

Effects of reduced-impact logging on medium and large-bodied forest vertebrates in eastern Amazonia

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Abstract: Standard line-transect census techniques were deployed to generate a checklist and quantify the abundance of medium and large-bodied vertebrate species in forest areas of eastern Amazonia with and without a history of reduced-impact logging (RIL). Three areas were allocated a total of 1,196.9 km of line-transect census effort. Sampling was conducted from April to June 2012 and from April to August 2013, and detected 29 forest vertebrate species considered in this study belonging to 15 orders, 20 families and 28 genera. Additionally, eight species were recorded outside census walks through direct and indirect observations. Of this total, six species are considered vulnerable according to IUCN (*Ateles paniscus*, *Myrmecophaga tridactyla*, *Priodontes maximus*, *Tapirus terrestris*, *Tayassu peccary*, *Chelonoidis denticulata*). Observed species richness ranged from 21 to 24 species in logged and unlogged areas, and encounter rates along transects were highly variable between treatments. However, the relative abundance of species per transect did not differ between transects in logged and unlogged forests. Of the species detected during censuses, only three showed different relative abundance between the two treatments (*Saguinus midas*, *Tinamus* spp. and *Dasyprocta leporina*). Our results show that the effect of RIL forest management was a relatively unimportant determinant of population abundance for most medium and large vertebrates over the time period of the survey.

Keywords: fauna, forest management, tropical rainforest, mammals, birds.

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Resumo: Técnicas padronizadas de censo por transecções lineares foram empregadas para gerar uma lista e quantificar a abundância de espécies de vertebrados de médio e grande porte em áreas de floresta na Amazônia oriental, com e sem uma história de exploração de impacto reduzido (EIR). Três áreas foram amostradas com um esforço total de 1.196,9 km de censo ao longo de transectos lineares. A amostragem foi realizada de abril-junho de 2012 e de abril-agosto de 2013, e detectou 29 espécies florestais de vertebrados consideradas neste estudo pertencentes a 15 ordens, 20 famílias e 28 gêneros. Adicionalmente, oito espécies foram registradas fora dos censos ao longo dos transectos por meio de observações diretas e indiretas. Desse total, seis espécies são consideradas vulneráveis de acordo com a IUCN (*Ateles paniscus*, *Myrmecophaga tridactyla*, *Priodontes maximus*, *Tapirus terrestris*, *Tayassu pecari*, *Chelonoidis denticulata*). A riqueza das espécies observada variou de 21 a 24 espécies em áreas com e sem corte seletivo, e as taxas de encontro ao longo dos transectos foram bastante variáveis entre os tratamentos. No entanto, a abundância relativa das espécies por transecto não diferiu entre florestas não exploradas e exploradas. Das espécies detectadas durante o censo, apenas três apresentaram diferentes abundâncias relativas entre os dois tratamentos (*Saguinus midas*, *Tinamus* spp. e *Dasyprocta leporina*). Nossos resultados mostram que o efeito do manejo florestal EIR não foi relativamente determinante para abundância populacional da maioria dos vertebrados de médio e grande porte.

Palavras-chave: Fauna, manejo florestal, floresta tropical, mamíferos, aves.

Introduction

Maintaining viable populations of medium and large-bodied vertebrates is essential if tropical forests are to maintain their current structure and composition (Wright et al. 2007, Terborgh et al. 2008, Gutierrez-Granados et al. 2010, Beck et al. 2013). For example, most Amazonian tree species are dispersed by forest vertebrates. In the Guiana Shield and Central Amazonia, frugivorous vertebrates disperse over 94% of all woody plant species (Peres & van Roosmalen 2002). Thus, surveys to assess the impact of any anthropogenic forest disturbance on faunal assemblages are essential to the understanding of biodiversity and ecological processes, as well as planning management and conservation strategies for forests and their constituent faunas (Willis et al. 2007).

However, despite the importance of medium and large vertebrates, extensive knowledge gaps still remain on these species (Paglia & Fonseca 2009). In Amazonia, this lack of knowledge comes partly from the vast area and ensuing difficulties in accessing many areas, both of which hinder studies over much of the basin. Despite the physical remoteness of some areas, between 1988 and 2013 more than 9.5% of primary forests across the Brazilian Amazon was either converted or severely degraded (INPE 2014) by various anthropogenic drivers including deforestation, forest fires, and fragmentation (Fearnside 2005, Michalski et al. 2008, Peres et al. 2010). To help minimize this impact, some 90 million hectares of Amazonian forests have been designated as Sustainable Use Protected Areas (SUPAs) (Peres 2011). Such areas are set aside for the sustainable use of natural resources, in addition to maintaining biodiversity and other ecological functions (Brazil 2000). Timber extraction is therefore a key economic activity in achieving the often intractable goal of reconciling financially viable land-use revenues and forest conservation within SUPAs.

Although controversial, selective logging has been widely promoted as one of the least harmful patterns of land use for tropical forest animal and plant communities (Johns 1991, Grove 2002, Meijaard & Sheil 2008, Gibson et al. 2011, Kudavidanage et al. 2012). However, this activity can alter the composition and structure of the original forest (Peres et al. 2010). Observed changes include modifications in the amount of litter, leaves, flowers and the elimination of fruiting trees important to the trophic viability of frugivore populations (Johns 1988, Uhl & Vieira 1989, Johns 1992, Chapman et al. 2000). In addition, a post-logging forest landscape may become more homogeneous (Kitching et al. 2013), potentially degrading habitats available for the vertebrate fauna. Studies across the humid tropics on the impacts of logging on forest biodiversity are plagued by a myriad of methodological problems (Laufer et al. 2013). Ideally, effectively assessing the impacts of selective logging requires a proper understanding of the structure and composition of forests and their wildlife both before and after logging (Johns 1986, Kohler et al. 2002, Potts 2011, Samejima et al. 2012). This prevents spatially biased, pseudo-replicated, or intrinsically flawed assessments of the effects of selective logging on wildlife, because it retains the original distribution and composition of resident species across treatments (Peres et al. 2010).

The potentially detrimental effects of logging on wildlife can be reduced with the use of management techniques that minimize the effects of disturbances, such as different forms

of reduced-impact logging (Putz et al. 2008). This technique consists of planning management actions to minimize the direct and indirect impacts of logging, and to maintain both ecosystem processes and the economic and environmental viability of the activity (Barreto et al. 1998, Putz et al. 2008). RIL typically has a lower cutting intensity than other forms of timber extraction and studies typically report lower levels of collateral damage than those induced by more traditional techniques. RIL is reported to induce lower rates of species loss (Whitman et al. 1998, Azevedo-Ramos et al. 2006, Samejima et al. 2012), minimize the amount of canopy openings, reduce collateral damage (Uhl & Vieira 1989, Bicknell & Peres 2010) and thereby reduce the probability of post-cutting forest fires (Nepstad et al. 1999).

However, our understanding of the effects of forest perturbation associated with RIL on forest fauna, particularly on medium and large-bodied vertebrates, remains very poor. The aim of this study, therefore, was to use standardized wildlife census techniques to inventory the medium and large vertebrate fauna in order to provide both a species checklist and estimate the richness and relative abundance of vertebrate populations at an eastern Amazonian forest landscape providing a RIL-disturbed and undisturbed forest mosaic. For this we collected data within three different areas: one that had never been exposed to selective logging, another 2-3 years after RIL disturbance, and the third including both pre- and post-disturbance one year after a selective cutting operation had occurred. We predict that patterns of species abundance, if not species composition, would remain unchanged. This prediction can be expected due the well conserved landscape, proximity to unlogged forest, and the management forest applied on the forests (RIL). However, we expect to detect the influence of RIL on the abundance of at least some species, particularly on the abundance of those strict forest specialist species, due to their undisturbed old growth ecological requirements.

Methods

1. Study Area

The study was conducted in the Rio Jari basin of north-eastern Pará, eastern Brazilian Amazonia, within a vast private landholding controlled by Jari Florestal (hereafter, Jari landscape) (00°27'00"–01°30'00" S; 51°40'00"–53°20'00" W; Figure 1). This company manages an area of approximately 1,260,000 ha in the transition region between the lowland Amazon and the Guianan Highlands (Souza 2009). Between the 1960s and 1990s, approximately 10% of the landholding area consisting of primary forest was converted to plantations of fast-growing exotic trees (Barlow et al. 2010). The site is currently characterized by a large-scale mosaic of *Eucalyptus* plantations (~ 45,000 ha), secondary forest abandoned for some 20-25 years (> 50,000 ha), and a vast area of primary forest (~ 1 million ha) subjected to extremely low levels of human disturbance (Barlow et al. 2007, Gardner et al. 2007, Parry et al. 2007). The predominant vegetation within the Jari study landscape is dense lowland, submontane and montane rain forest, seasonally-flooded forest (igapó), open evergreen lowland forest, submontane forest with lianas and submontane forest with palms (Souza 2009). The canopy cover (25-50 m tall) is continuous (Souza 2009), and the dominant emergent tree species is the commercially valuable Angelim Vermelho (*Dinizia excelsa* Ducke).

The average annual rainfall is 2,115 mm, with an average annual temperature of 26°C (22°-34°C) (Ribeiro et al. 2008, Souza 2009). The three driest months of the year experience 60 mm lower precipitation (RADAM 1974). Soils consist mostly of yellow oxisols, inceptisols and podzolics. Other soil types, such as the ultisol and plinthosols, occur in smaller patches. The soils of upland forests vary in their proportions of sand, clay and silt, and include gravel to a greater or lesser extent (Souza 2009).

2. Survey Areas

Our field sampling took place in three Annual Operating Plots (POAs – from the Portuguese acronym, *Planos Operacionais Anuais*) (Figure 1). These contiguous areas span over 450 km². We sampled two areas before the intervention of selective logging: control area (POA-08) and POA-07_{PRE}. These areas had been exposed to low levels of human impact (e.g.: subsistence hunting and a low density of narrow unpaved roads). In POA-07, two long-established roads (> 20 years) were supplemented by 8 km of recent logging roads (> 2 years) to support forest management activities. The control area had some 20 km of much older roads (> 25 years) built by the company for forest inventories of the area. Two other areas were sampled after they had been exposed to RIL, POA-07_{POST} (logged in 2012) and POA-06 (logged in 2010-2011). POAs-07 and 08 were surrounded to the north by > 20 year-old

secondary forests and tree plantations (*Eucalyptus* plantations). To the south of POA-06 (> 2 km) lay a region where RIL disturbance had taken place between 2006 and 2008. The other sampling areas were embedded within a vast matrix of undisturbed primary forest. All areas had been exposed to little or no hunting pressure. Throughout the entire time period of eight months of fieldwork, we detected fewer than ten signs of any present or past hunting activity (including vehicle tracks, hunting traps, direct encounters with hunters, spent shells, and gunfire shots).

POA-07 and POA-06 were cut according to reduced-impact logging techniques. These aim to minimize logging impacts through careful planning of access roads and transportation, a 100% forest inventory of the area to be managed, selection of individual trees for cutting (DBH > 50 cm), and control of tree felling direction, among other mitigating measures to minimize collateral damage. The maximum cutting intensity allowed for these areas was 3-4 individual trees • ha⁻¹ (or 30 m³ of sawable timber per ha), which is similar to other Amazonian sites (Uhl & Vieira 1989). The minimum cut-off of logging intensity applied to the surveyed areas varied according to the spatial distribution of species of high commercial value and abiotic characteristics of the region (e.g. topography and drainages). The logged areas (POA-07_{POST} and POA-06) were harvested at low intensity (22.8 m³ • ha⁻¹). This logging intensity and the resulting collateral damage amounted to a 16.9% reduction in

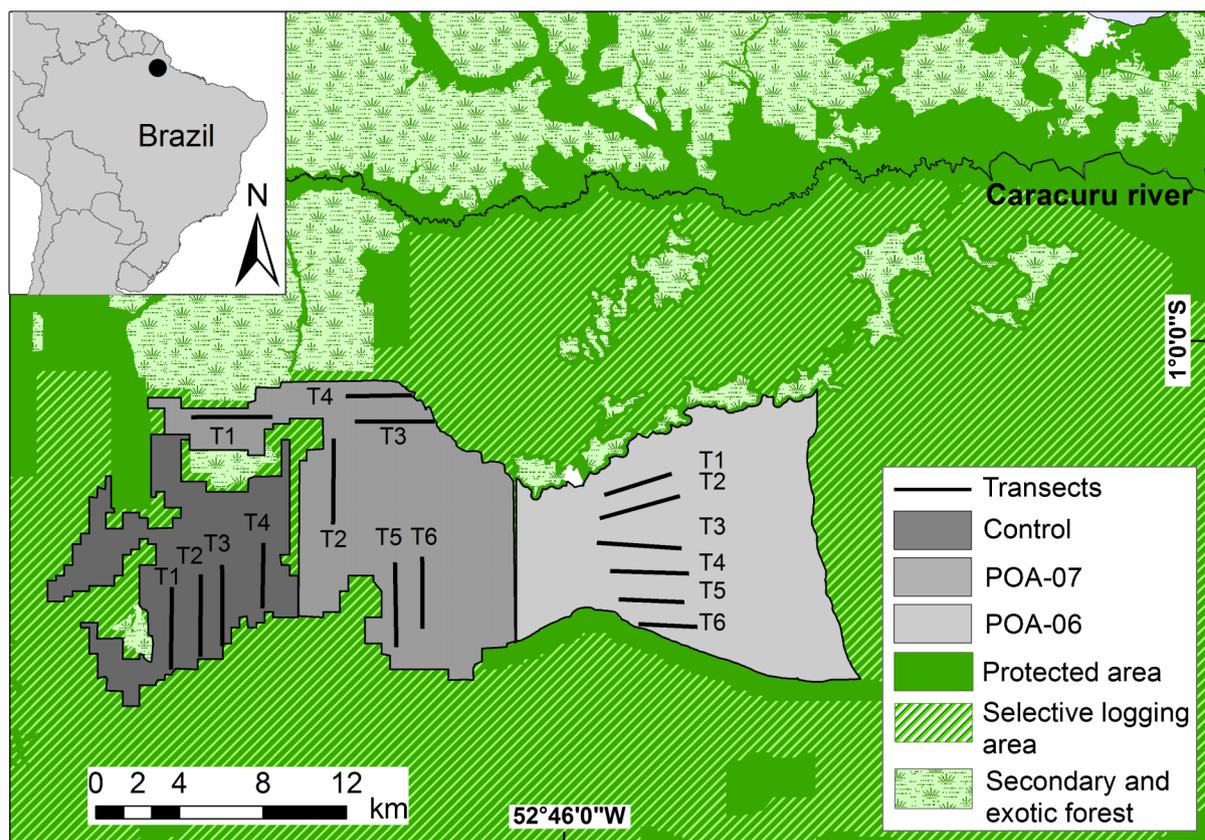


Figure 1. Location of the three study sites where medium and large-bodied vertebrates were surveyed in the municipal county of Almeirim, Pará, Brazil. Gray areas indicate those selected for the study, control, POA-07 (pre- and post-logging) and POA-06 areas. The green area indicates a legal forest reserve (LR) within the Jari study landscape and the hatched area, superimposed onto the LR, is the total area allocated to low-impact selective logging. Therefore, only the area south of POA-06 had been previously logged prior to this study (< 6 years).

forest basal area, compared to the basal area of the unlogged forest used as a control (J. Laufer, unpublished data).

3. Vertebrate censuses

We conducted two sessions of line-transect censuses of vertebrates over a 2-year period. The first sampling session occurred between April and June 2012, when we sampled POA-07 before selective logging intervention (POA-07_{PRE}). The second, between April and August 2013, sampled an area without intervention of selective logging, and another two with one and 2-3 years post-harvesting, respectively (POA_{Control}, POA-07_{POST} and POA-06). We avoided sampling any site during the months of July-December, when selective cutting normally takes place. To sample medium and large (> 250 g) vertebrates, we used a standardized line-transects census technique adjusted to local conditions (Peres & Cunha 2011). The census was conducted by observers with at least three years of experience of monitoring neotropical forest fauna. In total, a census effort of 1,196.9 km of line transect walks was accumulated in both unlogged treatments, POA-07_{PRE} and POA_{Control} (henceforth, UL), and logged forest (LF) treatments, POA-07_{POST} and POA-06. In each area between four and six linear transects of 3.2 to 4.5 km in length were cut, marked every 50 m, and mapped using a handheld GPS (Table 1). To maintain spatial independence, we spaced all transects by a minimum distance of 1 km (1-1.9 km, mean = 1.2 km, SD = ± 0.2). Each transect was walked at least 7 times in the morning and 3 to 7 times in the afternoon. To minimize possible sampling bias and randomly reshuffle observer effects, observers in each treatment were systematically rotated.

We followed the sampling protocol proposed by Peres & Cunha (2011) to census all diurnal forest vertebrate species larger than 250 g. Transects were walked at an average velocity of 1.25 km • h⁻¹ (Buckland et al. 2010a, b), which allows the use of both auditory and visual detections across all strata of

the forest (Peres & Cunha 2011). We systematically stopped for up to 1 min approximately every 100 m along transects to increase the likelihood of acoustic detections. Census work took place in the morning between 06:00 h and 11:00 h and in the afternoon from 13:30 h to 16:30 h. The sampling period varied with the logistics of each area and the vagaries of weather conditions. Censuses were discontinued during periods of mild to heavy rainfall, because under such conditions auditory detection is impaired and animals become less active (Peres 1999).

For each detection we recorded time, species and distance along the transect. For all small and large tinamous species (*Crypturellus* spp. and *Tinamus* spp., respectively), we grouped detection data by genus, due to inherent difficulties in identifying these birds to species during censuses (Bicknell & Peres 2010). To boost the detection power of vertebrate species occupancy (presence/absence) data we used both direct and indirect observations (presence of tracks, feces, hair and burrows) obtained along transects, as well as along the survey areas. Those ancillary data were also obtained when survey transects were being initially opened and during movements on foot between transects.

4. Data Analysis

To analyse whether the cumulative sampling effort in different areas was representative of the medium and large vertebrate assemblage we constructed per-transect species richness rarefaction curves, in which all visual and acoustic observations were combined. We analyzed data using the *vegan* (Oksanen et al. 2013) and *indicspecies* packages (De Cáceres & Jansen, 2014) with the R program function *specaccum* and *multipatt*, respectively (R Development Core Team 2013). ANOVAs were applied to perpendicular detection distances from transects (for both visual and acoustic records) to examine the variation in lateral detectability between the two treatments

Table 1. Sampling effort along different line transects in both logged and unlogged forest, length of transects (km), total distance censused (km), and encounter rates for all vertebrate species (visual and acoustic detections per 10 km walked) for each transect/treatment.

Unlogged Forest							
POA-07 (PRE)				Control			
Transect	Length (km)	Total (km)	Encounter rate	Transect	Length (km)	Total (km)	Encounter rate
T1	4.1	51.4	11.7	T1	3.9	75.0	14.1
T2	4.2	49.8	13.1	T2	3.9	65.9	13.5
T3	4.0	40.0	14.3	T3	4.0	69.1	23.7
T4	3.2	37.8	15.1	T4	3.2	66.6	15.9
T5	4.1	53.0	11.9				
T6	3.4	44.2	9.5				
TOTAL	22.9	276.2	12.4	TOTAL	15.0	276.5	16.8
Logged Forest							
POA-07 (POST)				POA-06 (POST)			
Transect	Length (km)	Total (km)	Encounter rate	Transect	Length (km)	Total (km)	Encounter rate
T1	4.1	55.9	13.8	T1	3.8	52.5	10.5
T2	4.2	58.1	7.7	T2	4.5	63.0	11.0
T3	4.0	54.5	9.9	T3	3.8	62.3	9.5
T4	3.2	43.6	15.3	T4	4.5	57.4	8.9
T5	4.1	57.1	12.1	T5	3.8	49.0	11.4
T6	3.4	47.6	13.9	T6	4.5	43.4	14.1
TOTAL	22.9	316.6	11.9	TOTAL	24.8	327.6	10.7

Vertebrates in selectively logged forests

Table 2. Form of detection for medium and large vertebrate species recorded along different logging treatments in this study. D = direct visual and acoustic observations; I = indirect observations (tracks, feces, hair and burrows). Unlogged Forest (UL) and Logged Forest (LF) correspond to relative abundance (detections per 10 km walked) of species in the two forest treatments. * Observations recorded outside censuses.

Group	Species	POA-07 _{PRE}	Control	POA-07 _{POST}	POA-06	Detection type	UL	LF
Birds	<i>Ara</i> spp.	X	X	X	X	D	0.29	0.31
	<i>Harpia harpyja</i> (Linnaeus, 1758)	X		X*		D	0.02	
	<i>Psophia crepitans</i> (Linnaeus, 1758)	X	X	X	X	D	0.22	0.12
	<i>Penelope marail</i> (Müller, 1776)	X	X	X	X	D	1.70	1.43
	<i>Crax allector</i> (Linnaeus, 1766)	X	X	X	X	D	0.58	0.42
	<i>Tinamus</i> spp.	X	X	X	X	D	2.88	1.82
	<i>Ramphastos tucanus</i> (Linnaeus, 1758)	X	X	X	X	D	1.94	1.46
	<i>Amazona ochrocephala</i> (Gmelin, 1788)	X	X	X	X	D	1.32	0.95
	<i>Ibycter americanus</i> (Boddaert, 1783)	X	X	X	X	D	0.20	0.06
	<i>Alouatta macconnelli</i> (Linnaeus, 1766)	X	X	X	X	D	0.58	0.50
	<i>Ateles paniscus</i> (Linnaeus, 1758) ^v	X	X	X	X	D	0.69	0.73
	<i>Pithecia pithecia</i> (Linnaeus, 1766)	X	X	X	X	D	0.07	0.06
	<i>Saguinus midas</i> (Linnaeus, 1758)	X	X	X	X	D	2.50	1.06
	<i>Saimiri sciureus</i> (Linnaeus, 1758)	X	X	X	X	D	0.02	
	<i>Sapajus apella</i> (Linnaeus, 1758) ^v	X	X	X	X	D	0.45	0.68
Ungulata	<i>Tapirus terrestris</i> (Linnaeus, 1758) ^v	X	X	X	X	D, I	0.16	0.06
	<i>Pecari tajacu</i> (Linnaeus, 1758)	X	X	X	X	D, I	0.13	0.30
	<i>Tayassu pecari</i> (Link, 1795) ^v	X	X	X	X	I		
	<i>Mazama americana</i> (Erxleben, 1777)	X	X	X	X	D, I	0.11	0.23
	<i>Mazama gouazoubira</i> (G. Fischer [von Waldheim], 1814)	X	X	X	X	D, I	0.18	0.30
	<i>Myoprocta exilis</i> (Wagler, 1831)	X	X	X	X	D	0.02	0.06
	<i>Sciurus aestuans</i> (Linnaeus, 1766)	X	X	X	X	D	0.22	0.19
	<i>Dasyprocta leporina</i> (Linnaeus, 1758)	X	X	X	X	D, I	0.20	0.39
	<i>Cuniculus paca</i> (Linnaeus, 1766)	X	X	X	X	I		
	<i>Myrmecophaga tridactyla</i> (Linnaeus, 1758) ^v	X	X	X	X	D	0.04	0.02
Cingulata	<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	X	X	X	X	D	0.07	0.02
	<i>Cabassous unicinctus</i> (Linnaeus, 1758)	X	X	X	X	D, I	0.04	0.02
	<i>Euphractus sexinctus</i> (Linnaeus, 1758)	X	X	X	X	D		0.02
	<i>Dasyppus kappleri</i> (Krauss, 1862)	X	X	X	X	I		
	<i>Priodontes maximus</i> (Kerr, 1792) ^v	X	X	X	X	I		
Carnivore	<i>Eira barbara</i> (Linnaeus, 1758)	X*	X	X	X	D	0.04	0.14
	<i>Puma yagouaroundi</i> (É. Geoffroy Saint-Hilaire, 1803)	X*	X	X	X	D		
	<i>Leopardus</i> spp.	X*	X	X*	X*	I		
Chelonia	<i>Panthera onca</i> (Linnaeus, 1758)	X*	X*	X*	X*	D, I		0.02
	<i>Puma concolor</i> (Linnaeus, 1771)	X*	X*	X*	X*	I		
	<i>Chelonoidis denticulata</i> (Linnaeus, 1766) ^v	X*	X	X*	X*	D, I	0.02	
	<i>Platemys platycephala</i> (Schneider, 1792)	X*	X*	X*	X*	D		

^vSpecies considered to be vulnerable according to IUCN.

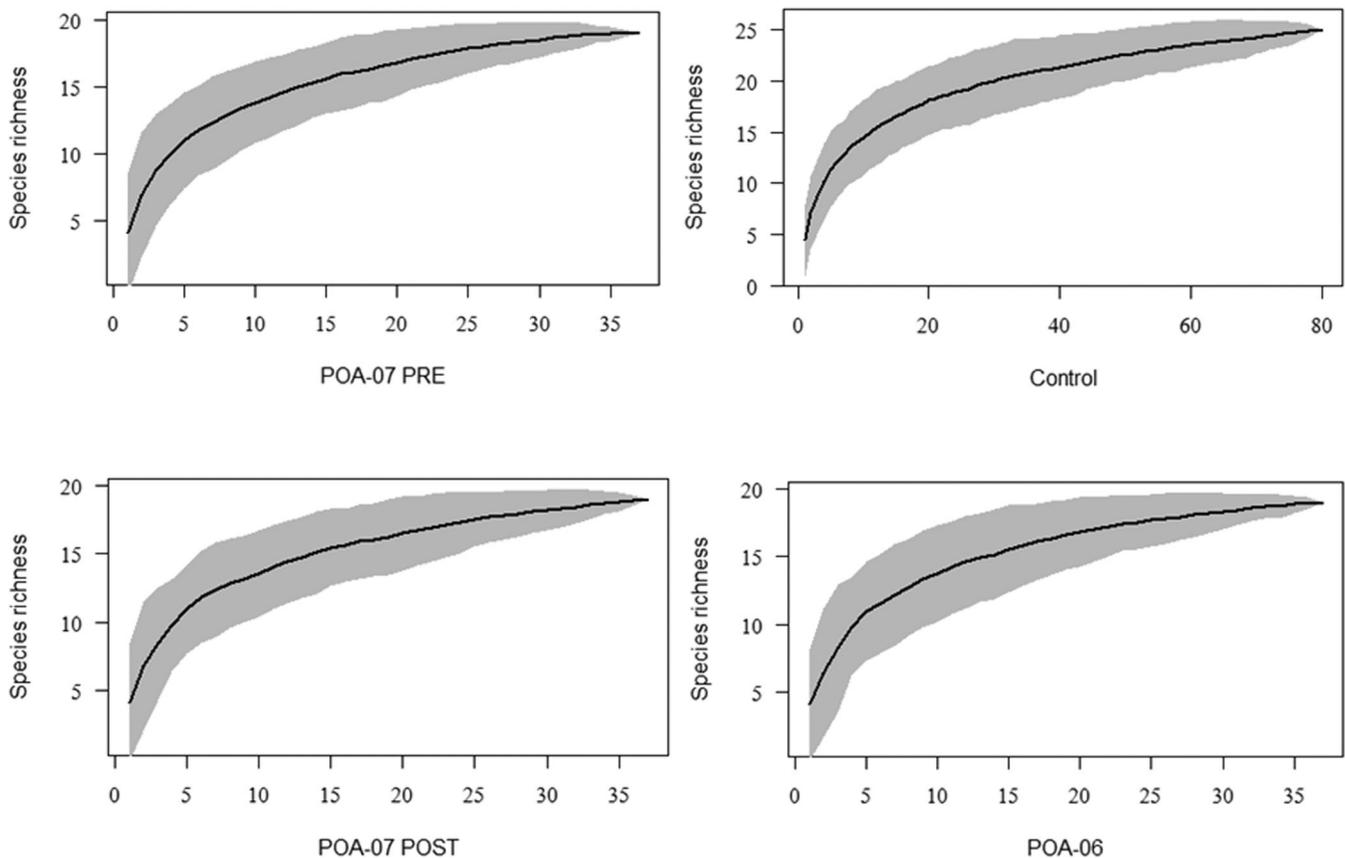


Figure 2. Cumulative species richness curve for medium and large vertebrates across the four study sites showing the 95% confidence intervals (gray areas). All four sampling areas reached asymptotes.

(Endo et al. 2010). We use the canonical significance threshold of $P > 0.05$ to accept the null hypothesis that there were no significant differences between treatments.

We combined data from visual and acoustic records to calculate the relative abundance of different species (detections every 10 km traveled on linear transects). We excluded from estimates of relative abundance all perpendicular distances farther than 50 m from transects to minimize the influence of detectability bias (Michalski & Peres 2007). Due to the low number of detections ($N < 30$) for most species, we did not attempt to derive a population density index (Buckland et al. 2010b). We used a non-parametric, Mann-Whitney test to examine differences between treatments (logged and unlogged areas). We considered transects in each POA as independent samples due to the minimum distance of 1.0 km between them. We also used an indicator analysis to understand which species differ in abundance between logged and unlogged areas (De Cáceres & Legendre 2009). For this analysis we used the relative frequency of each species in the indicator value index between unlogged and logged forests.

Results

Considering all line-transect censuses, we recorded a total of 29 species of medium and large vertebrates from 20 families, 15 orders and 28 genera. We also recorded eight additional species through direct and indirect observations outside systematic census routines (Table 2). Of the species total, six are considered Vulnerable by the International Union for Conservation of

Nature (IUCN) (Table 2). Of all 1,537 detection events (visual and acoustic) obtained in 2012 (POA-07_{PRE}) and 2013 (other POAs), 809 took place in unlogged areas and 728 in logged areas. Overall encounter rates along transects in unlogged areas was significantly higher than in logged areas ($U_{10,12} = 90$, $P = 0.05$). The average encounter rate per 10 km walked in unlogged and logged areas was 14.27 ($SD = \pm 3.80$) and 11.48 ($SD = \pm 2.33$), respectively (Table 1). The ANOVAs of overall lateral detectability of all species detected among the four sampling areas was not significantly different ($P = 0.056-0.881$, mean \pm SD = 0.499 ± 0.270). Species accumulation curves for the four areas suggest that the overall sampling effort deployed adequately sampled the medium and large vertebrate fauna of the Jari landscape (Figure 2).

The overall species richness detected in UL and LF areas was similar, ranging from 21 to 24 species. This variation was greater (10 - 19 species) if we consider individual transects within unlogged and logged forest treatments. Species richness was lower in transects at unlogged areas than in transects at logged areas, although the difference was not significant ($U_{10,12} = 40.5$, $P = 0.20$). The unlogged area had an average of 14.4 species ($SD = \pm 2.6$) detected every 10 km walked, while logged areas had an average of 15.8 species ($SD = \pm 1.48$). Only one species occurred exclusively in UL areas, the squirrel monkey (*Saimiri sciureus*), while the six-banded armadillo (*Euphractus sexcinctus*) was only detected in LF areas, but none of these species can be considered specialists of either logged or unlogged forests. The indicator analysis revealed the association of distribution pattern of four species (*Ara* spp. ($P = 0.001$), *Dasyprocta leporina* ($P = 0.006$), *Pecari tajacu* ($P = 0.022$) and *Eira barbara* ($P = 0.028$)) with

Vertebrates in selectively logged forests

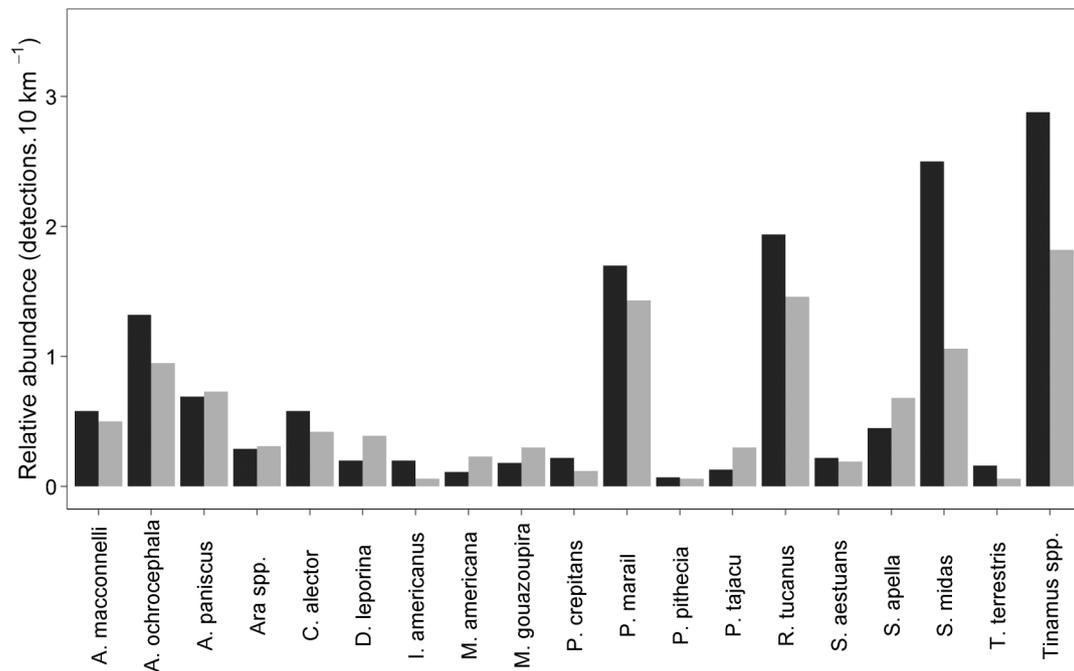


Figure 3. Change in relative abundance (detections \cdot 10km⁻¹ walked) of the main species detected in the two forest treatments (black: Unlogged Forest; gray: Logged Forest).

LF areas. On the other hand, we did not find any species that were significantly associated with UL areas.

Relative species abundance per transect did not differ between UL and LF areas ($U_{144, 190} = 14744.5$, $P = 0.19$) (Figure 3). The mean abundance was $0.99 (\pm 1.02)$ and $0.73 (\pm 0.65)$ detections \cdot 10 km⁻¹, respectively. The five most abundant species in UL and LF areas were the same (except for POA-06). These included a small-bodied callitrichid primate, the golden-handed tamarin (*Saguinus midas*) and four birds: white-throated toucan (*Ramphastos tucanus*), large tinamous (*Tinamus* spp.), yellow-crowned amazon (*Amazona ochrocephala*) and marail guan (*Penelope marail*). The difference in POA-06 is attributed to the presence of spider monkey (*Ateles paniscus*), the fourth most abundant species (1.0 detection \cdot 10 km⁻¹) at this site.

Three species showed significantly different relative abundances between the two treatments. *S. midas* showed increased abundance in unlogged forest compared to logged forest ($U_{10,12} = 100$, $P < 0.001$), with means of $2.3 (\pm 1.1)$ and $1.0 (\pm 0.7)$ detections \cdot 10 km⁻¹, respectively. The same pattern was observed for large tinamous, in that their relative abundance was 62% lower in logged compared to unlogged areas ($U_{10,12} = 108$, $P < 0.001$). Agouti (*D. leporina*) was the only species with the highest relative abundance in logged areas ($U_{10,12} = 26.5$, $P = 0.03$), with mean encounter rates of $0.14 (\pm 0.25)$ and $0.41 (\pm 0.31)$ for unlogged and logged forest areas, respectively. Moreover, this species was detected in 11 of 12 transects censused in logged areas, but in only three of the 10 transects censused in unlogged areas.

Discussion

Timber extraction in Amazonian forests holds a huge potential for growth in terms of both spatial extent and revenue (FAO 2010, Shearman et al. 2012), and this is often considered

a relatively benign land-use in terms of biodiversity responses to selective logging (Gibson et al. 2011). Despite its importance in the neotropics, there are still insufficient studies attempting to understand the effects of tropical forest timber extraction on medium and large vertebrates (Laufer et al. 2013). In addition, whether logging induces either positive or negative impacts on forest fauna remains unclear, as studies have found different results. For example, studies conducted in similar forests on the French Guiana showed opposite results for the trends on abundance of two species groups (*Psophia crepitans* and Tinamus) (Thiollay 1997, Bicknell & Peres, 2010). As we predicted, this study suggests that reduced-impact selective logging in itself did not strongly affect the species composition and relative abundance of the medium and large vertebrate populations, except for a few species. These results are consistent with other assessments of the degree to which RIL disturbance in tropical forests affects forest biotas (Azevedo-Ramos et al. 2006, Bicknell et al. 2014). The largely unaltered population abundances may result from the interaction of several factors, such as low levels of basal area removal and collateral damage, conserved landscape context and proximity to unlogged forest, and resilient life histories of several species.

A total of 28 of the 37 medium and large-bodied vertebrate species recorded had already been detected in other studies conducted in the Jari study landscape (e.g. Parry et al. 2007, 2009). However, our study detected nine additional taxa, including harpy eagle (*Harpia harpyja*), jaguarundi (*Puma yagouaroundi*), Brazilian squirrel (*Sciurus aestuans*), southern anteater (*Tamandua tretradactyla*), greater long-nosed armadillo (*Dasypus kappleri*), six-banded armadillo (*E. sexcinctus*), southern naked-tailed armadillo (*Cabassous unicinctus*), yellow-footed tortoise (*Chelonoidis denticulata*) and twist-neck turtle (*Platemys platycephala*) (Table 2). This is largely a function of our greater sampling effort compared to previous studies in the area, which increased the detection probability of these species.

In addition, earlier studies in the region partly focused on secondary forests after 18-23 years of regeneration. In these species, *E. sexcinctus* and *D. kapleri* were exclusively observed in logged and unlogged forests, respectively (Table 2). *E. sexcinctus* is known to use dry areas of wooded scrub (*cerrados*) and the boundaries between secondary and primary forest (Sousa e Silva Junior & Nunes 2001). The fact that this species was restricted to logged forests therefore supports the disturbance effect induced by RIL. On the other hand, *D. kappleri* is a well known primary forest species (Eisenberg 1989), but is often missing from hunted disturbed forests (e.g. Stone et al. 2009, Sampaio et al. 2010). *P. yagouaroundi* was recorded while moving between different sites within unlogged forest, but this species occurs in a broad range of both open and closed habitats, as well as fragmented and disturbed areas with exotic tree plantations (Michalski et al. 2006). The other six species did not show any clear pattern, being recorded in both unlogged and logged forests.

We uncovered widely variable encounter rates on transects within different forest treatments. This variation was largely due to the higher encounter rates in the control area (Table 1). However, the overall relative abundance did not differ across the two treatments. This indicates that RIL did not induce detectable changes in the relative abundance of medium and large vertebrates between UL and LF areas, at least within 6-18 month recovery time frame documented here. Only three taxa (*S. midas*, *Tinamus* spp. and *D. leporina*) showed significant differences in their relative abundances between treatments. This likely reflects the different ecological requirements of individual species (Bicknell & Peres 2010), variation in their resilience to different disturbance levels, and time required to recovery from RIL disturbance.

Two species that were more significantly abundant in UL areas — golden-handed tamarin and large tinamous — which *Tinamus* spp. is relatively intolerant to selective logging (Thiollay 1992, 1997, Mason 1996). However, the response of golden-handed tamarin was unexpected, given that this species is a generalist insectivore-frugivore (Pack et al. 1999), and are widely found in secondary forest (Rylands & Keuroghlian 1988). As such, we would expect this species to increase in relative abundance in logged areas. Lower food resource availability in logged areas is a possible explanation, as some key food trees for this species, such as *Manilkara bidentata* (Oliveira & Ferrari 2000), were exploited in the study area. Moreover, other food trees could have been affected by collateral damage from RIL. During the planning and execution phases of RIL cutting activities, several commercially valuable tree species bearing large fruits and seeds may be safeguarded (Putz et al. 2008), whereas forest species with minor or no commercial value are more often damaged during the implementation of roads, skid trails and roundlog storage areas. However, trees earmarked to be logged may have their felling planned so as to not damage seedlings and saplings for a second cutting cycle (Putz et al. 2008, Macpherson et al. 2012). So, until sufficient regeneration occurs in areas exposed to collateral damage, the abundance of golden-handed tamarin in recently-logged areas may decline because they prefer fruits with medium and small seeds (Oliveira & Ferrari 2000), and preferentially inhabit low-and middle strata vegetation (Randarshan et al. 2011).

The only species that apparently benefited from the structural disturbance accompanying RIL was *D. leporina*.

This is consistent with studies evaluating this species in other selective logged neotropical forests (Bicknell & Peres 2010). The increase in relative abundance in the area logged is possibly due to behavioral plasticity of this species, which can subsist in even small forest fragments (Jorge 2008, Norris et al. 2010). Moreover, our indicator analysis suggests that *D. leporina* could be defined as an indicator species of logged forests. The same applies to *E. barbara* that was more often recorded in logged forests. Both of these two species are known to prefer or tolerate disturbed forest habitats (Presley 2000, Jorge 2008), so their grouping with logging indicator taxa supports the notion that these species can subsist in large areas of RIL-disturbed forests.

In general, we found that reduced-impact logging did not affect the species composition and relative abundance of most medium and large-bodied vertebrates. The apparent lack of change in species composition and abundance can be explained by the life-history characteristics of the species in this study. Medium and large vertebrates are generally highly mobile, ensuring that they can move around the landscape, migrating to more suitable areas compared to areas affected by RIL (Azevedo-Ramos et al. 2006, Schleuning et al. 2011). In addition to species mobility, two important features of the landscape in the study area must be considered. The first feature is the presence of relatively large areas without any history of RIL disturbance immediately adjacent to areas with RIL activities. One of the guidelines of RIL planning is the choice of areas with gentle topography and high concentrations of tree species with high commercial value (Thiollay 1992, Putz et al. 2001). This fact allows for the persistence of “islands” of unlogged areas surrounded by logged ones. The second is the relatively well preserved matrix of the survey areas. Areas without any RIL disturbance can become a refuge for vertebrate species during reduced-impact logging operations, later acting as a recolonization source for the harvested areas (Johns 1996, Willot et al. 2000). Thus, interstitial areas of unlogged forests in our study landscape are likely to play a critical role in maintaining medium and large vertebrate populations throughout the RIL long-term cutting cycles of the overall forest mosaic.

However, there are other factors that can influence species responses to selective timber extraction. Recovery time, for example, can strongly influence assessments of the effects of selective logging (Putz et al. 2001, Jones et al. 2003, Clark et al. 2009). The response of organisms may have a time lag due to species-specific ecological factors, such as low reproductive rates and high longevity (Chapman et al. 2000, Owunji 2000). As the recovery time between the end of RIL disturbance associated and field sampling was relatively short in this study (6-18 months), our conclusions should be interpreted with caution. Indeed, longer-term studies should be carried out in selectively logged areas to track how resident populations respond over time (Michalski & Peres 2013). Ecological monitoring in such areas would also help researchers understand the synergistic interactions between RIL and conventional selective logging and other structural or non-structural human-induced forest disturbances (Peres et al. 2010). These may occur before or after selective cutting, and may include natural succession following droughts and hurricanes (Whitman et al. 1998, Chapman et al. 2000), overhunting of large-bodied vertebrates (De Thoisy et al. 2005, Poulsen et al. 2009) and forest wildfires (Uhl & Vieira 1989, Cochrane & Laurance 2002, Barlow & Peres 2008, FAO 2010).

This study has helped to understand the short-term responses of medium and large vertebrate populations to large-scale RIL operations in lowland tropical forests. However, there is still a long way to go to fully understand the effects of such RIL impacts in different areas, floristic contexts, landscapes and species assemblages, both within and outside Amazonia. This may yield data to improve our understanding of how to manage the > 45 million hectares of forest available for multiple natural resource use across the Brazilian Amazon alone (Bandeira et al. 2010). Monitoring of species contributing to forest regeneration (Wright et al. 2007, Terborgh et al. 2008) during the recovery process of selectively exploited forests should be undertaken by private companies, government agencies and local communities. With proper management, areas under low-impact selective logging can greatly contribute to the persistence of viable populations of most forest vertebrate species.

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