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# Vertebrate population responses to reduced-impact logging in a neotropical forest

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ABSTRACT

Vertebrate population densities were quantified in lowland central Guyana using line-transect censuses at three forest sites subjected to reduced-impact logging (RIL), and three adjacent unlogged sites. We censused a range of forest vertebrate species including large canopy-dwelling and terrestrial birds, three primates, one rodent and one tortoise. Two 4 km transects at each site were repeatedly surveyed during the wet season of 2008 to derive population density estimates on the basis of a cumulative survey effort of 416 km. RIL had ended within 16 months, and sites had been subjected to a mean extraction rate of 3.9 $m^3$ $ha^{-1}$, equivalent to only 1.1 trees $ha^{-1}$. Three of the 15 vertebrate species examined here exhibited significantly different abundances at forest RIL sites, two of which were negative. Large frugivores such as primates were less abundant in sites subject to RIL, whereas smaller frugivores, granivores, folivores and insectivores were more common in logged sites. We are unable to reliably distinguish between responses of different taxonomic groups, since robust abundance metrics could only be estimated for four mammal species. Despite this, species traits including dietary guild, body mass, home range size and vertical stratification of forest use are used to explain varying responses. Our findings suggest that responsible reduced-impact logging practices in neotropical forests can be considered as a relatively benign form of forest management that can coexist with the requirements of both local economies and biodiversity conservation. However, our study sites experienced comparably low extraction rates, and detrimental effects such as hunting were low. Our results therefore provide an opportunity to scrutinise the effects of best practice logging systems, though do not necessarily represent typical circumstances across tropical forests.

## 1. Introduction

The annual global trade in primary timber products from tropical forests is worth US$11.2 billion (ITTO, 2007), with most roundlogs extracted in south-east Asia. However, because of the growing appetite for tropical timber and the rapid depletion of Asian forests, much of the worldwide market-driven demand for tropical hardwood is now switching to neotropical forests. The neotropics contain over half the world's remaining tropical forests, yet are being deforested at a rate of 4.3 million ha $yr^{-1}$ (FAO, 2006). Additionally, each year 1.2 million ha of the Brazilian Amazon are selectively logged (Asner et al., 2005). It is therefore imperative that industrial scale forestry can be exercised sustainably in order to supply the global tropical timber markets into the future. Although many remote parts of Amazonia are currently unlogged, vast areas of the Brazilian Amazon have been allocated to private timber concessions, and hence in time, undisturbed forests will become confined to strictly protected reserves. While large forest reserves can maintain full complements of forest specialists, many species and populations will inevitably fall outside these reserves, thereby facing population declines or local extinctions in logged forests. To prevent the impoverishment of these landscapes, efforts must be made to minimise the impacts of selective logging on forest wildlife (Fimbel et al., 2001; Meijaard et al., 2005).

Across much of South America, especially the Guiana Shield, high value hardwoods comprise only a small portion of available species, so timber operations in these areas are highly selective, usually extracting fewer than 5 trees $ha^{-1}$ (ter Steege et al., 2002). In contrast, timber operations in south-east Asian dipterocarp forests typically extract three times this amount (Putz et al., 2001). In recent years, methods have been employed to minimise the detrimental effects of logging using a polycyclic system known as reduced-impact logging (RIL). Conventional selective logging can damage up to 15 times the number of trees extracted (Johns, 1988; Pinard and Putz, 1996; Putz et al., 2008). In comparison, RIL has been shown to reduce tree mortality by up to 27%, and total canopy gap fracture by 43% (Johns et al., 1996; Pinard and Putz, 1996). However,

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the implementation of RIL across worldwide tropical forests has been slow, and it remains poorly understood whether the reduced impacts of RIL on forest wildlife are proportional to that on forest structure (Azevedo-Ramos et al., 2006; Wunderle et al., 2006). RIL typically involves a 100% pre-harvest tree inventory used to ensure the efficient planning of skid trails, vine cutting to prevent damage to connecting trees, directional felling, and a number of methods ensuring minimal waste and maximum efficiency. In fact, RIL practices have become an essential component of international timber certification by the Forest Stewardship Council (FSC), and is described in detail elsewhere (Mason and Putz, 2001; Pinard and Putz, 1996; Vidal et al., 1997).

The impacts of selective logging on wildlife are broadly governed by two factors: the overall level of offtake and the extraction techniques. Conventionally logged forests subjected to high offtakes often succumb to high rates of faunal species loss (Fimbel et al., 2001; Mason, 1996; Thiollay, 1992, 1997). Logging intensity is frequently determined by the availability of large commercially valuable timber species, and consequently impacts are largely a function of forest structure and market-driven forces (Mason and Putz, 2001). However, extraction methods are a product of enforced governmental legislation, the environmental standards of a timber company, and the acquisition and maintenance of forestry certification. Many studies have reported highly species-specific impacts on wildlife, including both positive and negative abundance responses (Azevedo-Ramos et al., 2006; Chapman et al., 2000; Meijaard and Sheil, 2008; Plumptre and Reynolds, 1994). For instance, population abundance of some primate species increased in lightly logged (5.1 trees $\mathrm{ha}^{-1}$; 25% of trees damaged) forests in Uganda, but decreased significantly in moderately logged forests (7.4 trees $\mathrm{ha}^{-1}$; 50% of trees damaged), with frugivores being considerably more impacted than folivores (Chapman et al., 2000). It therefore seems likely that wildlife responses to a given logging operation are determined by logging intensity, level of collateral damage, and species-specific traits.

The mechanisms by which either hunting or logging affect tropical forest wildlife are considerably different, yet these effects are often spatially correlated (Cuaron, 2000; Laurance et al., 2006; Peres, 2001), thereby often confounding wildlife studies in logged forests. Logging operations usually facilitate hunter access to previously unhunted areas and/or increase demand for game meat. However, forests in central Guyana are remote and mostly void of human settlements, and animal protein requirements are primarily derived from freshwater fisheries resources (Watkins et al., 2005). These vast forest tracts therefore provide an opportunity to assess the impacts of RIL on wildlife, in a forest landscape context that is largely free of confounding effects such as hunting and other anthropogenic disturbances. However, this situation is relatively unique, and does not broadly represent typical circumstances in which hunting frequently co-occurs with most tropical forestry operations.

Large-bodied vertebrates represent appropriate candidates for assessing the effects of resource depletion and changes in forest structure induced by logging disturbance (Putz et al., 2001), because they can be feasibly censused and account for a large proportion of the faunal biomass in neotropical forests (Cuaron, 2000; Peres and Palacios, 2007). Logging studies to date in tropical forests have rarely sampled multiple taxa from the same sites simultaneously, or attempted to explain the varying responses of different species. Here we examine the responses of 15 mammal, bird and reptile species to forest disturbance generated by a recent reduced-impact logging operation. We interpret these responses in light of key species life-history traits such as body mass, home range size, vertical stratification (arboreal or terrestrial), and diet. We also report actual levels of timber extraction, which logging companies often fail to make available to investigators. In this study we worked closely with the logging companies who were interested in assessing the effects of their reduced-impact methods, and therefore we report accurate timber offtakes for each site as well as accurate skid trail density for one logged site, and estimated skid trail density for the two remaining logged sites.

## 2. Methods

### 2.1. Study area

The Iwokrama International Centre for Rainforest Conservation and Development (Iwokrama) forms an international partnership between Guyana and the Commonwealth, to demonstrate how tropical forests can be sustainably used in the interest of global scale climate change, local communities, and biodiversity conservation (Watkins, 2005). The 371,000 ha Iwokrama Forest lies between 4° and 5° north and 58.5° and 59.5° west (Fig. 1). Adjacent to the northern boundary of Iwokrama, 150,000 ha of forest is leased as a timber concession to Demerara Timbers Ltd (DTL). This entire area is characterised by low-lying *terra firme* tropical rainforest, dominated by *Chlorocardium rodiei*, *Eperua falcata*, *Dicorynia guianensis*, *Mora excelsa* and *Swartzia leiocalycina.* Rainfall averages ~3000 mm $\mathrm{yr}^{-1}$, with a rainy season from April to July (400–500 mm). Most other months experience ~200 mm. Temperatures range from an average minimum of 22 °C at night during the July rainy season to an average maximum of 36 °C during the October dry season. In 2008, exports of timber products from Guyana were worth US$25 million, and the Guyana forestry sector employs over 25,000 people (3% of the population).

### 2.2. Site and transect placement

Six sites were surveyed, comprising three logged and three unlogged (Fig. 1). All three unlogged sites were within the Iwokrama protected area. One logged site was also within the Iwokrama 'Sustainable Utilisation Area' and the two remaining logged sites were part of the DTL concession. Site comparability is critical in this type of study where baseline inference relies on 'pseudocontrol' or untreated sites (Plumptre and Reynolds, 1994). For this reason, transects were placed along relatively uniform forest type gradients and away from várzea forest areas subject to seasonal inundation during the high water period, as these areas were likely to exhibit elevated fruit availability and frugivore densities (Haugaasen and Peres, 2005; Lehman, 2004). Nevertheless, spatial and temporal differences in species abundance caused by the spatial distribution and phenology of plant resources cannot be completely discounted, particularly as our censuses were conducted during just one season.

While the Iwokrama Forest is a protected area, its collaboration with local indigenous peoples permits hunting for subsistence using traditional methods (Guyana Bill No. 7, 1995). However, there was only one community comprising approximately 200 people located within the Iwokrama boundary, and their subsistence was primarily based on fisheries resources from the large Essequibo River, and farming of the staple *cassava* (Watkins, 2005; Watkins et al., 2005). Low levels of hunting, primarily for collared (*Pecari tajacu*) and white-lipped peccary (*Tayassu pecari*), did occur within the Iwokrama Forest boundaries, but most of this was derived from the village buffer where no surveys were conducted. Illegal hunting was rare as movements by non-indigenous people were strictly monitored by both Iwokrama rangers and the Guyana Police Force. These low levels of hunting were also likely to be largely comparable at the remote DTL sites also. Although within the DTL concession there was no active hunting control, this area was largely inaccessible overland to persons other than small groups of DTL staff.

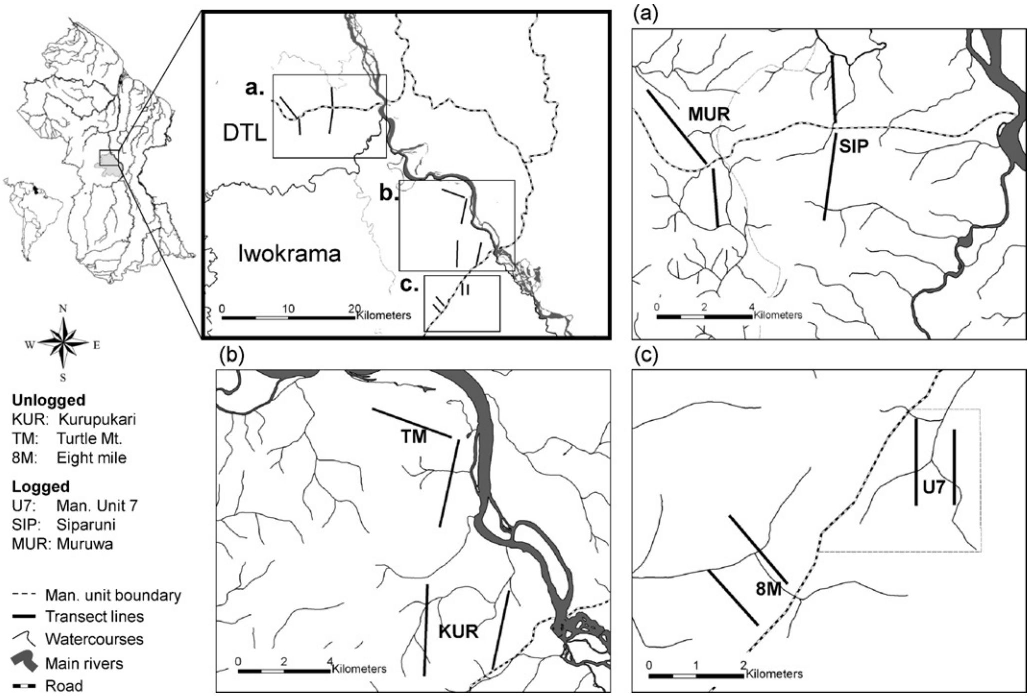

**Fig. 1.** Geographic location of forest sites and line-transects censused in central Guyana. Thick-bordered upper left panel shows the spatial arrangement of all forest sites sampled within the Iwokrama Forest boundary (delimited by grey polygon in top-left map) and DTL concession. Inset maps (a), (b) and (c) show the small-scale spatial distribution of survey transects within logged and unlogged sites (coded on the left).

The concession was cut-off by the Essequibo River, and only DTL vehicles could use the DTL-owned floating platform to cross the river. Outsider access to the concession was possible by a long boat journey, but this only facilitated three small riparian mining communities comprising fewer than 20 people each. These mining communities were never closer than 5 km from any part of our census transects and relied primarily on fisheries resources for protein. The closest permanent community was 40 km away. Informal interviews were held with one local fisherman, two miners, one small shop owner, one logger and one *Makushi* Iwokrama ranger, all of which stated that hunting was not prevalent in the DTL concession but what small offtakes did occur were again targeted at peccaries. All interviewees confirmed that primates were not hunted as they were considered to be a ‘dirty’ meat.

Sites were placed at least 2 km from one-another at the nearest point, and where transects ran parallel to one-another, they were placed farther than 1 km apart. Both transects within each site were surveyed simultaneously by different observers to avoid double counting between transects. Where a primary logging road was present, transects retained a 200 m road buffer, and ran at an approximately perpendicular angle from the road.

### 2.3. Sampling methods

Surveys were conducted during the rainy season from April to June 2008. Each site was surveyed using two transects of up to 4 km in length, resulting in a mean total effort of 70 km walked per site. Similar line-transect surveys in French Guiana showed that 40–90 km of census walks were required to reliably assess the abundance of some of the target species sampled in this study (Thoisy et al., 2008). A total of 416.1 km of surveys were completed, 214.9 km and 201.2 km in unlogged and logged forest, respectively.

Following Peres (1999), straight-line transects were cut along a compass bearing, measured with a Hip-Chain® and GPS, and marked using brightly coloured flagging at 50 m intervals to ensure mapping of vertebrate observations. Preparation of each transect was usually completed within 1 day, and surveys were never conducted within 24 h of line cutting.

Transects were walked early in the morning (0630–1000 h) and in the afternoon (1400–1700 h), when animals are most active. Surveys were always conducted by two observers who walked slowly (~1250 m/h) along the transect line, pausing at regular intervals to scan the forest (Mitani et al., 2000). Upon detection of target species, the distance along the transect, and perpendicular distance to the animal sighted were determined. In case of social species, we noted group size, group structure, and perpendicular distances were estimated to approximate geometric centre of the group. Surveys were conducted by trained native Amerindian observers who were very familiar with the forest and its wildlife.

### 2.4. Target species

Target species were selected based on the likelihood of obtaining robust population density estimates using line-transect sampling, and to provide a representative profile of species across dietary guilds. All mammal species were diurnal and included three primate and one large caviomorph rodent species. Birds were represented by three cracids, two tinamids, one trumpeter, nine parrots, two parakeet, three macaw, two toucan, one falconid, and one oropendola species. In addition, we censused *Geochelone* tortoises, which in this area were represented by a single species. Closely related congeners of a few of these species, which could not be reliably identified in the field (e.g. the tinamous and the parrots), were pooled together into a single functional group (Table 2) as in Peres and Palacios (2007). Other large vertebrate species, including ungulates and an additional primate species were censused during field surveys, but did not provide sufficient numbers of detections for comparison between logging treatments. Therefore, only species with ≥10 total detections at all sites are included in this paper. Our analysis of only four mammal species is biased towards primates and is therefore not representative of the forests overall

**Table 1**
Effort, forest characteristics, harvest, skid trail and time since logging finished for all sites, unlogged and logged.

| | Unlogged | | | | Logged | | | |
|---|---|---|---|---|---|---|---|---|
| | KUR | TM | 8M | All | U7 | SIP | MUR | All |
| Effort | | | | | | | | |
| Effort (km walked) | 77.0 | 68.7 | 69.2 | 214.9 | 70.0 | 70.0 | 61.2 | 201.2 |
| Total transect length (km) | 7.7 | 8.0 | 3.6 | 19.3 | 3.5 | 6.7 | 6.7 | 16.9 |
| Forest characteristics | | | | | | | | |
| Forest type[b] | MGK[c] | MMC[d] | MGK[c] | – | MGK[c] | MGK[c] | MMC[d] | – |
| Tree density (trees ha$^{-1}$) >10 cm DBH[b] | 403 | 421.5 | 403 | – | 403 | 403 | 421.5 | – |
| Tree density (trees ha$^{-1}$) >40 cm DBH[b] | 51 | 50.6 | 51 | – | 51 | 51 | 50.6 | – |
| Logging intensity | | | | | | | | |
| $\bar{X}$ ($\pm$SD) logging density (trees ha$^{-1}$)[b] | – | – | – | – | 2.5 (0.9) | 0.8 (1.1) | 0.8 (0.6) | 1.1 (1.1) |
| $\bar{X}$ ($\pm$SD) volume removal (m$^3$ ha$^{-1}$)[b] | – | – | – | – | 7.9 (2.2) | 2.5 (3.4) | 3.5 (2.6) | 3.9 (3.4) |
| Skid trail density | | | | | | | | |
| $\bar{X}$ ($\pm$SD) skid trail encounter rate (km$^{-1}$)[a] | – | – | – | – | 5.1 (3.9) | 2.9 (3.4) | 4.2 (3.6) | 4.1 (1.2) |
| $\bar{X}$ ($\pm$SD) skid trail density (m ha$^{-1}$)[b] | – | – | – | – | 59.4 (11.2) | No data | No data | – |
| Time | | | | | | | | |
| $\bar{X}$ ($\pm$SD) months since logging finished[b] | ∞ | ∞ | ∞ | ∞ | 2.3 (1.3) | 16.0 (2.4) | 11.4 (2.7) | 10.7 (5.5) |

[a] Data collected along transect lines.
[b] Data provided by timber operations.
[c] Mixed Greenheart, Kakaralli. Dominated by *Chorocadium rodiei, Epurua falcata, Dicorynia guianensis* (based on m$^3$ ha$^{-1}$ trees >40 cm DBH).
[d] Mora, Manicole, Crabwood, Trysil. Dominated by *Mora excelsa, C. rodiei, D. guianensis* (based on m$^3$ ha$^{-1}$ trees >40 cm DBH).

large-mammal fauna in Guiana forests, and should be interpreted accordingly.

### 2.5. *Logging methods and levels of disturbance*

This study was carried out in forests managed by two timber companies, whose methodologies were largely comparable, both adhering to the Guyana Forestry Commission's '*Code of practice for timber harvesting*' (GFC, 2002). *Management Unit 7* was part of Iwokrama's experimental timber operation. *Siparuni* and *Muruwa* sites were part of the DTL concession, whose reduced-impact methods have been shown to decrease skidding damage by up to 65%, and reduce the average size of tree-fell gaps by 40%, compared with conventional selective logging in Guyana (van der Hout, 1999). While there are currently no data on the exact damage levels of Iwokrama's logging practices, timber extraction methods endeavoured to minimise damage at every stage of the operation, which was awarded certification from the Forestry Stewardship Council (FSC) in early 2008.

Table 1 summarises the logging intensity at each site. A mean of 1.12 trees ha$^{-1}$ or 3.92 m$^3$ ha$^{-1}$ was removed from logged sites. This amounted to ~2.2% of trees >40 cm DBH, or ~0.3% including all trees >10 cm DBH. Just five tree species account for 98% of the total commercial timber harvest from central Guyana. At the sites surveyed, an average of ~73% of trees removed were *C. rodiei* (Lauraceae), ~15% *E. falcata* (Fabaceae), ~5% *D. guianensis* (Fabaceae), ~3% *Goupia glabra* (Goupiaceae), ~2% *Peltogyne* spp. (Fabaceae), with the remaining ~2% comprising 10 more species. Logged sites were harvested in 2007 or 2008, 2–16 months prior to surveys, with a mean of 11 months. Skid trail encounter rates at logged sites varied from three to five skid trails per km of transect, with five skid trails per km corresponding to ~59 m of skid trail per ha. Given that skid trails were ~5 m wide, this represents a loss of ~295 m$^2$ ha$^{-1}$ of forest understorey, or 2.96% of the horizontal plane. With a mean tree density of 409 stems ha$^{-1}$ (>10 cm DBH), skid trail damage therefore amounted to 12.1 trees ha$^{-1}$, or 3.0% of all trees >10 cm DBH. The overall damage was consequently 13.2 trees ha$^{-1}$ (<10 cm DBH) or 3.2% of all trees in RIL stands. These data do not include primary access roads or surrounding trees succumbing to collateral damage during felling, so the real figure is likely to be marginally higher.

### 2.6. *Data analysis*

Perpendicular distances were used for the estimation of densities using the DISTANCE 5.0 software (Thomas et al., 2006). For all species, detections used in analysis were truncated to an effective strip width of 100 m either side of the transect. This ensured that detections were not independent of the habitat and logging treatment being studied, and minimised errors in the estimation of distances. Model selection was based on the lowest Akaike Information Criterion (Buckland et al., 2001). Separate detection functions were fitted to logged and unlogged forests, to account for potential differences in visibility between logging treatments (Buckland et al., 2001; Johns, 1985). Where reliable density estimates were not possible due to small sample sizes, we used mean encounter rates per site as a substitute population abundance metric. All density estimates and encounter rates were calculated from both visual and acoustic detection events, with the exception of the black spider monkey (*Ateles paniscus*) which vocalised significantly more in logged forest ($t_{10}$ $-2.3$, $p=0.045$), despite lower densities. Data on spider monkeys were therefore analysed using visual detections only. A modified independent samples *t*-test, the *Z*-test was used to test for significant differences in abundance between logged and unlogged forest (Buckland et al., 2001; Owiunji and Plumptre, 1998; Plumptre and Reynolds, 1994).

$$Z = \frac{D1 - D2}{\sqrt{se(D1)^2 + se(D2)^2}}$$

where $D$ is the density estimate for area 'i', and $se$ is the standard error of the density estimate in area 'i'. $Z$ values greater than 1.96 or smaller than $-1.96$ are significant at the $p < 0.05$ level.

A general linear model (GLM) was used to interpret responses of each species to logging, by using their life-history variables as covariates. These variables included body mass, home range size, primary dietary guild and vertical stratification of forest use (arboreal or terrestrial) (Table 2). Because these variables are not independent across species, we also used principal components analysis (PCA) as a data reduction technique to collapse the effects of these four variables.

**Table 2**

Vertebrate species or functional groups of species censused, main detection methods, species life-history traits, total number of detections, and comparisons of population abundance estimates in unlogged ($N = 3$) and logged ($N = 3$) forest sites.

| Group<br>Family<br>Genus species | BM[a] | VS[b] | FG[c] | HR[d] | N[e] | Unlogged | | Logged | | % diff[h] | *p*[i] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Mean encounter rate (±SE)[f] | Density estimate (95% CI)[g] | Mean encounter rate (±SE)[f] | Density estimate (95% CI)[g] | | |
| Primates | | | | | | | | | | | |
| *Ateles paniscus* | 9.5 | A | Fr | 4 | 45 | 1.49 (0.3) | 6.9 (3.9–12.2) | 0.63 (0.2) | 3.6 (1.5–8.0) | −64 | <0.01[*] |
| *Alouatta macconnelli* | 6.5 | A | Fo | 2 | 44 | 0.84 (0.17) | 4.6 (2.4–9.0) | 0.67 (0.26) | 5.4 (2.6–11.1) | +17 | 0.72 |
| *Cebus olivaceus* | 2.7 | A | Fr | 3 | 10 | 0.42 (0.09) | – | 0.05 (0.05) | – | −88 | <0.001[*] |
| Rodents | | | | | | | | | | | |
| *Dasyprocta leporina* | 4.0 | T | Gr | 1 | 209 | 3.85 (1.0) | 10.5 (5.4–20.2) | 6.25 (0.87) | 14.9 (9.7–22.8) | +42 | 0.26 |
| Reptiles | | | | | | | | | | | |
| *Geochelone denticulata* | 6.5 | T | Fr | 4 | 14 | 0.45 (0.16) | – | 0.2 (0.04) | – | −56 | 0.13 |
| Birds | | | | | | | | | | | |
| Psophiidae (Trumpeters) | | | | | | | | | | | |
| *Psophia crepitans* | 1.5 | T | In | 4 | 60 | 1.14 (0.27) | 15.3 (7.9–30.1) | 1.74 (0.09) | 24.4 (14.5–40.1) | +59 | 0.24 |
| Cracidae (Guans) | | | | | | | | | | | |
| *Crax alector* | 3.2 | T | Fr | 2 | 61 | 1.74 (0.33) | 6.9 (2.5–19.0) | 1.18 (0.51) | 5.0 (2.2–11.5) | −28 | 0.61 |
| *Penelope marial, jacquacu* | 0.9 | T | Fr | 2 | 28 | 0.61 (0.06) | 2.8 (1.3–5.7) | 0.69 (0.16) | 2.3 (1.0–5.2) | −18 | 0.7 |
| Falconidae (Falcons) | | | | | | | | | | | |
| *Ibycter americanus* | 1.2 | A | In | 4 | 46 | 1.08 (0.2) | 3 (1.6–5.7) | 1.14 (0.58) | 3.8 (1.0–14.0) | +27 | 0.8 |
| Psittacidae (Parrots) | | | | | | | | | | | |
| *Ara* spp. | 1.2 | A | Gr | 4 | 80 | 2.04 (0.54) | 3.1 (1.6–6.0) | 1.82 (0.82) | 3.6 (1.4–9.0) | +16 | 0.76 |
| *Amazona* spp.; *Pionites melanocephalus*; *Pionopsitta caica*; *Deroptyus accipitrinus*; *Pionus fuscus*; *menstruus* | 0.3 | A | Gr | 4 | 247 | 5.78 (2.04) | 16.7 (7.8–35.7) | 6.21 (0.61) | 23.1 (15.4–34.6) | +38 | 0.35 |
| *Pyrrhura picta*; *Brotogeris chrysoptera* | 0.1 | A | Gr | 4 | 148 | 3.1 (1.1) | 19.2 (8.2–45.3) | 4.15 (0.38) | 21.1 (14.7–30.3) | +10 | 0.81 |
| Tinamidae (Tinamous) | | | | | | | | | | | |
| *Tinamus major*; *Crypturellus variegatus* | 0.6 | T | Fr | 1 | 118 | 2.45 (0.44) | 2.2 (1.5–3.1) | 3.31 (0.45) | 5.0 (3.5–7.3) | +127 | <0.01[*] |
| Ramphastidae (Toucans) | | | | | | | | | | | |
| *Ramphastos tucanus*; *vitellinus* | 0.58 | A | Fr | 3 | 143 | 3.46 (0.9) | 2.4 (1.3–4.4) | 3.53 (0.58) | 2.2 (1.6–3.0) | −8 | 0.77 |
| Icteridae (Oropendolas) | | | | | | | | | | | |
| *Psarocolius viridis* | 0.42 | A | Fr | 3 | 82 | 1.77 (0.63) | 1.2 (0.6–2.5) | 2.29 (0.62) | 1.5 (1.0–2.5) | +25 | 0.56 |

[a] Mean adult body mass (kg).

[b] Vertical stratification. T = Terrestrial; A = Arboreal.

[c] Primary feeding guild. Fr = Frugivore; Gr = Granivore; In = Insectivore; Fo = Folivore.

[d] Home range. 1 = 0–10 ha; 2 = 11–50 ha; 3 = 51–100 ha; 4 = > 100 ha.

[e] Total number of detection events, both acoustic and visual. Truncated to 100 m effective half strip width.

[f] Groups or individuals detected per 10 km of transect effort.

[g] Inds/km$^2$. Calculated using DISTANCE 5.0 software (Thomas et al., 2006). Model: half-normal key with cosine expansion series. For species detected acoustically, perpendicular distances were analysed in intervals according to the smallest Akaike Information Criterion (AIC). For visually detected species, exact distances were used.

[h] Percentage difference in density estimate (logged–unlogged). Where no density estimate, encounter rates were used.

[i] Calculated using *Z*-test (see Section 2).

[*] Significant at the <0.05 level.

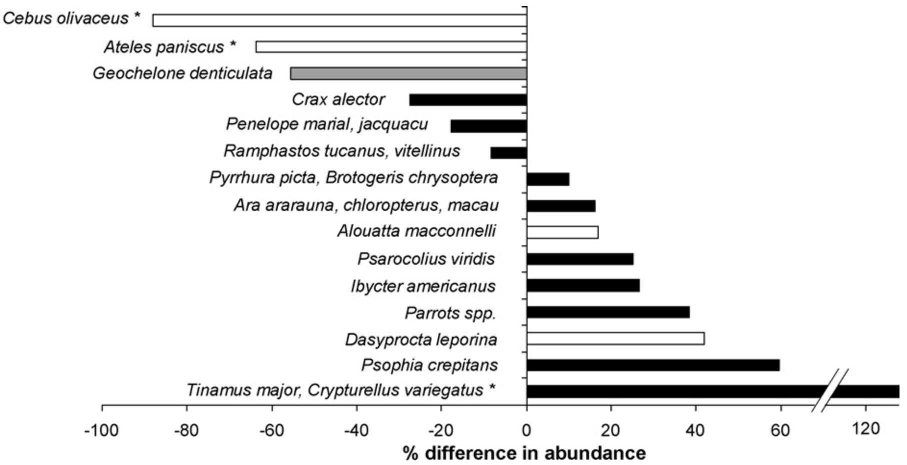

**Fig. 2.** Pooled percentage differences in population density estimates (but encounter rates for *C. olivaceus* and *G. denticulata*) between three unlogged and three logged forest sites surveyed in central Guyana. Lower and higher abundance in logged forests are represented by a negative (−ve) or positive (+ve) difference in abundance, respectively. Bird, mammal and tortoise species are represented by black, white, and grey bars, respectively. *Parrots* spp. refers to *Amazona* spp., *Pionites melanocephalus, Pionopsitta caica, Deroptyus accipitrinus, Pionus fuscus, and Pionus menstruus.* Asterisks (*) indicate significant differences at $p < 0.05$ level (calculated using a modified independent samples *t*-test).

## 3. Results

### 3.1. Impact of logging

Table 2 presents both the encounter rates and the population density estimates for target species in logged and unlogged forest sites. At the species level, three species exhibited significant differences in abundance between logged and unlogged forest. Only two species, however, were significantly less abundant in logged sites (Fig. 2). Wedge-capped capuchin monkeys (*Cebus olivaceus*) and spider monkeys (*A. paniscus*) were significantly less abundant in logged forests, whereas the tinamid species (*Tinamus major* and *Crypturellus variegatus*) were significantly more abundant in logged forests. Many other species showed only slight differences between logged and unlogged sites. In addition, no significant differences in group sizes, on the basis of reliable group counts, were detected for group-living species ($p > 0.1$ in all cases).

### 3.2. Life-history traits

The general linear model found just one marginally significant predictor ($\log_{10}$ body mass) of the proportional difference in abundance between unlogged and logged forest sites using the selected life-history traits ($\log_{10}$ body mass: $F_1 = 4.6$, $p = 0.06$; home range size: $F_1 = 2.6$, $p = 0.15$; feeding guild: $F_3 = 2.19$, $p = 0.17$; vertical stratification: $F_1 = 0.41$, $p = 0.54$). The remaining three variables independent of one-another did not explain responses to logging. However, when these traits are collapsed into one variable (using a PCA data reduction), through analysis of horizontal clustering, Fig. 3b shows that species with similar life-history traits exhibited comparable differences in abundance between logged and unlogged forest. Large frugivores were less abundant in logged forests, with small frugivores showing mixed differences, and insectivores and granivores slightly more abundant in logged forests. Abundance difference was also negatively correlated with

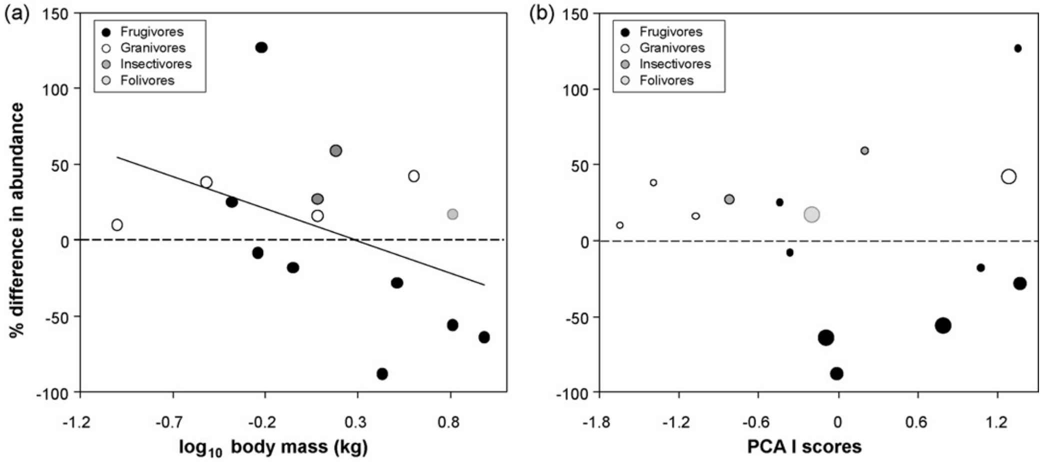

**Fig. 3.** (a) Relationship between mean adult $\log_{10}$ body mass (kg) and percentage difference in population density estimates (but encounter rates for *C. olivaceus* and *G. denticulata*) in three logged and three unlogged forest sites. ($y = -43x + 12.5$, $R^2 = 0.2$, $N = 15$, $p = 0.1$). (b) Relationship between percentage difference in density estimates (but encounter rates for *C. olivaceus* and *G. denticulata*) in logged and unlogged forest sites, and the first PCA axis extracted from the vertebrate species traits considered in this study (Table 2). Point size represents mean adult body mass. ($y = 1.6x + 6.6$, $R^2 = 0.001$, $N = 15$, $p = 0.92$). Points clustered horizontally, represent similar population response to reduced-impact logging.

body mass (Fig. 3a), with species larger than ∼800 g generally showing decreases in logged forests, while species smaller than ∼800 g often showing increases in logged forests.

## 4. Discussion

Only three of the 15 species (or functional groups of species) examined here exhibited significantly different abundances in forest sites subject to reduced-impact logging, two of which had lower abundances in logged sites. Differences in abundance between logged and unlogged sites varied considerably and can be partly explained by species life-history traits. Small arboreal frugivores appear to be largely unaffected by RIL, whereas large frugivores were negatively affected and insectivores, folivores and granivores were more common in logged sites. However, impacts on forest structure from the low intensity RIL operation in this study were relatively recent, and some of the patterns of abundance uncovered here could change over time.

Impacts of logging, subtle or otherwise, can be attributed to numerous factors. Logging can alter forest resource abundance to primary consumers as well as forest structure, forest microclimate and nesting or roosting sites (Grieser Johns, 1997). Although at high logging intensities and levels of collateral damage the availability of some food resources will decrease (Grieser Johns, 1997; Putz et al., 2001), in carefully implemented RIL sites overall resource abundance may not noticeably change, but the relative proportions of resources may be modified (Basset et al., 2001). Therefore where RIL is implemented, subtle changes in population abundances are expected, but the complete extirpation of species is unlikely.

The broad range and high functional diversity of vertebrates sampled in this study help to explain the varying responses to logging, as relative changes in resources may benefit some species, but be detrimental to others (Gray et al., 2007; Putz et al., 2001). In this study, species such as the tinamous (*T. major* and *C. variegatus*), agouti (*Dasyprocta leporina*), and grey-winged trumpeter (*Psophia crepitans*) may have responded to a species-specific increase in resource abundance in logged forests, and thereby profited from logging. However, species such as wedge-capped capuchins (*C. olivaceus*), and black spider monkey (*A. paniscus*) may have experienced a reduced resource supply following logging, and were therefore less common in logged sites. Although food resource abundance is important, a species dietary diversity and ability to adapt to a changing resource base is also likely to play an important role in determining responses to logging. Species with a broader dietary spectrum are less likely to be affected by logging where only relative proportions of foods change rather than an overall decrease in the resource base (1986, Grieser Johns 1997; Johns and Skorupa, 1987; Grieser Johns 1986, 1997; Johns and Skorupa, 1987; Meijaard et al., 2005). Additionally, species that can shift the relative proportions of different food types consumed may thrive in disturbed landscapes (Grieser Johns, 1997). In this study, red howler monkeys (*Alouatta macconnelli*) did not fit neatly into a pattern of lower abundance in logged forests as seen in other primates. This is likely because howlers are known to shift the proportions of food items in response to habitat modification (Grieser Johns, 1997) and they can rely almost entirely on young foliage for much of the year (Julliot, 1996; Julliot and Sabatier, 1993). Moreover, elevated light levels due to greater canopy fracture in logged forest often stimulate young leaf production (Johns, 1988; Plumptre and Reynolds, 1994), which are more easily digested than mature leaves (Simmen and Sabatier, 1996). Folivorous primates therefore often thrive in selectively logged or otherwise disturbed tropical forest habitats (Chapman et al., 2000; Plumptre and Reynolds, 1994). Conversely, species exhibiting a narrow dietary breadth may be heavily impacted by logging. For instance, *A. paniscus* are obligate sucrose-rich fruit pulp specialists, which form >79% of their diet (Simmen and Sabatier, 1996; van Roosmalen, 1985), and appear to be heavily impacted by logging.

Body mass and home range size are highly correlated within feeding guilds (Cotgreave and Harvey, 1992). Smaller species, with smaller home ranges, can often go unaffected by logging; as well planned reduced-impact logging such as that in central Guyana often retains large areas of undisturbed forest. For agoutis and tinamids, foraging ranges will therefore often be unaltered by skid trails, access roads or augmented densities of tree-fell gaps. Conversely, wide-ranging volant species such as parrots may be less sensitive to logging as they can forage opportunistically over large forest macro-mosaics (Mason and Thiollay, 2001), that may include both logged and unlogged areas. In general, small-bodied species are less likely to be affected by logging because they may be able to diverge through microhabitat specialisation into early successional and edge habitats, whereas the high metabolic demands of large-bodied species are too great to favour high population densities in fragmented or patchy habitats (Grieser Johns, 1997).

The indirect effects of both logging disturbance and biomass removal may lead to considerable microhabitat and microclimatic changes in the long-term, particularly in nutrient-poor tropical forests (Hammond et al., 1996; Thomas, 2001). Logging may affect nutrient cycling processes caused by compaction, erosion and reduction in litterfall (Thomas, 2001). Nutrient dynamics are particularly important for forests in the Guiana Shield which rely on a fairly closed system of nutrient cycling due to relatively infertile soils (Brouwer, 1996). If nutrient cycling processes in logged forests are altered or suppressed, knock-on bottom-up effects may be experienced by food species providing important resources for forest wildlife. Additionally, frugivores and granivores are critical components as dispersal mediators in forest regeneration processes following logging, and if lost, long-term changes may occur. A reduction in soil nutrients may decrease fruit-bearing potential, and additionally, elevated canopy fracture results in understorey desiccation, deficits in leaf moisture and greenness, and consequently disruptions in plant phenological cycles (Kultunov and Ustin, 2007). Responses to logging in the plant community depend on plant traits and forest type, as increasing light levels are known to inhibit some mature primary forest tree species in Guyana which require shade for seedling germination (Rose, 2000), yet encourage greater fruit and flower production in the understorey and herb layers, and in pioneer or edge plants (Costa and Magnusson, 2003; Dubuy and Chazdon, 1998; Grieser Johns, 1997; Johns, 1988; Putz et al., 2001). A long-term study from French Guiana found that natural tree-fell gap dynamics opened up the forest canopy by 0.6–1.3% $\text{yr}^{-1}$ (van der Meer and Bongers, 1996), whereas logging in central Guyana typically opens the canopy by 3% $\text{yr}^{-1}$ (Thomas, 2001). Many dominant tree species will therefore succumb to elevated light levels that may affect community-wide seedling recruitment dynamics (Thomas, 2001), with knock-on affects for primary vertebrate consumers. Where both timber extraction and collateral damage can be minimised through reduced-impact logging, these modifications to forest structure are considerably less apparent and therefore significant long-term impacts are less likely to occur (Pinard and Putz, 1996).

## 5. Conclusions

Although wildlife population responses to logging disturbance in tropical forests are highly species-specific, this study suggests that these can be partly explained by life-history variables. Conventional logging that results in high levels of disturbance is often associated with negative abundance responses for most species (Mason, 1996; Thiollay, 1992, 1997). In contrast, we find that many forest vertebrate species are not adversely affected by low levels of timber harvest using reduced-impact extraction methods, which is consistent with other studies (Azevedo-Ramos et al., 2006; Castro-Arellano et al., 2007; Felton et al., 2008; Presley et al., 2009). Compared with other forms of tropical forest disturbance, including recurrent wildfires, fragmentation, and forest conversion into fast-growing monocultures, reduced-impact logging provides a relatively benign land-use alternative that is more compatible with the requirements of full complements of biodiversity; selectively logged forests are more likely to retain wildlife assemblages that are largely indistinguishable from those in undisturbed forests (Barlow et al., 2006). However, given the apparent effect of any RIL on large canopy frugivores, and their vulnerability to other disturbances such as hunting, attempts should be made to reconcile RIL with the habitat requirements of these species. Additionally, as 50% of the mammal species considered in this study were detrimentally affected by RIL, future studies should aim to census a wider spectrum of the mammal fauna to enhance our understanding of the ecological responses of different taxa to reduced-impact logging.

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## References

Asner, G.P., Knapp, D.E., Broadbent, E.N., Oliveira, P.J.C., Keller, M., Silva, J.N., 2005. Selective logging in the Brazilian Amazon. Science 310, 480–482.

Azevedo-Ramos, C., de Carvalho, O., do Amaral, B.D., 2006. Short-term effects of reduced-impact logging on eastern Amazon fauna. Forest Ecol. Manage. 232, 26–35.

Barlow, J., Peres, C.A., Henriques, L.M.P., Stouffer, P.C., Wunderle, J.M., 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: an Amazonian synthesis. Biol. Conserv. 128, 182–192.

Basset, Y., Charles, E., Hammond, D.S., Brown, V.K., 2001. Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. J. Appl. Ecol. 38, 1045–1058.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford.

Brouwer, L.C., 1996. Nutrient cycling in pristine and logged tropical rain forest—A study in Guyana. Tropenbos-Guyana Series 1. Ph.D. thesis. University of Utrecht.

Castro-Arellano, I., Presleya, S.J., Saldanha, L.N., Willig, M.R., Wunderle, J.M., 2007. Effects of reduced impact logging on bat biodiversity in terra firme forest of lowland Amazonia. Biol. Conserv. 138, 269–285.

Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000. Long-term effects of logging on African primate communities: a 28 year comparison from Kibale National Park, Uganda. Conserv. Biol. 14, 207–217.

Costa, F.R.C., Magnusson, W.E., 2003. Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a central Amazonian forest. Biotropica 35, 103–114.

Cotgreave, P., Harvey, P.H., 1992. Relationships between body size, abundance and phylogeny in bird communities. Funct. Ecol. 6, 248–256.

Cuaron, A.D., 2000. A global perspective on habitat disturbance and tropical rainforest mammals. Conserv. Biol. 14, 1574–1579.

Dubuy, J.M., Chazdon, R.L., 1998. Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica. Biotropica 30, 223–237.

FAO, 2006. Forest resources assessment 2005: progress towards sustainable forest management. FAO Forestry Paper 147. FAO, Rome, Italy.

Felton, A., Wood, J., Felton, A.M., Hennessey, B., Lindenmayer, D.B., 2008. Bird community responses to reduced-impact logging in a certified forestry concession in lowland Bolivia. Biol. Conserv. 141, 545–555.

Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), 2001. The Cutting Edge. Columbia University Press, New York.

GFC, 2002. Guyana Forestry Commission. Code of Practice for Timber Harvesting, 2nd ed. GFC.

Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The response of avian feeding guilds to tropical forest disturbance. Conserv. Biol. 21, 133–141.

Grieser Johns, A., 1997. Timber Production and Biodiversity Conservation in Tropical Rain Forests. Cambridge University Press, Cambridge.

Guyana Bill No. 7, 1995. The Iwokrama International Centre for Rainforest Conservation and Development Act 1996. Government of Guyana, Georgetown.

Hammond, D.S., Gourlet-Fleury, S., van de Hout, P., ter Steege, H., Brown, V.K., 1996. A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. Forest Ecol. Manage. 83, 99–116.

Haugaasen, T., Peres, C.A., 2005. Mammal assemblage structure in Amazonian flooded and unflooded forests. J. Trop. Ecol. 21, 133–145.

ITTO, 2007. Annual Review and Assessment of the World Timber Situation 2007. International Tropical Timber Organization, Yokohama, Japan.

Johns, A.D., 1985. Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. Am. J. Primatol. 8, 31–36.

Johns, A.D., 1988. Effects of "selective" timber extraction on rain forest structure and composition and csme consequences for frugivores and folivores. Biotropica 20, 31–37.

Johns, A.D., Skorupa, J.P., 1987. Responses of rain-forest primates to habitat disturbance: a review. Int. J. Primatol. 8, 157–191.

Johns, J.S., Barreto, P., Uhl, C., 1996. Logging damage during planned and unplanned logging operations in the eastern Amazon. Forest Ecol. Manage. 89, 59–77.

Julliot, C., 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. Int. J. Primatol. 17, 239–258.

Julliot, C., Sabatier, D., 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. Int. J. Primatol. 14, 527–550.

Kultunov, A., Ustin, S.L., 2007. Impact of selective logging on phenology in Amazon rain-forests. American Geophysical Union, B51A-0060.

Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P., Ondzeano, C., 2006. Impacts of roads and hunting on central African rainforest mammals. Conserv. Biol. 20, 1251–1261.

Lehman, S.M., 2004. Distribution, and diversity of primates in Guyana: species-area relationships and riverine barriers. Int. J. Primatol. 25, 73–95.

Mason, D., 1996. Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting. Biotropica 28, 296–309.

Mason, D.J., Putz, F.E., 2001. Reducing the impacts of tropical forestry on wildlife. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York.

Mason, D.J., Thiollay, J.M., 2001. Tropical forestry and the conservation of neotropical birds. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York.

Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, A., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S., O'Brien, T., 2005. Life after Logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo. CIFOR, Bogor, Indonesia.

Meijaard, E., Sheil, D., 2008. The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecol. Res. 23, 21–34.

Mitani, J.C., Struhsaker, T.T., Lwanga, J.S., 2000. Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. Int. J. Primatol. 21, 269–286.

Owiunji, I., Plumptre, A.J., 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. Forest Ecol. Manage. 108, 115–126.

Peres, C.A., 1999. General guidelines for standardising line-transect surveys of tropical forest primates. Neotrop. Primates 7, 11–16.

Peres, C.A., 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conserv. Biol. 15, 1490–1505.

Peres, C.A., Palacios, E., 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. Biotropica 39, 304–315.

Pinard, M.A., Putz, F.E., 1996. Retaining forest biomass by reducing logging damage. Biotropica 28, 278–295.

Plumptre, A.J., Reynolds, V., 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve. J. Appl. Ecol. 31, 631–641.

Presley, S.J., Willig, M.R., Saldanha, L.N., Wunderle, J.M., Castro-Arellano, I., 2009. Reduced-impact logging has little effect on temporal activity of frugivorous bats (Chiroptera) in lowland, Amazonia. Biotropica 41, 369–378.

Putz, F.E., Sirot, L.K., Pinard, M.A., 2001. Tropical forest management and wildlife: silvicultural effects on forest structure, fruit production, and locomotion of arboreal mammals. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York.

Putz, F.E., Zuidema, P.A., Pinard, M.A., Boot, R.G.A., Sayer, J.A., Sheil, D., Sist, P., Elias, Vanclay, J.K., 2008. Improved tropical forest management for carbon retention. PLoS Biol. 6, 1368–1369.

Rose, S., 2000. Seeds, seedlings and gaps—size matters: a study in the tropical rain forest of Guyana. Tropenbos-Guyana Series 9. Ph.D. thesis. University of Utrecht.

Simmen, B., Sabatier, D., 1996. Diets of some French Guianan primates: food composition and food choices. Int. J. Primatol. 17, 661–693.

ter Steege, H., Welch, I., Zagt, R., 2002. Long-term effect of timber harvesting in the Bartica Triangle, Central Guyana. Forest Ecol. Manage. 170, 127–144.

Thoisy, B., Brosse, S., Dubois, M.A., 2008. Assessment of large-vertebrate species richness and relative abundance in Neotropical forest using line-transect censuses: what is the minimal effort required? Biodivers. Conserv. 17, 2627–2644.

Thiollay, J.M., 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. Conserv. Biol. 6, 47–63.

Thiollay, J.M., 1997. Disturbance, selective logging and bird diversity: a Neotropical forest study. Biodivers. Conserv. 6, 1155–1173.

Thomas, R.S., 2001. Forest productivity and resource availability in lowland tropical forests of Guyana. Tropenbos-Guyana Series 7. Ph.D. thesis. Imperial College, University of London.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., Marques, T.A., 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment. University of St. Andrews, UK.

van der Hout, P., 1999. Reduced Impact Logging in the Tropical Rain Forest of Guyana: Ecological, Economic and Silvicultural Consequences. Tropenbos Guyana Series 6.

van der Meer, P.J., Bongers, F., 1996. Formation and closure of canopy gaps in rain forest at Nouregues, French Guiana. Vegetation 126, 167–179.

van Roosmalen, M.G.M., 1985. Habitat preferences, diet, feeding behavior and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Suriname. Acta Amazonica 15, 1–238.

Vidal, E., Johns, J., Gerwing, J.J., Barreto, P., Uhl, C., 1997. Vine management for reduced-impact logging in eastern Amazonia. Forest Ecol. Manage. 98, 105–114.

Watkins, G.G., 2005. The Iwokrama Centre and forest: introduction to special papers. Proc. Acad. Nat. Sci. Phila. 154, 1–5.

Watkins, G., Saul, W., Holm, E., Watson, C., Arjoon, D., Bicknell, J., 2005. The fish fauna of the Iwokrama Forest. Proc. Acad. Nat. Sci. Phila. 154, 39–53.

Wunderle, J.M., Henriques, L.M.P., Willig, M.R., 2006. Short-term responses of birds to reduced-impact logging in a lowland Amazon forest: can reduced-impact methods help to retain avian biodiversity in tropical timber production forests? J. Ornithol. 147, 114–115.