

Large-vertebrate assemblages of primary and secondary forests in the Brazilian Amazon

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Abstract: Secondary forests account for 40% of all tropical forests yet little is known regarding their suitability as habitat for diurnal large mammals and game birds. This is especially so for second-growth that develops on large areas of degraded land. We address this by investigating assemblages of large-bodied birds and mammals in extensive patches of secondary forest in the Jari region of the north-eastern Brazilian Amazon, comparing species richness and abundance against that of adjacent undisturbed primary forests. We conducted 184 km of line-transect censuses over a period of 3 mo, and found that although primary and secondary forests held a similar abundance of large vertebrates, the species composition was very different. Secondary forests supported a high abundance of ungulate browsers (0.85 vs 0.44 indiv. per 10 km) and smaller-bodied primates (15.6 vs 4.6 indiv. per 10 km) compared with primary forests. However, large prehensile-tailed primates were absent (black spider monkey *Ateles paniscus*) or at very low abundance (Guyanan red howler monkey *Alouatta macconelli*) in secondary forest. The abundance of large frugivorous/granivorous birds was also low in secondary forests compared with primary forests (22.6 vs 37.1 individuals per 10 km, respectively). Faunal assemblages appear to reflect food resource availability. Concurrent vegetation surveys indicated that secondary forests had high levels of terrestrial and understorey browse. Fruit production was largely restricted to pioneer trees such as *Bellucia* and *Inga* spp. Although these regenerating forests were an important habitat for large mammals and birds, they were limited in terms of faunal richness, particularly dispersers of large-seeded plants.

Key Words: Amazon, frugivory, herbivory, large mammals, regeneration, secondary forest

INTRODUCTION

Tropical secondary forests account for some 40% of all tropical forest regions, and are being formed at a rate of 9 million ha y^{-1} (Moran *et al.* 1994), reflecting a worldwide acceleration in the rate of tropical forest degradation and conversion (Brown & Lugo 1990, Foody *et al.* 2003). Indeed some countries may soon only have secondary forest remaining (Castelletta *et al.* 2000, Lugo & Helmer 2004, Wright & Muller-Landau 2006). Regenerating forests in the Brazilian Amazon cover a third of deforested land (Perz & Skole 2003), as converted land is frequently abandoned due to low productivity (Nepstad *et al.* 1991). However, little is known about the response of faunal communities to large-scale tropical forest regeneration (DeWalt *et al.* 2003, Gascon *et al.*

1999, Vandermeer & Perfecto 1997, but see Dunn 2004), and they remain poorly studied in the Amazon.

Large vertebrates serve important ecological roles in the functioning of tropical ecosystems, especially seed dispersal (Howe & Smallwood 1982, Jansen & Zuidema 2001, Wunderle 1997). In Amazonian and Guianan forests, the vast majority of plant species require animals for seed dispersal (Peres & van Roosmalen 2002). The vertebrate assemblage within second-growth will therefore influence the rate and nature of forest regeneration. Although previous research in southern Mexico has reported a reduced species richness and abundance of large mammals in secondary forest (Estrada *et al.* 1994), results were confounded by the small size of habitat patches and methodological problems such as not accounting for differences in detection distance among habitats surveyed. Indeed other studies have suggested that secondary forests serve as productive hunting grounds in the tropics (Gavin 2004, Wilkie 1989). Secondary forests may

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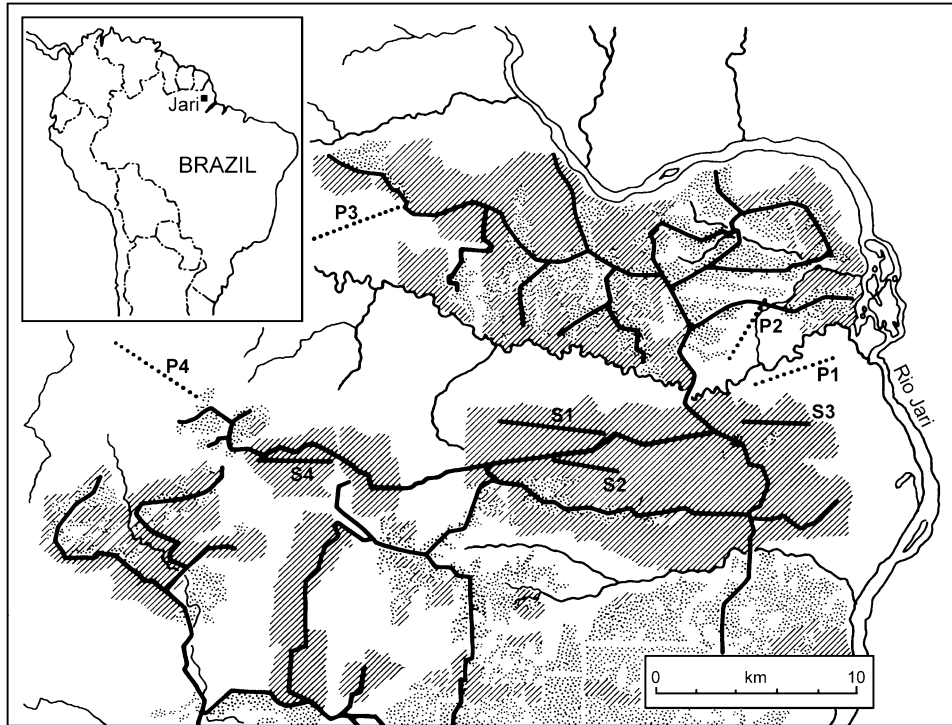


Figure 1. Map of the study area within the 1.7-Mha Jari landholding in the north-eastern Brazilian Amazon. Faunal line-transects are indicated in hatched areas of secondary forest (S1–S4 unbroken lines) and unshaded areas of primary forest (P1–P4 dotted lines). Stippled areas indicate active *Eucalyptus* plantations.

therefore support sizeable densities of large vertebrates, and may be an important though overlooked large vertebrate habitat in fragmented tropical landscapes.

We present an investigation of the large-vertebrate community structure within extensive areas of secondary forest in north-eastern Brazilian Amazonia. Comparisons are made with adjacent areas of undisturbed primary (*terra firme*) forest. We predict that secondary forests will hold high abundances of disturbance-tolerant species, with broad diets which enable consumption of a range of fruits and pioneer browse (DeWalt *et al.* 2003). We predict that specialist frugivores will be absent or at low abundance in secondary forest. To our knowledge, this study provides the first quantitative assessment of large-vertebrate communities within Amazonian second-growth forests, and should therefore be considered the first step towards a critical evaluation of the conservation value of abandoned or fallow agricultural lands for large vertebrates in the Amazon.

METHODS

Study area

The study took place in the Rio Jari watershed ($0^{\circ}53'S$, $52^{\circ}36'W$) within the State of Pará in the north-eastern

Amazon basin (Figure 1). The existing 1.7-Mha landholding currently managed by a large forestry company was originally purchased in 1967, with *c.* 10% (145 000 ha) of the primary forest converted into large-scale exotic tree plantations. Currently, the region consists of a mosaic of active tree plantations (45 000 ha), regenerating secondary forest (100 000 ha), and the remainder largely undisturbed *terra firme* primary forest. The secondary forests have naturally regrown after the clearing and subsequent abandonment of 6-y rotation *Gmelina arborea* Roxb. and *Eucalyptus* hybrid (*E. grandis* \times *E. urophylla*) plantations. Secondary forest patches were intersected by forestry access roads and some derelict timber-yarding areas. Average annual rainfall (1968–1986) is 2115 mm (Coutinho & Pires 1996), with a marked wet season from January to June, and a distinct dry season from September to November. Levels of human disturbance are generally low within the primary and secondary forests of the experimental matrix, and primarily restricted to seasonal collection of wild seed crops from Brazil nut trees (*Bertholletia excelsa* Humb. & Bonpl.). This study was carried out in four areas of even-aged secondary forest and four areas of primary forest (Figure 1). The secondary forests were originally cleared with bulldozers and were abandoned between 13 and 18 y ago, which is also the typical age of secondary forest from smallholder agriculture in the Brazilian Amazon (Smith *et al.* 2003).

All fieldwork was conducted between March and July 2004. One-metre-wide straight-line transects of 3.1 to 5 km in length (secondary forest transects: 5.0, 4.0, 4.0, 3.1 km; primary forest: 4.0, 4.0, 5.0, 4.0 km) were cut at each site prior to surveying. Each transect was in a distinct patch of secondary forest, with a unique history of clearance, cultivation and abandonment. Transects were orientated to avoid potentially confounding effects of forest edges. Primary and secondary forest patches were large (>1000 ha) though we accept that for some wide-ranging species such as jaguar (*Panthera onca*), a single animal could incorporate primary and secondary forest within its home range.

Habitat data

Trees and lianas were sampled in two 0.25-ha plots (10 × 250 m) placed alongside each transect from 250–500 m, and 2250–2500 m from point zero. The status (dead/alive) was recorded, as were all stumps and tree falls within the plots. All trees (≥10 cm dbh) with more than half their stem within each plot were recorded.

Forest structure was assessed every 100 m along each transect. Height of the canopy was visually estimated to the nearest metre. Understorey density was assessed by examining a vertically held 2.5-m graduated pole from 15 m, using binoculars to count number of 10 cm pole-sections clearly visible (following Barlow *et al.* 2002). Forest floor cover was assessed using a 2 × 2-m quadrat at the side of the trail. Canopy cover was measured using a spherical densiometer, following Lemmon (1957).

Each transect was surveyed for fruit patches in June 2004, separately from faunal surveys. Terrestrial fruit trail surveys were used as they are both effective and efficient to conduct (Sabatier 1985, Wallace & Painter 2002), and may provide a better measure of mammalian food availability than fruit traps by capturing a greater diversity of fruit types (Hemingway & Overdorff 1999). Terrestrial trails also avoid the chance concentration effects that can occur given the relatively small area sampled by traps (Stevenson *et al.* 1998). When a patch of fruit was detected on the trail binoculars were used to locate and check whether there was still ripe fruit on the parent tree. If there was, the local name, fruit type (fleshy or non-fleshy) and dbh of the tree was recorded. Stem diameter provides a good index of fruit production (Leighton & Leighton 1982, Stevenson *et al.* 1998).

Faunal surveys

All sites were surveyed for diurnal large-bodied mammals and large easily detectable bird species using a standardized line-transect census protocol as described in

Peres (1999). Censuses were conducted between April and July 2004. Surveys alternated on a daily basis between primary and secondary forest sites to minimize any seasonal bias and maximize temporal independence. All sites were censused six times, providing a cumulative census effort of 184.3 km. Censuses were undertaken in the morning (06h00–10h30) but were discontinued during periods of rain. Due to rain, transects could not always be completed though secondary forest effort was 93.1 km in total (mean = 3.9 km per census) and primary forest survey effort of 91.25 km (mean = 3.8 km per census). Transects were walked slowly (1.25 km h⁻¹) by LP and a highly experienced independent observer. Birds can be effectively surveyed using line transects (Brooks & Begazo 2001, Hill *et al.* 2003, Peres 2000, Peres *et al.* 2003), though we restricted our surveys to relatively large species that are easily detectable by sight, call or flush. All medium- to large-bodied mammals and birds (>250 g) encountered were identified, noting species, detection cue, distance along transect, and perpendicular distance from the transect to the centre of the cluster in the case of social species. Reliable group size counts were obtained whenever possible. Tracks are a useful means of assessing the relative abundance of terrestrial mammals (Reyna-Hurtado & Tanner 2005) and recent indirect signs of large vertebrate activity were also recorded whenever possible, including tracks, scrapes, faeces and holes in the ground used for shelter or foraging. As surveys were conducted in the rainy season all soil substrates were constantly saturated and track detectability is likely to be comparable in primary and secondary forest habitat. 'Tracks' were defined as a cluster of tracks from the same animal. Tracks of jaguar (*Panthera onca*) and puma (*Puma concolor*) were pooled as they could not always be reliably distinguished. In addition, detection data for several species of small tinamous (*Crypturellus* spp.) and large tinamous (*Tinamus* spp.) were pooled as flushed tinamous were difficult to identify to species during censuses.

Data analysis

The number of direct encounters (acoustic or visual) was small for many species so a simple encounter rate per 10 km walked was used, rather than calculating density and biomass estimates. A bias can arise when comparing abundances from line-transect censuses if there are structural differences between study habitats, which can affect detectability (Johns 1985). As such we truncated the census data of certain species to exclude the greater perpendicular detection distances in primary forest (excluded all data beyond: Guyanan howler monkey *Alouatta macconnelli*, 300 m; brown capuchin *Cebus apella*, 100 m; Brazilian agouti *Dasyprocta leporina*, 40 m;

red-throated caracara *Ibycter americanus*, 200 m; white-throated toucan *Ramphastos tucanus*, 400 m).

Non-parametric Mann–Whitney tests were used to test for differences, unless otherwise stated.

The statistical package PRIMER[®] v.5 (Clarke 1993) was used to explore vertebrate community differences among sites. Initially, cross-site similarities were calculated using Bray Curtis as the coefficient for faunal matrices, as it is often used for biological data (containing unimodal and linear responses) and ignores joint absences. The matrix was constructed using the encounter rates of individuals for large vertebrates surveyed, though excluding species observed only once in the study (e.g. paca *Agouti paca*, giant anteater *Myrmecophaga tridactyla* and bushdog *Speothos venaticus*). Cross-site similarities were explored visually using non-metric multidimensional ordination (NMDS), in which sites are positioned visually in accordance with their relative similarities to each other (Clarke & Warwick 2001). Analysis of similarity tests (ANOSIM) were then performed (Clarke & Green 1988) to assess whether primary and secondary forest sites differed more from each other than replicates within the same forest types. A high *R* value indicates that replicates within site types are more similar to each other than replicates from the different site type. Similarity percentage (SIMPER) analysis was used to identify which species contribute to similarities within transects of the same forest type and to dissimilarities between transects in different forest types (Clarke 1993).

RESULTS

Habitat structure and food resources

Secondary forest was structurally very different to primary forest (Table 1). Secondary forests were characterized by low basal area, due largely to lower average tree size rather than the only marginally lower tree density. Secondary forest canopy was lower and more open. Secondary forest was dominated by a few tree families, namely Myrtaceae (which included exotic *Eucalyptus* resprouts) and Mimosaceae (mainly *Inga* spp.). The availability of food resources was markedly different in primary and secondary forest (Table 1). Secondary forest had higher levels of terrestrial browse and a denser understorey shrub layer. Although the summed basal area of fruiting trees was higher in primary forest, the difference was not statistically significant due to some overlap between primary and secondary forest sites, and the relatively small sample sizes. Fruit walks along primary forest transects yielded 142 patches of fleshy and 25 non-fleshy fruit, whereas those in secondary forest yielded 205 and 3 patches of fleshy and non-fleshy fruit, respectively. The frequency and combined basal area

Table 1. Mean (\pm SE) habitat structure and large-vertebrate feeding resource availability in primary forest (PF) and secondary forest (SF) of Jari in the north-eastern Brazilian Amazon ($df=4$ in all cases). Significance tests were performed using Mann–Whitney *U*-tests, * $P < 0.05$; ns = not significant.

Resource	PF	SF	<i>U</i>
Structure			
Basal area (m ²)	7.3 \pm 0.7	3.5 \pm 0.8	–2.31*
Canopy height (m)	23 \pm 0	7 \pm 1	–2.31*
Canopy openness (%)	2.5 \pm 0.2	8.5 \pm 1.5	–2.31*
Understorey			
Understorey openness (%)	40 \pm 5	18 \pm 2	–2.31*
Terrestrial browse (%)	16 \pm 2	29 \pm 3	–2.31*
Fruit			
Fruiting basal area per km	5.2 \pm 2.8	1.0 \pm 0.5	–1.73 ns
Fruiting trees per km	7.6 \pm 2.7	12.0 \pm 4.1	0.87 ns
Fruiting tree dbh	36.0 \pm 2.4	11.6 \pm 1.7	–2.31*

of fruiting trees was not significantly different between primary and secondary forest, but fruiting trees were significantly smaller in secondary forest sites.

Fruiting in secondary forests was largely restricted to two genera, *Inga* (Mimosaceae) and *Bellucia* (Melastomataceae), which accounted for 18.6% and 68.3% of the secondary forest fruit patches, respectively. These two tree genera alone contributed 42.0% and 46.8% of the summed fruiting basal area, respectively.

Mammals

Mammalian species richness was slightly lower in secondary forests (SF) than in the primary forest (PF) controls, although this was not statistically significant (PF: mean \pm SE = 11.5 \pm 0.7 species, SF: mean = 10.5 \pm 1.3 species; $U_{4,4} = -0.726$, $P = 0.486$). The highest mammalian encounter rates were in secondary forest sites, though there was no significant difference between primary and secondary forest ($U_{4,4} = -0.289$, $P = 0.886$).

The multivariate patterns of community composition was significantly different for large mammals between primary and secondary forest sites (ANOSIM, $R = 0.37$, $P < 0.05$). Nine mammal species were important in distinguishing community composition. Of these, primates varied widely in their tolerance of secondary forest and were important discriminators of community composition in the SIMPER analysis (Table 2). Brown capuchins were considerably more abundant in secondary forest than primary forest. Common squirrel monkeys (*Saimiri s. sciureus*) and golden-handed tamarins (*Saguinus m. midas*) were not detected in primary forest during censuses. Conversely, the largest prehensile-tailed primate, the black spider monkey (*Ateles paniscus*), was restricted to primary forest. Guyanan red howler monkey was largely restricted

Table 2. Breakdown of the average dissimilarity (Av. diss.) in encounter rates of larger mammals (>250 g) and easily detectable larger birds in primary forest (PF) and secondary forest (SF), in descending order of contribution to community dissimilarity. Overall dissimilarity = 78.2% (mammals), and 64.1% (birds).

	Average abundance (indiv. per 10 km)		Av. diss. measure	Cumulative % diss.
	PF	SF		
Mammals				
<i>Ateles paniscus</i>	1.39	0	14.7	18.8
<i>Cebus apella</i>	0.78	1.55	11.9	34
<i>Alouatta macconnelli</i>	1.12	0.13	11.3	48.5
<i>Dasyprocta leporina</i>	0.54	1.44	11.1	62.7
<i>Saguinus m. midas</i>	0	0.91	6.3	70.7
<i>Mazama americana</i>	0.23	0.76	6.29	78.8
<i>M. gouazoupira</i>	0.44	0	5.37	85.6
<i>Pithecia pithecia</i>	0.21	0.13	2.18	88.4
<i>Myoprocta exilis</i>	0.21	0	2.02	91
Birds				
<i>Amazona ochrocephala</i>	4.01	0.22	13.0	20.3
<i>Ortalis m. motmot</i>	0	3.17	11.1	37.7
<i>Ramphastos tucanus</i>	3.08	1.22	7.9	50
<i>Tinamus spp.</i>	2.48	0.55	7.6	61.8
<i>Ibycter americanus</i>	2.2	0.52	5.76	70.8
<i>Psarocolius spp.</i>	2.23	2.14	5.1	78.8
<i>Pyrrhura picta</i>	0.98	0	3.27	83.7
<i>Ara spp.</i>	1.19	0.37	3.25	88.9
<i>Crypterellus spp.</i>	1.42	1.71	2.84	93.4

to primary forest and was at very low abundance in secondary forest. Guianan saki monkeys (*Pithecia pithecia*) were only observed on three occasions, in both habitats.

Some closely related species appeared to have different habitat preferences. For example, Brazilian agouti was more abundant in secondary forest, whereas the opposite was true for red acouchi (*Myoprocta exilis*). Agouti track densities were variable across sites (Table 3). The same pattern was found for *Mazama* spp.; red brocket deer (*M. americana*) was more abundant in secondary forest than primary forest sites whereas grey brocket deer

(*M. gouazoupira*) was rare in primary and secondary forest sites. Track densities of red brocket deer were also much higher in secondary forest (21.3 ± 8.9 tracks per 10 km compared with 1.8 ± 0.5 , respectively, $U_{4,4} = -2.31$, $P < 0.05$). Grey brocket deer track density was similar in primary forest and secondary forest. Collared peccary (*Pecari tajacu*) were never observed directly in secondary forest though they were seen or heard on four occasions in primary forest. Their tracks were seen in three out of four SF and PF sites. There were few direct detection events of other ungulates (white-lipped peccaries *Tayassu pecari* and tapir *Tapirus terrestris*) although tracks of both species were seen in both habitats. Tapir tracks were second only to red brocket deer in terms of terrestrial mammal track densities. The paca is predominantly nocturnal and was encountered only once. However, track data indicated that paca were fairly abundant in secondary forests.

Direct observations of large carnivores were too rare to assess their abundance although tracks were detected in both secondary and primary forests (Table 3). In one of the secondary forest sites, there was one sighting of two bush dogs, which are listed in CITES Appendix 1. There were also sightings of coati (*Nasua nasua*) and giant anteater (*Myrmecophaga tridactyla*) in secondary forest. Tracks of armadillo (*Dasybus spp.*) and giant anteater were recorded in primary and secondary forest, though at variable densities.

Birds

Species richness in secondary forests of the large-bodied birds included in our censuses was similar to that in primary forest (PF = 14.3 ± 0.5 species per site, SF = 12.3 ± 1.0 species per site, Mann–Whitney $U_{4,4} = -1.49$, $P = 0.2$). However, the abundance of large-bodied birds was significantly higher in primary forest than in secondary forest (PF = 18.5 ± 2.5 encounters per 10 km, SF = 10.2 ± 0.4 encounters per 10 km, Mann–Whitney $U_{4,4} = -2.31$, $P < 0.05$).

Table 3. The number of transects ($n = 4$) in which large mammal tracks were observed in primary and secondary forest, and track rate per 10 km (\pm SE) surveyed in the Jarí region of the north-eastern Brazilian Amazon. Significance tests were performed using Mann–Whitney U -tests. * $P < 0.05$; ns = not significant ($df = 4$, 4 in all cases).

Species	Primary forest		Secondary forest		U
	N (of 4)	Tracks per 10 km	N (of 4)	Tracks per 10 km	
<i>Dasyprocta leporina</i>	4	2.47 ± 1.09	3	1.95 ± 0.76	0.00 ns
<i>Mazama americana</i>	4	1.80 ± 0.52	4	21.3 ± 8.91	-2.31*
<i>M. gouazoupira</i>	2	1.29 ± 1.02	3	1.09 ± 0.57	-0.30 ns
<i>Pecari tajacu</i>	3	2.02 ± 0.93	3	0.80 ± 0.43	-1.02 ns
<i>Tayassu pecari</i>	2	0.65 ± 0.42	1	0.25 ± 0.25	-0.67 ns
<i>Tapirus terrestris</i>	4	6.69 ± 2.03	4	8.57 ± 2.34	-0.58 ns
<i>Agouti paca</i>	1	0.42 ± 0.42	3	1.06 ± 0.76	-1.07 ns
Large felids	1	0.36 ± 0.36	2	1.00 ± 0.61	0.99 ns
<i>Dasybus spp.</i>	3	1.81 ± 0.65	4	1.41 ± 0.52	-0.29 ns
<i>Myrmecophaga tridactyla</i>	3	0.94 ± 0.40	1	0.46 ± 0.46	-0.77 ns

The community composition of the bird species surveyed was also significantly different between primary and secondary forest sites (ANOSIM, $R = 0.771$, $P < 0.05$). Secondary forest sites were characterized by a high abundance of little chachalaca (*Ortalis m. motmot*), though also by an absence or much lower abundance of nearly all the other bird species censused (Appendix I). The largely terrestrial frugivore-insectivores, grey-winged trumpeter (*Psophia c. crepitans*) and marail guan (*Penelope marail*), were never encountered in secondary forest. Large tinamous were observed in both habitats, though were more abundant in primary forest. Black curassow (*Crax alector*), a large terrestrial game bird, had a higher encounter rate in secondary forest, though sample sizes were small. Small tinamous were fairly abundant in both habitats and were not important discriminators of differences in primary and secondary forest bird communities (Appendix 1).

SIMPER analysis emphasizes the general paucity of most canopy birds in secondary forest (*Amazona* spp., white-throated toucan, red-throated caracara, and painted parakeet *Pyrrhura p. picta*; Table 2). Oropendolas (*Psarocolius* spp.) had similar abundances in primary and secondary forest.

DISCUSSION

Secondary forests appear to support mammal abundances comparable with those of primary forest, including many species harvested by subsistence hunters in Amazonian forests (Peres 2000). We report a high abundance of large vertebrates in secondary forests (cf. Wilkie 1989), indicating a large prey base for both predators and people. However, community composition was very different between primary and secondary forest, with high species turnover between habitats. Species vary in their resilience to changes in habitat and food supply, and tend to be affected by disturbance in different ways (Lawton *et al.* 1998). As predicted, primates with a generalist diet were abundant in secondary forests, as were terrestrial ungulate browsers and agoutis. However, secondary forests were probably unsuitable for large primates, and held an impoverished avian frugivore assemblage in comparison to primary forest sites.

Frugivores

The large-scale secondary forests surveyed were a relatively poor habitat for specialist frugivores, and the majority of mammalian and avian frugivores of the Jari region were either absent or rare in secondary forests. The complete absence of the largest frugivorous Amazonian primate, the black spider monkey, suggests

an impoverished flora in second-growth areas, as well as structural constraints for these upper canopy semi-brachiators. Spider monkeys feed on large mature fruit pulp of primary forest trees and lianas (Peres & van Roosmalen 2002, van Roosmalen 1980) and apparently cannot survive exclusively on small fruits from pioneer tree and shrub species. The low abundance of howler monkeys in secondary forests could perhaps be attributed to a lack of large canopy trees upon which this largely folivorous primate depends (Julliot & Sabatier 1993, Leighton & Leighton 1982, Schwarzkopf & Rylands 1989). The response of large primates reflects their decline after logging, which is also attributed to a lack of preferred large fruiting trees (Grieser-Johns 1997). However, abundance of large primates was relatively low even in primary forests at Jari, reflecting the lower regional scale productivity of this region (Phillips *et al.* 2004, Peres in press).

Although highly mobile, large avian frugivores responded in a similar way to large primates. The marked scarcity of macaws, parrots and toucans, which specialize on young seeds or mature fruit, is consistent with the general vulnerability of these species to forest disturbance (Thiollay 1992). Generalist species, such as the red-throated caracara were present in all secondary forest sites, as were small cracids such as little chachalacas. Little chachalacas have been previously recorded as highly tolerant of second-growth habitat, as has *Crax alector* (Borges 1999). Curassows appear to be more resilient to habitat disturbance as they were observed in two of the four secondary forest sites. Oropendolas were also common in secondary forest, possibly because they feed on ripe pods of *Inga* spp. (Hilty 2003), which are generally abundant in secondary forests (Guariguata & Ostertag 2001), including those of Jari. Terrestrial avian frugivores were largely absent from the secondary forests studied, and this is consistent with their responses to logging (Thiollay 1992). Grey-winged trumpeters are primary forest specialists (Stotz *et al.* 1996), and appear to be unable to subsist on food resources in secondary forest as they were restricted to primary forest. The absence of marail guans from our secondary forest sites may be due to a small sample size as guans have previously been found to feed on pioneer plants such as *Cecropia* spp. and *Bellucia* spp. (Borges 1999), but are normally less abundant in secondary forest than primary forest (Johns 1991a). This raises questions over the degree to which seed dispersal limitation may hinder secondary forest succession. For example, large frugivorous birds and mammals almost certainly increase the rate of forest succession through seed dispersal (Howe 1977, Wunderle 1997), particularly for large-seeded plants dispersed by a few species of specialized and often large-bodied seed vectors (Peres & van Roosmalen 2002, Poulsen *et al.* 2002).

Dietary breadth

The high abundance of several primate species with broad diets (extending to insectivory) in this study can be related to the resources available in secondary forest, in agreement with DeWalt *et al.* (2003), who predicted that primate biomass in secondary forest will be dominated by species that subsist on a mixed diet of fruits and insects. Tamarins are known to prefer secondary forest over primary forest habitat (Schwarzopf & Rylands 1989), and it has been speculated that they benefit from the abundant arthropods in secondary forest (Lovejoy *et al.* 1986). Light-trapping in the same region showed higher Orthoptera abundance per unit volume of forest in second-growth than primary forest (A. L. Gutjahr unpubl. data). Squirrel monkeys are often abundant in highly degraded forest habitat (Barlow & Peres 2006, Boinski 1987), probably due to a broad diet that includes many insects as well as *Bellucia* and *Inga* fruits (Lima & Ferrari 2003). Pioneer trees are associated with high and frequent production of fruit (Levey 1988) and secondary forest fruiting in Jari was characterized by an almost complete dominance of *Bellucia* and *Inga* spp. However, our study took place just after the peak months of fruiting in Jari (Coutinho & Pires 1996) so we may have underestimated fruit production in primary forest as compared to secondary forest. The higher abundance of brown capuchins in secondary forests was similar to their density response to logging in central Amazonia (Johns 1991b). Their resilience to disturbance may be due to dietary elasticity (Simmen & Sabatier 1996), and a tolerance of forest fragmentation and landscape 'patchiness' (Michalski & Peres 2005).

The occurrence of tapirs in secondary forest is of conservation importance given their vulnerability to hunting and generally low densities across their range (Bodmer & Brooks 1997). Tapirs thrive on herbaceous plants and saplings of forest gaps (Fragoso 1991, Salas & Fuller 1996), and consume a substantial amount of *Bellucia* fruit (Henry *et al.* 2000), all of which were common in secondary forests. Red brocket deer also subsist on browse and fruits (Gayot *et al.* 2004), explaining their high abundance in secondary forests. Grey brocket deer are more frugivorous than red brocket deer, and consume a lower proportion of browse and pioneer species (Gayot *et al.* 2004).

Although hunting can severely impact vertebrate assemblage structure (Peres 2000), our findings are unlikely to have been affected by differential levels of hunting pressure in primary and secondary forest as our survey sites were deliberately remote from human communities. Participatory mapping with hunters in the region also indicates that the areas surveyed are subjected to only low levels of hunting pressure (L. Parry unpubl. data).

Conservation implications

The pace of land conversion in tropical forest regions looks set to continue (Foody *et al.* 2003) and an increasing proportion of tropical forest cover will become second-growth (Wright & Muller-Landau 2006). It is therefore essential to understand the value of secondary forest to large vertebrates, firstly to determine which species are absent from secondary forest due to a low tolerance to regrowth habitat. Secondly, the case for preventing indiscriminate re-clearance of regenerating forests is stronger given some baseline abundance data. This study goes some way to redress a chronic lack of information regarding large vertebrate community composition within secondary forest (Dunn 2004), although longer-term studies examining inter- and intra-annual changes in vertebrate abundances are essential to gain a full appreciation of the conservation relevance of this habitat. Further research could also clarify the extent to which secondary forests may serve as feeding rather than breeding areas, as has been suggested for birds (Petit *et al.* 1999).

The high abundance of many bird and mammal species in secondary forest warrants greater consideration by landowners when planning conversion of existing second-growth forests into agriculture, or increasingly, exotic tree plantations (Malhi *et al.* 2002). However, the lower suitability of second-growth habitat to many specialist bird and mammal species means that 13–18-y-old secondary forests are of limited conservation value compared with primary forest. Conservationists are encouraged to argue for the protection of existing tropical secondary forests as a useful resource for nature conservation, rather than as an adequate alternative to primary forests.

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LITERATURE CITED

- BARLOW, J. & PERES, C. A. 2006. Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest. *Biodiversity and Conservation* 15:985–1012.
- BARLOW, J., HAUGAASEN, T. & PERES, C. A. 2002. Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biological Conservation* 105:157–169.

- BODMER, R. E. & BROOKS, D. M. 1997. Status and action plan of the lowland tapir (*Tapirus terrestris*). Pp. 46–56 in Brooks, D. M., Bodmer, R. E. & Matola, S. (eds.). *Tapirs – status survey and conservation action plan*. IUCN, Gland.
- BOINSKI, S. 1987. Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia Primatologica* 49:151–167.
- BORGES, S. H. 1999. Relative use of secondary forests by cracids in Central Amazonia. *Ornitologia Neotropical* 10:77–80.
- BROOKS, D. M. & BEGAZO, A. J. 2001. Macaw density variation in the western Amazonian basin. Pp. 427–438 in Marzluff, J. M., Bowman, R. & Donnelly, R. (eds.). *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Dordrecht.
- BROWN, S. & LUGO, A. E. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1–32.
- CASTELLETTA, M., SODHI, N. S. & SUBARAJ, R. 2000. Heavy extinction of forest avifauna in Singapore: lessons for biodiversity conservation in Southeast Asia. *Conservation Biology* 14:1870–1880.
- CLARKE, K. R. 1993. Nonparametric analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- CLARKE, K. R. & GREEN, R. H. 1988. Statistical design and analysis for a “biological effects” study. *Marine Ecology Programme Series* 46: 213–226.
- CLARKE, K. R. & WARWICK, R. M. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. Primer-E Ltd, Plymouth. 172 pp.
- COUTINHO, S. D. C. & PIRES, M. J. P. 1996. *Jari: um banco genético para o futuro*. Imago Editora Ltda., Rio de Janeiro. 242 pp.
- DEWALT, S. J., MALIAKAL, S. K. & DENSLOW, J. S. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management* 182:139–151.
- DUNN, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18:302–309.
- ESTRADA, A., COATES-ESTRADA, R. & MERITT, D. J. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* 17:229–241.
- FOODY, G. M., BOYD, D. S. & CUTLER, M. E. J. 2003. Predictive relations of tropical forest biomass from Landsat TM data and their transferability between regions. *Remote Sensing of Environment* 85:463–474.
- FRAGOSO, J. M. 1991. The effect of selective logging on Baird’s tapir. Pp. 295–304 in Mares, M. & Schmidly, D. J. (eds.). *Latin American mammalogy: history, biodiversity and conservation*. University of Oklahoma Press, Norman.
- GASCON, C., LOVEJOY, T. E., BIERREGAARD, R. O., MALCOM, J. R., STOUFFER, P. C., VASCONCELES, H. L., LAURANCE, W. F., ZIMMERMAN, B., TOCHER, M. & BORGES, S. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91:223–229.
- GAVIN, M. C. 2004. Changes in forest use value through ecological succession and their implications for land management in the Peruvian Amazon. *Conservation Biology* 18:1562–1570.
- GAYOT, M., HENRY, O., DUBOST, G. & SABATIER, D. 2004. Comparative diet of the two forest cervids of the genus *Mazama* in French Guiana. *Journal of Tropical Ecology* 20:31–43.
- GRIESER-JOHNS, A. 1997. *Timber production and biodiversity conservation in tropical rain forests*. Cambridge University Press, Cambridge. 247 pp.
- GUARIGUATA, M. R. & OSTERTAG, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148:185–206.
- HEMINGWAY, C. A. & OVERDORFF, D. J. 1999. Sampling effects on food availability estimates: phenological method, sample size, and species composition. *Biotropica* 31:354–364.
- HENRY, O., FEER, F. & SABATIER, D. 2000. Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. *Biotropica* 32:364–368.
- HILL, K., MCMILLAN, G. & FARINA, R. 2003. Hunting-related changes in game encounter rates from 1994 to 2001 in the Mbaracayu Reserve, Paraguay. *Conservation Biology* 17:1312–1323.
- HILTY, S. L. 2003. *Birds of Venezuela*. Christopher Helm, London. 878 pp.
- HOWE, H. F. 1977. Bird activity and seed dispersal of a wet tropical forest tree. *Ecology* 58:539–550.
- HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- JANSEN, P. A. & ZUIDEMA, P. A. 2001. Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees. Pp. 35–60 in Fimbel, R. A., Grajal, A. & Robinson, J. (eds.). *The cutting edge: conserving wildlife in logged tropical forests*. Columbia University Press, New York.
- JOHNS, A. D. 1985. Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. *American Journal of Primatology* 8:31–36.
- JOHNS, A. 1991a. Responses of Amazonian rain forest birds to habitat modification. *Journal of Tropical Ecology* 7:417–437.
- JOHNS, A. 1991b. Forest disturbance and Amazonian primates. Pp. 115–135 in Box, E. O. (ed.). *Primate responses to environmental change*. Chapman & Hall, London.
- JULLIOT, C. & SABATIER, D. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *International Journal of Primatology* 14:527–550.
- LAWTON, J. H., BIGNELL, D. E., BOLTON, B., BLOEMERS, G. F., EGGLETON, P., HAMMOND, P. M., HODDA, M., HOLT, R. D., LARSEN, T. B., MAWDSLEY, N. A., STORK, N. E., SRIVASTAVA, D. S. & WATT, A. D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72–76.
- LEIGHTON, M. & LEIGHTON, D. R. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14:81–90.
- LEMMON, P. E. 1957. A new instrument for measuring forest overstorey density. *Journal of Forestry* 55.
- LEVEY, D. J. 1988. Spatial and temporal variation in Cost Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251–269.
- LIMA, E. M. & FERRARI, S. F. 2003. Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in eastern Brazilian Amazonia. *Folia Primatologica* 74:150–158.
- LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOM, J. R., QUINTELA, C. E. & HARPER, L. E. 1986. Edge and other effects

- of isolation on Amazon forest fragments. Pp. 257–285 in Soulé, M. (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, MA.
- LUGO, A. E. & HELMER, E. H. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190: 145–161.
- MALHI, Y., MEIR, P. & BROWN, S. 2002. Forests, carbon and global climate. *Philosophical Transactions of the Royal Society of London, Series A-Mathematical Physical and Engineering Sciences* 360:1567–1591.
- MICHALSKI, F. & PERES, C. A. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation* 124: 383–396.
- MORAN, E. F., BRONDÍZIO, E., MAUSEL, P. & WU, Y. 1994. Integrating vegetation, land-use and satellite data. *BioScience* 44:329–338.
- NEPSTAD, D. C., UHL, C. & SERRÁO, A. S. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* 20:248–255.
- PERES, C. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. *Neotropical Primates* 7:11–16.
- PERES, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14:240–253.
- PERES, C. A. in press. Soil fertility and arboreal mammal biomass in tropical forests. In Schnitzer, S. & Carson, W. (eds.). *Tropical forest community ecology*. Blackwell Publishing, Oxford.
- PERES, C. A. & VAN ROOSMALEN, M. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted tropical forests. Pp. 407–423 in Levey, W., Silva, D. & Galetti, M. (eds.). *Frugivory and seed dispersal: ecological, evolutionary and conservation issues*. CAB International, Wallingford.
- PERES, C. A., BARLOW, J. & HAUGAASEN, T. 2003. Vertebrate responses to surface wildfires in a central Amazonian forest. *Oryx* 37:97–109.
- PERZ, S. G. & SKOLE, D. L. 2003. Secondary forest expansion in the Brazilian Amazon and the refinement of forest transition theory. *Society and Natural Resources* 16:277–294.
- PETIT, L. J., PETIT, D. R. & CHRISTIAN, D. G. 1999. Bird communities of natural and modified habitats in Panama. *Ecography* 22:292–304.
- PHILLIPS, O. L., BAKER, T. R., ARROYO, L., HIGUCHI, N., KILLEEN, T. J., LAURANCE, W. F., LEWIS, S. L., LLOYD, J. & MALHI, Y. 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of Royal Society, Series B* 359:381–407.
- POULSEN, J. R., CLARK, C. J., CONNOR, E. F. & SMITH, T. B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83:228–240.
- REYNA-HURTADO, R. & TANNER, G. W. 2005. Habitat preferences of ungulates in hunted and nonhunted areas in the Calakmul Forest, Campeche, Mexico. *Biotropica* 37:676–685.
- SABATIER, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Ecologie (Terre et Vie)* 40:289–320.
- SALAS, L. A. & FULLER, T. 1996. Diet of the lowland tapir (*Tapirus terrestris* L) in the Tabaro River valley, southern Venezuela. *Canadian Journal of Zoology* 74:1444–1451.
- SCHWARZKOPF, L. & RYLANDS, A. B. 1989. Primate species richness in relation to habitat structure in Amazonian forest fragments. *Biological Conservation* 48:1–12.
- SIMMEN, B. & SABATIER, D. 1996. Diets of some French Guianan primates: food composition and food choices. *International Journal of Primatology* 17:661–693.
- SMITH, J., FERREIRA, S., KOP, P. V. D. & SABOGAL, C. 2003. The persistence of secondary forests on colonist farms in the Brazilian Amazon. *Agroforestry Systems* 58:125–135.
- STEVENSON, P. R., QUINONES, M. J. & AHUMUDA, J. A. 1998. Annual variation in fruiting pattern using two different methods in a lowland tropical forest, Tinigua National Park, Columbia. *Biotropica* 30: 129–134.
- STOTZ, D. F., FITZPATRICK, J. W., PARKER, T. A. & MOSKOVITS, D. K. 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago. 502 pp.
- THIOLLAY, J. M. 1992. The influence of selective logging on bird species diversity in a Guianan rain forest. *Conservation Biology* 6:47–63.
- VAN ROOSMALEN, M. V. 1980. *Habitat preferences, diet, feeding preferences, and social organization of the black spider monkey*. Ph.D. thesis, University of Wageningen, Netherlands.
- VANDERMEER, J. & PERFECTO, I. 1997. The agroecosystem: a need for the conservation biologist's lens. *Conservation Biology* 11:591–592.
- WALLACE, R. B. & PAINTER, R. L. E. 2002. Phenological patterns in a southern Amazonian tropical forest: implications for sustainable management. *Forest Ecology and Management* 160:19–33.
- WILKIE, D. S. 1989. Impact of roadside agriculture on subsistence hunting in the Ituri Forest of northeastern Zaire. *American Journal of Physical Anthropology* 78:485–494.
- WRIGHT, S. J. & MULLER-LANDAU, H. C. 2006. The future of tropical forest species. *Biotropica* 38:287–301.
- WUNDERLE, J. M. J. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99:223–235.

Appendix 1. Number of large mammals and birds detected (visual and acoustic) per 10 km of line-transect surveys in primary forest (PF) and secondary forest (SF) in the Jari region of the north-eastern Brazilian Amazon. Direct detection events are the number of individual visual and acoustic detection events. Mean group size is based on all visual detection events, including times other than during census. C = observed during census; P = detection at time other than census (visual, acoustic, tracks).

Species	English name	Direct detection events		Encounters per 10 km		Mean group size		Individuals per 10 km		Detection	
		PF	SF	PF	SF	PF	SF	PF	SF	PF	SF
Primates											
<i>Alouatta macconnelli</i> Elliot, 1910	Guyan red howler monkey	10	1	1.12 ± 0.54	0.13 ± 0.13	4.5	4.5	5.02	0.58	C	C
<i>Ateles paniscus</i> (L., 1758)	Black spider monkey	13	0	1.39 ± 0.62	0	4.5	–	6.24	0	C	–
<i>Cebus apella</i> (L., 1758)	Brown capuchin	7	14	0.78 ± 0.28	1.55 ± 0.62	5.1	6.2	3.99	9.61	C	C
<i>Pithecia pithecia</i> (L., 1766)	Guianan saki monkey	2	1	0.21 ± 0.12	0.13 ± 0.13	3.0	1.0	0.64	0.13	C	C
<i>Saguinus m. midas</i> (L., 1758)	Golden-handed tamarin	0	8	0	0.91 ± 0.54	–	3.6	0	3.27	P	C
<i>Samiri s. sciureus</i> (L., 1758)	Common squirrel monkey	0	1	0	0.13 ± 0.13	–	20.0	0	2.58	–	C
	Total			3.50 ± 0.86	2.84 ± 1.36						
Ungulates											
<i>Mazama americana</i> (Erxleben, 1777)	Red brocket deer	2	7	0.22 ± 0.13	0.76 ± 0.27	1.0	1.0	0.22	0.76	C	C
<i>M. gouazoubira</i> (G. Fischer, 1814)	Grey brocket deer	1	1	0.11 ± 0.11	0.10 ± 0.10	1.0	0.9	0.11	0.09	C	C
<i>Tapirus terrestris</i> (L., 1758)	Brazilian tapir	1	0	0.11 ± 0.11	0	1.0	–	0.11	0	C	P
<i>Tayassu pecari</i> (Link, 1795)	White-lipped peccary	1	0	0.10 ± 0.10	0	200	–	20.0	0	C	P
<i>Pecari tajacu</i> (L. 1758)	Collared peccary	4	0	0.44 ± 0.01	0	4.8	–	2.11	0	C	P
	Total			0.99 ± 0.11	0.86 ± 0.35						
Rodents											
<i>Agouti paca</i> (L., 1766)	Paca	0	1	0	0.10 ± 0.10	–	1.0	0.00	0.10	P	C
<i>Dasyprocta leporina</i> (L., 1758)	Brazilian agouti	5	13	0.54 ± 0.20	1.44 ± 0.53	1.1	1.2	0.60	1.78	C	C
<i>Myoprocta exilis</i> (Wagler, 1831)	Red acouchi	2	0	0.21 ± 0.21	0	1.0	–	0.21	0.00	C	?
Other mammals											
<i>Eira barbara</i> (L., 1758)	Tayra									P	–
<i>Leopardus pardalis</i> (L., 1758)	Ocelot									P	–
<i>Myrmecophaga tridactyla</i> (L., 1758)	Giant anteater									P	P
<i>Nasua nasua</i> (L., 1766)	South American coati	0	2	0	0.21 ± 0.21	–	22.5	0	4.69	–	C
<i>Puma concolor</i> (L., 1771)	Puma									P	P
<i>Panthera onca</i> (L., 1758)	Jaguar									P	P
<i>Speothos venaticus</i> (Lund, 1842)	Bush dog	0	1	0	0.10 ± 0.10	–	2.0	0	0.21	–	C
Game Birds											
<i>Crax alector</i> (L., 1766)	Black currawong	1	3	0.11 ± 0.11	0.32 ± 0.20	2.0	2.3	0.22	0.73	C	C
<i>Crypterellus</i> spp. ^a	Small tinamous	13	16	1.42 ± 0.46	1.71 ± 0.20	1.0	1.3	1.42	2.22	C	C
<i>Ortalis m. motmot</i> (L., 1766)	Little chachalaca	0	30	0	3.18 ± 1.13	–	3.0	0	9.53	–	C
<i>Penelope marail</i> (Müller, 1776)	Marail guan	3	0	0.34 ± 0.11	0	1.8	–	0.60	0	C	–
<i>Psophia crepitans</i> (L., 1758)	Grey-winged trumpeter	5	0	0.52 ± 0.39	0	5.8	–	3.03	0	C	–
<i>Tinamus</i> spp.	Large tinamous	23	5	2.48 ± 0.84	0.55 ± 0.27	1.0	1.1	2.48	0.60	C	C
	Total			4.87 ± 1.07	5.75 ± 0.75						
Canopy birds											
<i>Amazona ochrocephala</i> (Gmelin, 1788)	Yellow-crowned parrot	36	2	4.01 ± 0.99	0.22 ± 0.22	2.7	2.0	10.81	0.44	C	C
<i>Ara</i> spp.	Macaws	11	3	1.18 ± 0.43	0.37 ± 0.24	2.4	3.3	2.84	1.21	C	C
<i>Ibycter americanus</i> (Boddaert, 1783)	Red-throated caracara	20	5	2.20 ± 1.08	0.51 ± 0.32	2.2	1.8	4.84	0.92	C	C
<i>Psarocolius</i> spp. ^b	Oropendola	20	20	2.23 ± 0.97	2.13 ± 0.54	1.7	2.3	3.79	4.91	C	C
<i>Pyrrhura picta</i> (Müller, 1776)	Painted parakeet	9	0	0.97 ± 0.37	0	2.5	–	2.44	0	C	–
<i>Ramphastos tucanus</i> (L., 1758)	White-throated toucan	28	11	3.08 ± 0.96	1.22 ± 0.38	1.5	1.7	4.62	2.07	C	C
	Total			13.67 ± 3.29	4.45 ± 0.70						

^aPooled data of four species, including *C. soui*, *C. e. erythropus*, *C. cinereus* and *C. variegatus*.

^bIt is acknowledged that these encounters may include the morphologically similar caciques (*Cacicus* spp.) which can be difficult to distinguish from *Psarocolius*.