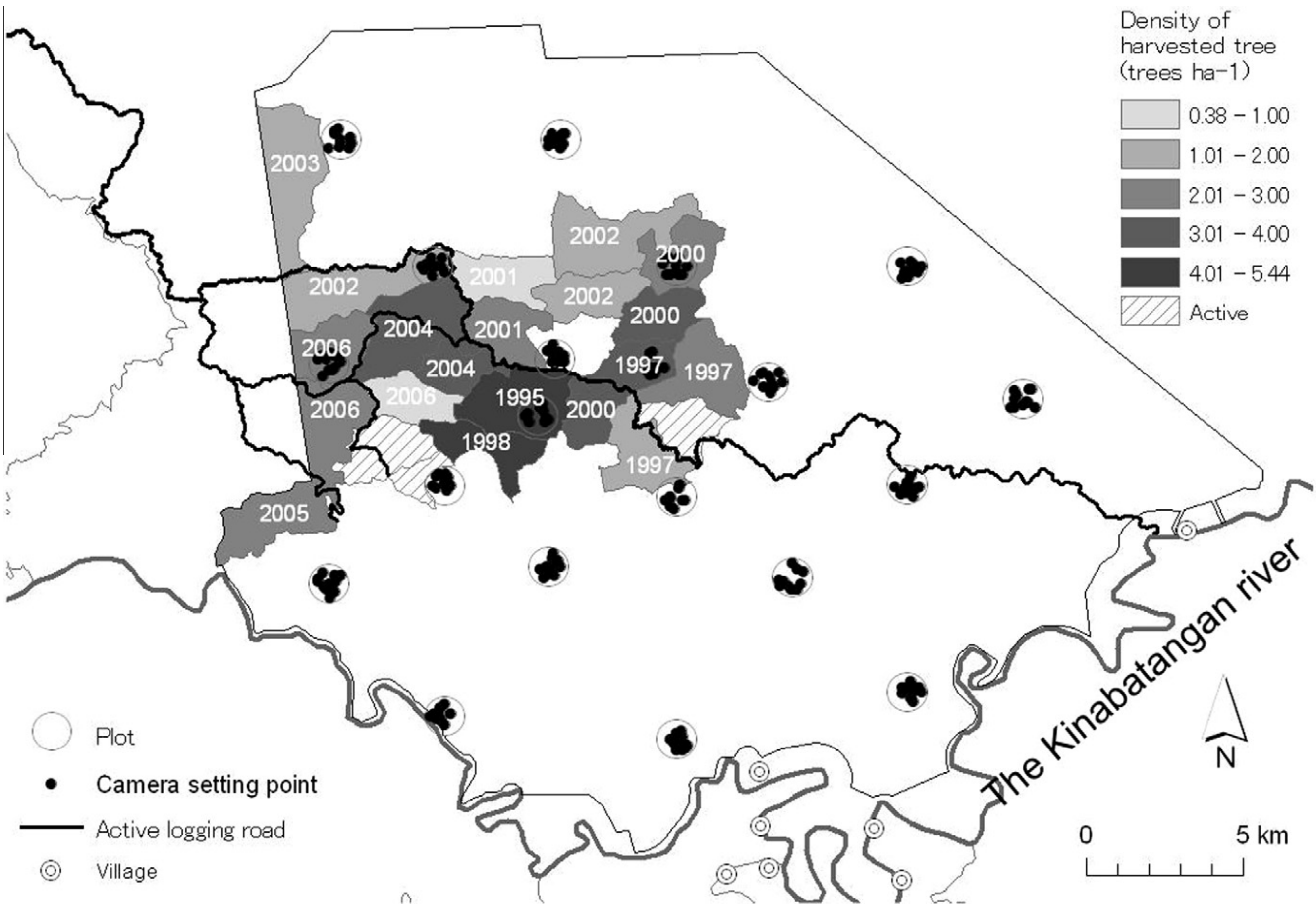


**Fig. 1.** One hundred and thirty-five compartments in Deramakot Forest Reserve, density of trees harvested by reduced-impact logging (RIL) and the localities of camera points. The number in each compartment indicates the most recent year in which timber was harvested.

of 24,934 trees (2.36 trees $ha^{-1}$) with a volume of 145,399 $m^3$ (13.74 $m^3$ $ha^{-1}$) were harvested.

Hunting pressure is low in Deramakot. There are no villages or other human settlements in Deramakot except those directly related to the forest management. Although there are five villages along the Kinabatangan River near Deramakot, with a total population of 789, 77.7% of the inhabitants are Muslim (Sabah Forestry Department, 2005) and do not generally eat wild meat. Furthermore, poaching from the surrounding area and all hunting activity by logging workers has been strongly discouraged by the staff of the FMU.

Many tree species of mixed dipterocarp forest synchronically flower and fruit for a few months every 1–5 years, known as the general flowering and mast fruiting phenomenon (Janzen, 1974; Ashton et al., 1988; Sakai, 2002). Many frugivorous mammals and birds are known to change their activity during the mast fruiting period (Leighton and Leighton, 1983; Curran and Leighton, 2000). The mast fruiting events happened in 2007 and 2010 in this study area, but during this study period, there was no mast fruiting period and fruiting activity of the forest was continuously low (Samejima, personal observation).

### 2.2. Relative abundance index

To evaluate the abundance of medium to large ground-dwelling vertebrates and their species composition, we used a relative abundance index: the mean trapping rate (MTR) of photos of each species and the total species composition taken by multiple automatic sensor cameras (camera traps) set at random points in a plot over a period.

We chose 20 plots in a systematic manner throughout Deramakot (Fig. 1). Plots were established at an interval of approximately 5 km. All plots were harvested at least once by conventional logging before it ceased in 1987. Five plots were located in the area harvested again under RIL guidelines in 1995, 1997, 2000, 2002, and 2006 (taken to represent postharvested forest conditions), and the other 15 plots were located in the area that had not been harvested since 1988 (preharvested forest conditions). Each plot was a circle with diameter of 1 km. We randomly selected 12 set points within each plot using the statistical software R 2.10.0 (R Development Core Team, 2009). We used an automatic film camera with a passive infrared sensor (Field Note II, Marifu, Iwakuni, Japan). In each plot, we could only use three cameras at any given time. Thus, we set the cameras at three set points for a particular period and then moved them to another three points every 3–5 months. We located each point using a GPS (GPSmap60CSx, Garmin Ltd., Olathe, KS) and set the camera on a tree approximately 50 cm above the ground. Each camera was set to face open ground, avoiding intrusive large trees and bushes which make it difficult to identify photographed species. We confined the area of field-of-view as 2–7 $m^2$. At a sloped set point, we faced the camera to upper slope to obtain easily identified images. At a flat set point, we faced the camera downward to limit the field-of-view from becoming too large. The films and batteries were changed every 1–2 months. All plots were assessed nearly simultaneously for the 19 months.

After a film was developed, we identified the animal species in each photo and recorded the time and date. Photographs were assessed for all animal species larger than the western tarsier (*Tarsius bancanus*) and moonrat (*Echinosorex gymnurus*). We excluded photos of animals that we could not identify. Rats, squirrels, tree shrews, bats, and small birds were excluded because of the difficulties of species identification. As the greater mouse-deer (*Tragulus napu*) and lesser mouse-deer (*Tragulus kanchil*) were sometimes hard to distinguish from each other, we treated these species as one morphospecies, *Tragulus* spp. We were also unsure about the precise identification of otters. Most pictures of otters looked like the oriental small-clawed otter (*Aonyx cinerea*). However, because Wilting et al. (2010b) reported two more species of otter in Deramakot and we are not certain of our identification, we categorized all of them simply as otters.

As the total active camera days for a plot was at least 770 camera-days, we counted the total number of photos for each species taken in a plot over 770 active camera-days and calculated the MTR for each plot. We excluded photos that we considered redundant in cases where the same species was photographed more than twice within 30 min. We defined the active camera-days as follows: if the camera had remaining exposure when we changed the film, we defined the active camera-days from the date when the camera was mounted until the film was changed. If the film was fully exposed when it was changed, we defined the active camera-days until the date stamped on the final exposure. Periods during which a camera malfunctioned were also excluded from the active camera-days. The 770 active camera-days were selected from the total active camera days in each plot, as the number of camera days are not much different among the set points in each plot.

Many previous studies have used automatic sensor cameras, or camera traps, to conduct basic inventories of medium to large ground-dwelling vertebrates (Foresman and Pearson, 1998; Silveira et al., 2003; Trolle, 2003; Srbek-Araujo and Chiarello, 2005; Pettorelli et al., 2010). Compared to survey methods that rely on direct sightings of animals, camera trapping is useful for detecting elusive species (Kays and Slauson, 2008). Since the 1990s, camera traps have also been used to evaluate animal abundance (Karanth and Nichols, 1998). The most numerous studies using camera traps to evaluate abundance are applications of a capture–recapture technique, which can be used only for species with recognizable pelage patterns that allow individual identification (Karanth and Nichols, 1998; Karanth et al., 2006; Trolle et al., 2007; Kays and Slauson, 2008; Balmea et al., 2009). Another recently developed method is occupancy estimation (MacKenzie et al., 2004, 2006). Using the maximum likelihood estimation or Bayesian statistics, the detection probability across the trap points was estimated. Based on this, a robust index of presence called the occupancy probability (proportion of area occupied by the species) can be estimated. O'Brien et al. (2010) further developed the wildlife picture index (WPI), a geometric mean of occupancy probabilities of species in a unit area.

For this study, we used the mean trapping rate (MTR), which is the number of photos of a certain species taken by a number of cameras set in a plot over a certain period, as a relative abundance index (Carbone et al., 2001; O'Brien et al., 2003). The correlation of the MTR with true density has been shown by Carbone et al. (2001), O'Brien et al. (2003), Rowcliffe et al. (2008, 2011) and Rovero and Marshall (2009). However, the correlation is still controversial because the stability of detection probability among plots is uncertified (Carbone et al., 2001, 2002; Jennelle et al., 2002; Karanth et al., 2004; Kays and Slauson, 2008; Rowcliffe and Carbone, 2008; Tobler et al., 2008; Rovero and Marshall, 2009; O'Brien, 2011).

We set cameras at many points to calculate the MTR of a plot with precision. If there are dense bushes or clear logging roads in a plot or if the target species has a stable nest site or feeding area, the time the animal spends at each point may be highly variable in the plot. Based on simulations, Rowcliffe et al. (2008) estimated 20 setting points is absolute minimum to precise estimation to the abundance. However, for four ungulate species, they detected a good correlation between true densities and MTR using only three to six set points. Rovero and Marshall (2009) also found that the trapping rate of a duiker from five to eight set points correlated well with the density estimated by a distance method.

However, MTR could not be used as an abundance index if the detection probability were different between plots in pre- and postharvested areas. The number of set points can improve the problem of low precision, but cannot solve the problem of low accuracy. In terms of the vegetation of this study area, the detection probability is considered not much different between the two areas. Even just a few years after RIL, the vegetation of our study area was relatively homogeneous and mostly covered by forest. If the vegetation of some plots were mixed with different vegetation types like forests and large open areas, and if the moving speed or grope size of the target species was different among the habitat types, then the detection probability may vary among the plots, but these condition was not in this study area. Furthermore, we devised the setting methods in several ways to reduce the differences of detection probability between plots in the two areas. (1) We excluded arboreal species to interpret. As the density of trees differs among plots, the proportion of time spent on the ground (the detection probability) may be different between plots in pre- and postharvested area. (2) We set cameras randomly. This differed from the mark-recapture method and occupancy estimation, which used to set cameras on clear trails to increase detection probability. Setting points for MTR should be selected randomly to reduce the difference of mean detection probability between the two areas (Rowcliffe et al., 2008). The frequency of animal stays may be different among habitats. If the habitat of set points were biased to specific habitats, such as trail, the mean detection probability varied among plots (Harmsen et al., 2010). However, if the proportion of habitat cameras set were corresponding with the proportion of the habitats in the plot by the random setting, such bias can be avoided (Rowcliffe et al., 2011). Recent innovations in GPS have enabled accurate positioning under dense canopies with little error (less than approximately 30 m), making it possible to place cameras in ideal locations. (3) We confined the area of a field-of-view in small areas (2–7 $m^2$) to ensure that it varied little across the setting points. At a flat point with no dense bush, it is easy to obtain a large field-of-view by setting camera parallel to the ground; however, large field-of-view is unable to obtain at a steep point or a plot with dense bushes. Therefore, we confirmed the field-of-view in small areas at all set points. (4) We set the cameras for a long time (19 months) at every plot to reduce the differences, such as weather, between the plots in the two areas. Animal daily movement distance (the averaged moving speed including resting time) and group size can be affected by weather or reproduction cycle, which may be different between plots in the two areas. These effects are considered to be reduced by long study periods. However, there is still a possibility that the detection probabilities were different between plots in the two areas. Several factors in a plot, such terrain steepness, the density of dense bush on the ground, and the density of the target species itself, may affect the daily movement distance or grope size of each individual and vary the detection probabilities between the two areas.

### 2.3. Statistical test

We tested differences in the MTR of medium to large vertebrates and also differences in the species composition between plots in pre- and postharvested areas. The differences in MTR were tested by Welch's $t$-test. As species with low MTR may not have enough statistical power for analysis and may cause a type II error, we also analyzed the statistical power for each $t$-test. To examine temporal changes in the effects of RIL for each species, we compared the MTR in each of the five postharvested plots to the MTR in the 15 preharvested plots using a Wilcox rank sum test, and we also compared the MTR among the five postharvested plots. The similarity of species composition between any combinations of two plots was evaluated using the Jaccard index. Using Mantel tests, we compared Jaccard indices between pre- and postharvested plots and Jaccard indices between two preharvested plots or between two postharvested plots. All statistical tests were conducted using R 2.10.0 (R Development Core Team, 2009).

## 3. Results

Among the 12 set points in which we set cameras in each plot, we could not obtain any active camera-days from several set points due to camera malfunctions. Therefore, the number of set points from which we could obtain data varied from 9 to 12. Active camera days in a plot ranged from 770 to 1181.

During the total 15,400 camera days (770 camera days $\times$ 20 plots), we obtained 5444 photos of 39 medium to large vertebrates: 35 mammal species (34 morphospecies), three terrestrial bird species, and a water monitor lizard (Table 1). Seven were endangered species, and 10 were vulnerable species as classified by the 2009 IUCN Red List of threatened species (IUCN, 2009). In addition, 12 mammal species and the three bird species were at least partially arboreal (Payne et al., 2005).

Among the 38 morphospecies, 15 had adequate statistical power for the Welch's $t$-test (power > 0.7). Before Bonferroni correction, the MTR of two species (the chestnut-necklaced partridge (*Arborophila charltonii*) and the thick-spined porcupine (*Thecurus crassispinis*)) were lower in postharvested than in preharvested areas, and the MTR of the sun bear (*Helarctos malayanus*) was higher in postharvested areas (Welch's $t$-test, $p < 0.05$). However, no species showed a significant difference in MTR between pre- and postharvested areas after Bonferroni correction. Although insectivorous and frugivorous species are known to be sensitive to logging (Heydon and Bulloh, 1996; Meijaard et al., 2005), the MTR of such species in Deramakot (the short-tailed mongoose (*Herpestes brachyurus*), the pig-tailed macaque (*Macaca nemestrina*), the bearded pig (*Sus barbatus*), greater and lesser mouse-deer (*Tragulus* spp.), the Malay badger (*Mydaus javanensis*), the common palm civet (*Paradoxurus hermaphroditus*), and the Malay civet (*Viverra tangalunga*)) did not show significant declines in postharvested areas. In addition, even though the mean MTR of the crested fireback (*Lophura ignita nobilis*) was notably higher in preharvested than that in postharvested areas, this was because the MTR of this species was very high at two plots along the Kinabatangan River. The difference between the pre- and postharvested areas was not significant.

Among the five postharvested plots, the MTR was smallest in the most recently harvested plot (2 years after harvest) for five species: the sambar deer (*Rusa unicolor*), the long-tailed porcupine (*Trichys fasciculate*), the Bornean yellow muntjac (*Muntiacus atherodes*), the bearded pig (*S. barbatus*), and *V. tangalunga*. In contrast, the MTR was highest in the most recently harvested plot for the bay cat (*Catopuma badia*) and the flat-headed cat (*Felis planiceps*). However, the MTR of the second most recently harvested plot (6 years after harvest) was not the second smallest or the second largest for these species. Compared to the MTR in preharvested plots, the MTR in any postharvested plots was not significantly lower for any species. In contrast, the MTR of three cat species (*C. badia*, *F. planiceps*, and the leopard cat *Neofelis diardi*) and *V. tangalunga* in some postharvested plots was significantly higher than those in preharvested plots ($p < 0.05$).

The number of species photographed per plot was also not significantly different between pre- and postharvested areas (Welch's $t$-test, $p < 0.05$). The Jaccard index between pre- and postharvested plots was $0.58 \pm 0.10$ (mean ± SD) and was not significantly different from that between preharvested plots ($0.59 \pm 0.19$) or that between postharvested plots ($0.59 \pm 0.19$) (Mantel test statistic $r = -0.181$, $p < 0.05$).

## 4. Discussion

In spite of continuous logging activity for the past 15 years, only a few ground-dwelling species showed weak, but not significant, differences in MTR between the pre- and postharvested areas. The composition of photographed species also did not show significant differences between the two forest conditions. Based on our results, we speculate that the density of each species and the species composition were not significantly different between them. Previous studies have indicated that insectivores and frugivores are sensitive to disturbances caused by conventional logging (Meijaard et al., 2005). However, in this study, the MTR of species belonging to these guilds did not show significant differences between pre- and postharvested areas. The MTR of herbivorous species that are known to increase in conventionally logged forests, such as Bornean yellow muntjac (*M. atherodes*) and *R. unicolor*, were also not different between the two areas. These results are in contrast to the finding that MTR of several species in the forest reserve adjacent to Deramakot were significantly lower than that in Deramakot (Imai et al., 2009). The lack of significant differences in photographed species composition also implies that the species composition of the two different areas are not much different. Assuming that the species compositions and abundance in pre- and postharvested areas were not significantly different from each other before RIL started in 1995, we suggest that the SFM in Deramakot has been effective in reducing the impacts of logging on medium to large ground-dwelling vertebrates.

However, the detection probability of some species still might be different between the plots in pre- and postharvested areas. The verification of the correlation between MTR and the true density estimated by other methods is necessary. The mark-recapture method, however, requires a huge effort to conduct, and the distance method is not practical in the steep condition of this study area. Another viable method is to measure the average moving speed and number of individuals (grope size) in an image in each plot. The average moving speed is measurable with the recent model of camera-trap which can record video images (Rowcliffe et al., 2011). If the averaged moving speed and number of individuals are not different among plots, then the detection probability can be considered to be stable among the plots. If the average moving speed and the number of individuals are indeed different among plots, MTR should be adjusted by the moving speed to use as relative abundance index. Further study is necessary.

Fifteen of the 39 species detected in this study were partially arboreal. We do not know the impacts of logging on these species because even if their populations declined after logging, MTR may be maintained by increases in the amount of their time spent on the ground. Surveying by line transect (Heydon and Bulloh, 1996) is necessary to confirm the impacts of logging on these species.

We suggest that the reduction of logging impact detected in this study was caused not only by the practice of RIL techniques, but also by other SFM practices. Although the density of trees harvested was suppressed and skid trails were planned to minimize

**Table 1**
Mean ± standard deviation of trapping rate (the number of photos in 770 camera-days per plot) for each species in pre- and postharvested areas in Deramakot Forest Reserve. $p$ is the probability by Welch's $t$-test before Bonferroni correction. A $p > 0.05$ is indicated as "–". Power is the statistical power for the $t$-test. EN: endangered species, VU: vulnerable species on the IUCN Red List (IUCN, 2009). Main food habitat is based on Matsubayashi et al. (2007), Smythies (1999), and Myers (2009). C: carnivore, HF: herbivore and frugivore, I: insectivore, O: omnivore.

| Common name | Species | Threatened status | Main food habit | Pre-harvested area | Post-harvested area | | | | | | $p$ (Welch's $t$-test) | Power |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Year after RIL | | | | | Average | | |
| | | | | | 2 | 6 | 8 | 11 | 13 | | | |
| Great argus | *Argusianus argus grayi* | | O | 23.20 ± 18.68 | 8 | 21 | 40 | 8 | 9 | 17.20 ± 13.88 | – | 1.00 |
| Crested fireback | *Lophura ignita nobilis* | | O | 13.27 ± 32.06 | 3 | 2 | 3 | 0 | 0 | 1.60 ± 1.52 | – | 1.00 |
| Pig-tailed macaque | *Macaca nemestrina*[†] | VU | O | 19.60 ± 13.27 | 13 | 25 | 26 | 43 | 11 | 23.60 ± 12.80 | – | 1.00 |
| Sambar deer | *Rusa unicolor* | VU | HF | 8.20 ± 7.39 | 0 | 5 | 4 | 8 | 4 | 4.20 ± 2.86 | – | 1.00 |
| Chestnut-necklaced partridge | *Arborophila charltonii* | | O | 4.73 ± 4.96 | 0 | 3 | 1 | 1 | 0 | 1.00 ± 1.22 | 0.02 | 1.00 |
| Sun bear | *Helarctos malayanus* | VU | O | 1.93 ± 1.67 | 7 | 7 | 6 | 4 | 2 | 5.20 ± 2.17 | 0.02 | 1.00 |
| Greater mouse-deer and Lesser mouse-deer | *Tragulus napu* and *T. kanchil* | | HF | 59.53 ± 46.89 | 62 | 56 | 63 | 91 | 41 | 62.60 ± 18.15 | – | 1.00 |
| Malay badger | *Mydaus javanensis* | | C | 6.20 ± 5.14 | 3 | 3 | 2 | 7 | 1 | 3.20 ± 2.28 | – | 1.00 |
| Long-tailed porcupine | *Trichys fasciculate* | | HF | 16.00 ± 12.73 | 2 | 31 | 37 | 19 | 5 | 18.80 ± 15.43 | – | 1.00 |
| Common porcupine | *Hystrix brachyura* | | HF | 5.07 ± 6.76 | 0 | 3 | 8 | 0 | 1 | 2.40 ± 3.36 | | 0.99 |
| Bornean yellow muntjac | *Muntiacus atherodes* | | HF | 28.40 ± 20.48 | 7 | 24 | 40 | 44 | 17 | 26.40 ± 15.53 | – | 0.92 |
| Thick-spined porcupine | *Thecurus crassispinis* | | HF | 2.00 ± 3.40 | 0 | 0 | 0 | 0 | 0 | 0.00 | 0.04 | 0.92 |
| Banded palm civet | *Hemigalus derbyanus* | VU | O | 11.47 ± 8.07 | 9 | 9 | 8 | 13 | 9 | 9.60 ± 1.95 | – | 0.88 |
| Tembadau | *Bos javanicus* | EN | HF | 1.53 ± 4.90 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.74 |
| Common palm civet | *Paradoxurus hermaphroditus*[a] | | O | 2.47 ± 3.85 | 0 | 0 | 2 | 2 | 1 | 1.00 ± 1.00 | – | 0.70 |
| Water monitor | *Varanus salvator* | | C | 2.00 ± 2.67 | 1 | 1 | 0 | 2 | 1 | 1.00 ± 0.71 | – | 0.40 |
| Bearded pig | *Sus barbatus* | VU | O | 16.93 ± 14.19 | 6 | 22 | 11 | 36 | 14 | 17.80 ± 11.71 | – | 0.31 |
| Asian elephant | *Elephas maximus* | EN | HF | 0.87 ± 1.73 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.31 |
| Short-tailed mongoose | *Herpestes brachyurus* | | C | 1.80 ± 1.52 | 3 | 4 | 0 | 5 | 0 | 2.40 ± 2.30 | – | 0.17 |
| Orangutan | *Pongo pygmaeus* [a] | EN | HF | 1.53 ± 1.64 | 0 | 1 | 3 | 1 | 0 | 1.00 ± 1.22 | | 0.15 |
| Bay cat | *Catopuma badia* | EN | C | 0.07 ± 0.26 | 3 | 0 | 0 | 0 | 0 | 0.60 ± 1.34 | – | 0.15 |
| Malay civet | *Viverra tangalunga* | | O | 16.07 ± 11.46 | 6 | 45 | 9 | 11 | 7 | 15.60 ± 16.55 | – | 0.12 |
| Yellow-throated marten | *Martes flavigula*[a] | | C | 0.87 ± 0.92 | 0 | 0 | 1 | 0 | 1 | 0.40 ± 0.55 | – | 0.12 |
| Banded linsang | *Prionodon linsang*[a] | | C | 0.47 ± 0.92 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.12 |
| Pangolin | *Manis javanica* | EN | I | 0.93 ± 1.10 | 1 | 0 | 1 | 0 | 1 | 0.60 ± 0.55 | – | 0.09 |
| Otter | *Aonyx cinerea* and *Lutra* spp. | VU | C | 0.33 ± 0.62 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.09 |
| Flat-headed cat | *Felis planiceps* | EN | C | 0.00 | 1 | 0 | 0 | 0 | 0 | 0.20 ± 0.45 | – | 0.06 |
| Long-tailed Macaque | *Macaca fascicularis*[a] | | O | 0.53 ± 0.99 | 1 | 0 | 0 | 1 | 0 | 0.40 ± 0.55 | – | 0.06 |
| Binturong | *Arctictis binturong*[a] | VU | O | 0.13 ± 0.35 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.06 |
| Leopard cat | *Prionailurus bengalensis* | | C | 0.13 ± 0.35 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.06 |
| Collared mongoose | *Herpestes semitorquatus* | | C | 0.07 ± 0.26 | 0 | 0 | 0 | 1 | 0 | 0.20 ± 0.45 | – | 0.06 |
| Marbled cat | *Felis marmorata*[a] | VU | C | 0.27 ± 0.80 | 0 | 1 | 0 | 0 | 0 | 0.20 ± 0.45 | – | 0.05 |
| Otter civet | *Cynogale bennettii* | EN | C | 0.07 ± 0.26 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.05 |
| Red leaf monkey | *Presbytis rubicunda*[a] | | HF | 0.07 ± 0.26 | 0 | 0 | 0 | 0 | 0 | 0.00 ± 0.00 | – | 0.05 |
| Small-toothed palm civet | *Arctogalidia trivirgata*[a] | | O | 0.07 ± 0.26 | 0 | 0 | 0 | 0 | 0 | 0.00 | – | 0.05 |
| Moonrat | *Echinosorex gymnurus* | | I | 11.60 ± 12.64 | 7 | 9 | 8 | 4 | 30 | 11.60 ± 10.45 | – | 0.05 |
| Clouded leopard | *Neofelis diardi*[a] | VU | C | 0.40 ± 0.51 | 0 | 2 | 0 | 0 | 0 | 0.40 ± 0.89 | – | 0.05 |
| Western tarsier | *Tarsius bancanus*[a] | VU | I | 0.40 ± 0.74 | 2 | 0 | 0 | 0 | 0 | 0.40 ± 0.89 | – | 0.05 |
| Number of species | | | | 20.93 ± 2.96 | 19 | 20 | 19 | 19 | 17 | 18.80 ± 1.10 | 0.03 | 0.95 |

[a] Indicates at least partially arboreal mammal species (Payne et al., 2005).

their total length, 58.8% of the area in targeted compartments was disturbed. Thus, we suspect that most ground-dwelling vertebrates must have escaped from the harvesting area, at least during the logging operation. Therefore, we conclude that the preservation of the original species composition after RIL was assisted by three factors: (1) confining the annual harvest to only a small part of the FMU supports rapid population recovery by immigration from surrounding compartments after harvesting; (2) RIL prevents irreversible reductions in food and shelter resources to support populations inside the compartment; and (3) the access of hunters to the logging area is limited.

Considering temporal variation after RIL, while the MTR in any postharvested plots was not significantly lower than that in preharvested plots for all species, the MTR for five species in a plot only 2 years after harvest were the lowest of all postharvest plots. Logging disturbance may impact these species. However, the MTR in the plot 6 years after harvest were not lower than that in other plots, indicating that the population might recover during the second to sixth years after RIL. It is notable that the MTR of some wild cat species and *V. tangalunga* were somewhat higher in some plots of recently logged forest than in preharvested plots. This is a surprising result because the wild cat species, especially *C. badia* and *F. planiceps*, are known to be some of the most rare and endangered species in Borneo (Mohamed et al., 2009; Wilting et al., 2010a,b). Although populations of these species may be sustained by good forest condition in Deramakot, small-scale disturbances by RIL may be preferred by these species as foraging sites. The disturbance by RIL may increase the abundance of terrestrial insects and other small animals, which are food resources for these carnivorous species.

Recently, the importance of production forests in conserving biodiversity in tropical regions became widely accepted (Putz et al., 2001; Zarin, 2004; Ancrenaz et al., 2005, 2010; Meijaard and Sheil, 2007; Imai et al., 2009; Patterson and Coelho, 2009; Edwards et al., 2010). Although Borneo is a global hotspot for biodiversity, fully protected areas, such as national parks, comprise only a small part of Borneo's area and are isolated from each other. The continuous production forests under proper management between the fully protected areas can increase the long-term survival of many species. Our study shows that FMU under SFM schemes such as Deramakot can play a role in this function.

Indeed, Deramakot supports a rich diversity of mammals, including many elusive and endangered species. In addition to our records, nine mammal species (the flying lemur (*Cynocephalus variegates*), the slow loris (*Nycticebus coucang*), the silvered langur (*Presbytis cristata*), the Bornean gibbon (*Hylobates Muelleri*), the proboscis monkey (*Nasalis larvatus*), the Malay weasel (*Mustela nudipes*), the hairy-nosed otter (*Lutra sumatrana*), the smooth otter (*Lutrogale perspicillata*), and the masked palm civet (*Paguma larvata*)) have been observed by us or documented by Matsubayashi et al. (2007) and Wilting et al. (2010a,b). Thus, at least 42 medium-to-large mammalian species inhabit Deramakot. Considering that 51 medium-to-large mammal species have been recorded in all of Borneo (Payne et al., 2005), 82.3% of the species inhabit this small forest reserve, which covers only 0.007% of the total area of Borneo.

To confirm the mitigation effects of SFM, the long-term monitoring of a site is required before the start of RIL operations. In this study, we assumed that mammalian density and species composition were not significantly different between pre- and postharvested areas prior to RIL harvest. However, because the standing volume in the postharvested area before harvest was relatively higher than that in the preharvested area, the population densities of several species in the postharvested area before harvesting could have been higher than those in the preharvested area. Although we can conclude from this study that logging operations with RIL techniques do not cause irreversible differences in species composition, a long-term monitoring study is necessary to confirm this effect.

The mitigation effects of SFM practices detected in our study might be due to the much-reduced harvest intensity employed in Deramakot. Deramakot was almost entirely logged prior to the introduction of RIL. Compared to primary forest, damage to the forest environment during road construction was less severe in Deramakot because old existing roads could be reused (Samejima, personal observation). The density of the harvestable trees before logging were obviously lower than that in primary forests. The mean standing volume of trees >60 cm DBH was only 83.3 $m^3\ ha^{-1}$ in Deramakot, which was considerably lower than the 185 $m^3\ ha^{-1}$ recorded in a primary forest of East Kalimantan (Sist et al., 1998). As a result, only 2.36 trees $ha^{-1}$, with a volume of 13.74 $m^3\ ha^{-1}$, were harvested in Deramakot. This is in contrast with the $7.0 \pm 3.0$ trees $ha^{-1}$ ($56.5 \pm 23.3\ m^3\ ha^{-1}$) harvested by RIL in the primary forest (Sist et al., 1998). Sist et al. (2003) indicated that even RIL could cause severe damage to tree populations and delay the recovery of standing stock when the harvesting intensity was at more than 8 trees $ha^{-1}$. Therefore, the effectiveness of SFM in maintaining biodiversity may not be assured if logging intensity is high. Comparable camera-trapping studies in different FMUs will provide more reliable information about the effectiveness of SFM in maintaining biodiversity.

Meijaard et al. (2005) strongly recommended practical studies for improving forest management for biodiversity conservation. There have already been several studies on the effects of RIL on biodiversity at the compartment level (Foody and Cutler, 2003). However, the net effects of SFM can also be derived from the adequate allocation and layout of conservation areas over an entire FMU and by the length of the cutting cycle. The impact of SFM on the compartment level can be misperceived if the impact assessment is conducted only just after logging (Azevedo-Ramos et al., 2006; Felton et al., 2008; Bicknell and Peres, 2010). As in this study, impact assessments of SFM on biodiversity conservation need to be conducted over the entire FMU.

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