

Assessing Vertebrate Abundance and the Effects of Anthropogenic Disturbance on
Tropical Forest Dynamics

by

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Abstract

The Madre de Dios river basin in southeastern Peru is one of the largest and most diverse forest ecosystems on the planet. Though conservation zones with strict protection do exist in the basin, human population growth and development are having a considerable effect on forest dynamics. One major threat is the hunting-induced reduction or local extinction of large-bodied vertebrates. Vertebrate fauna contribute substantially to the maintenance of biodiversity and ecosystem processes – most notably through the dispersal of seeds by frugivores – and their loss may have disastrous consequences both to forest community composition and to the human populations which rely on ecosystem health and functioning. On the basis of 300km of standardized line-transect sampling, I documented the current densities of vertebrate frugivores across three forest sites under varying degrees of hunting pressure. I compared results across sites and interpreted them in terms of current pressures as well as site-specific trends in seedfall and tree recruitment. Increasing hunting pressure reduced large-bodied frugivores, corresponding with distinct shifts in vertebrate community composition and seedfall patterns. In response to these results, future efforts should promote strict protection of large-bodied vertebrate frugivores, with continued expansive multi-taxa forest monitoring across ontogenetic stages.

Table of Contents

List of Tables.....	iii
List of Figures.....	iii
Introduction.....	1
Objectives.....	2
Field Sites	
<i>i) Site 1: Reserva Amazónica.....</i>	3
<i>ii) Site 2: The Los Amigos Biological Station.....</i>	4
<i>iii) Site 3: The Tambopata Research Center.....</i>	4
Methods	
<i>i) Documenting vertebrate abundance.....</i>	5
<i>ii) Analyzing transect data.....</i>	10
Results.....	11
Discussion	
<i>i) Density modeling.....</i>	12
<i>ii) Hunting: Direct Effects.....</i>	15
<i>iii) Hunting: Effects on Forest Dynamics.....</i>	17
<i>iv) Conservation Implications.....</i>	18
Acknowledgements.....	21
References.....	21
Appendix	
<i>i) PD ANOVA Results.....</i>	25
<i>ii) Density Estimate Associated Values and Observational Information.....</i>	28

List of Tables

Table 1: Body mass and hunter preference of focal species.....	9
Table 2: Encounter rates of focal species.....	11
Table 3: Density estimates and effects of hunting on focal species.....	12
Table 4: Basin-wide density estimates of large frugivores.....	13
Table 5: Density estimates of two primate species at the Los Amigos Biological Station.....	14
Tables A1-A8: PD ANOVA results.....	25
Table A9: Observational information and density estimate associated values.....	28

List of Figures

Figure 1: The Janzen-Connell model of tree recruitment.....	2
Figure 2: Field sites in the Madre de Dios river basin.....	3
Figure 3: Reserva Amazónica transects and surroundings.....	6
Figure 4: The Los Amigos Biological Station transects and surroundings.....	7
Figure 5: The Tambopata Research Center transects and surroundings.....	8
Figure 6: <i>Distance</i> -generated detection function (<i>Cebus spp.</i>).....	10
Figure 7: Seedfall distribution of <i>Pseudolmedia laevis</i> at two sites.....	18

Introduction

The Madre de Dios river basin in southeastern Peru is one of the largest and most diverse forest ecosystems on the planet. The basin comprises 80,000 km² of lowland tropical forest, including several protected areas. The region boasts staggering biodiversity over several ecological zones, with more than 1,000 species of birds, 200 species of mammals, and 15,000 species of plants. Though conservation zones with strict protection do exist in the basin, human population growth and development are having a considerable effect on forest dynamics. Human use of the area ranges from small-scale swidden agriculture to more destructive logging and hunting, and rapid population growth and development around city centers such as Puerto Maldonado. Human hunting pressures in the region can significantly reduce and in some cases even eliminate local fauna. Indeed a main threat posed to biodiversity of the region is the human-induced local extinction of large-bodied vertebrates.

Vertebrate fauna contribute substantially to the maintenance of biodiversity and ecosystem processes – most notably through the dispersal of seeds by frugivores – and their loss may have disastrous consequences both to biodiversity and to the human populations which rely on ecosystem health and functioning. To date, however, the effects of these local extinctions have not been systematically documented. Current knowledge suggests that vertebrate frugivores play a crucial role in the recruitment of seedlings by dispersing seeds from parent plants. Janzen (1970) and Connell (1971) offer a mechanism by which vertebrate fauna contribute to the maintenance of high tree diversity in tropical forests, and through which the effects of vertebrate extinctions can be examined. In the absence of vertebrate seed dispersers, seeds dropped near their parent trees are subject to dramatically reduced success rates due to the pressures of localized host-specific predators, pathogens, and parasites; these actors are collectively termed “natural enemies,” predominantly arthropods, fungi, and other small organisms. Seeds must “escape in space” from the parent tree to avoid these density dependent pressures, and seed dispersal by vertebrate fauna is the primary mechanism through which recruitment is possible (see Figure 1).

In this regard, it is possible that human hunting pressures directly affect recruitment of new trees, thus reducing diversity and reshaping forest structure. An understanding of how and to what degree anthropogenic disturbance alters forest dynamics will allow conservationists to best address existing threats to biodiversity, while promoting the sustainable use of natural resources. As ecosystem health directly affects the human inhabitants of those natural systems, developing a comprehensive strategy for forest use and conservation will be critical for the long-term wellbeing of local communities.

TREE RECRUITMENT IN AN EMPTY FOREST

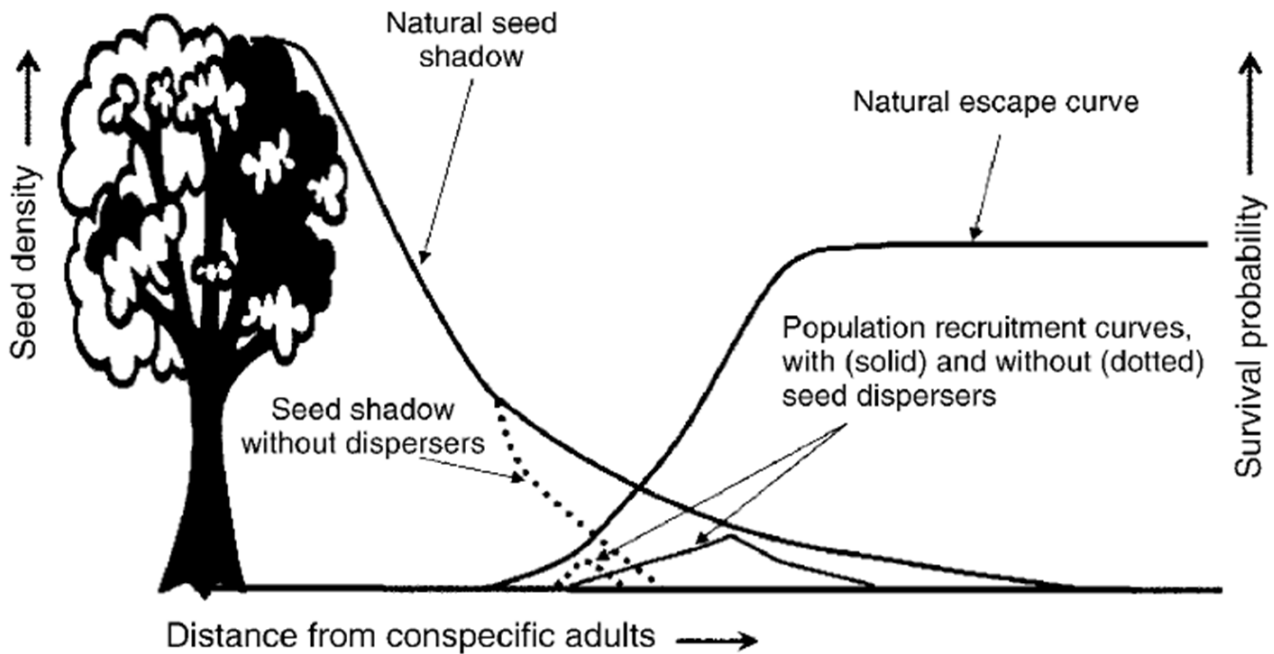


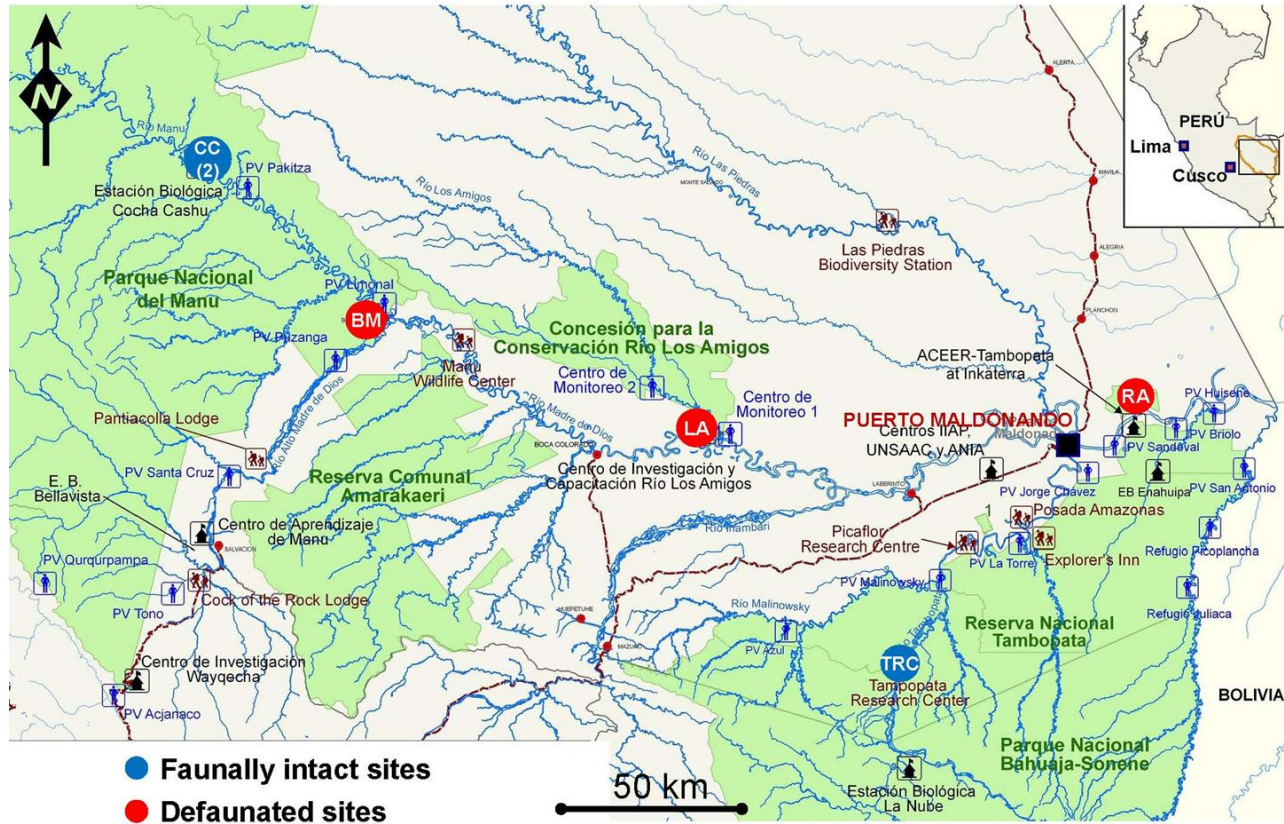
Figure 1: From Terborgh *et al.* (2008); The Janzen-Connell model of tree recruitment, with predicted alterations to the seed shadow and recruitment window. Recruitment occurs in the spatial overlap between the seed shadow and the escape curve. Reduction of this overlap, as by removal of seed dispersing vertebrates, results in a limiting of recruitment potential.

Objectives

The primary objectives of the project are: i) to document the current abundances of vertebrate frugivores across three forest sites and gauge the extent of hunting-induced reductions and local extinctions; ii) to gain an understanding of forest regeneration dynamics and the effects of anthropogenic disturbance on high biodiversity forest systems using integrated short- and long-term data; and iii) to present stakeholders in the local community and international conservation field with an empirical analysis of the effects of current resource use, and the potential ecosystem-level consequences of unsustainable hunting.

Produced directly by this study are systematic short-term data on vertebrate frugivore abundances across three forest sites under varying degrees of anthropogenic disturbance. Collected concurrently are long-term data on forest regeneration dynamics from three additional sites spread across the Madre de Dios river basin (collected by the Center for Tropical Conservation). Complementary analysis will focus on an integration of this data with existing data on seedfall and tree recruitment, in order to describe the effects of anthropogenic disturbance on forest dynamics, as they relate to frugivory, seed dispersal, and tree community regeneration.

Field Sites



*adapted from original base map created by Nelson Gutiérrez, Amazon Conservation Association GIS Lab, Puerto Maldonado, 2007

Figure 2: Field sites in the Madre de Dios river basin. Note distinction between faunally intact and defaunated sites. A subset of these sites – RA, LA, and TRC – represent the extent of field survey effort for the immediate study.

i) Site 1: Reserva Amazónica

Reserva Amazónica (RA; 69°3'13"W, 12°32'4"S) is a 17,000 hectare private ecological reserve, owned and managed by the Asociación Inkaterrea, an ecotourism company promoting sustainable luxury travel in Peru. The site is located approximately 15km from the region's capital city, Puerto Maldonado, along the Madre de Dios River.

Past and current pressures

Given its relatively small size and proximity to Puerto Maldonado, the Reserva Amazónica forests face substantial human pressure. The lands surrounding the reserve are dominated by human use, with forests converted for farming, mining, and habitation. The large human population of Puerto Maldonado (estimated at approximately 100,000 people and growing rapidly) contributes to the extensive use of forest resources in the surrounding region. Large-bodied vertebrates venturing outside the small conservation zone thus face intensive hunting pressure, and the site is believed to be at least partially defaunated as a result. Overall, though the small conservation zone itself is well-protected, Reserva Amazónica represents a forest under considerable human disturbance.

ii) Site 2: The Los Amigos Biological Station

The Los Amigos Biological Station / Centro de Investigación y Capacitación Rio Los Amigos: CICRA (LA; 70°4'52"W, 12°34'10"S) is a 453 hectare research center adjacent to the 146,000 hectare Los Amigos Conservation Concession. The Concession was established in 2001 by two non-governmental organizations: the Peruvian Asociación para la Conservación de la Cuenca Amazónica (ACCA) and the US-based Amazon Conservation Association (ACA). While the land is managed for conservation by these two NGOs, it is owned by the state.

Past and current pressures

Prior to its designation as a conservation concession, the area surrounding Los Amigos was inhabited by ephemeral artisanal gold miners. The immediate grounds and many of the station facilities themselves were used as a more permanent mining settlement. As riverside gold mining requires the heavy use of mercury during refinement, the process can itself be environmentally damaging. The heaviest ecological impact, however, is through other factors associated with high human presence. During the peak period of activity on the station grounds, from the late 1980s to early 1990s, the high density of permanent miners – up to 120 at one point (Pitman 2010) – necessitated substantial bushmeat hunting for subsistence. Professional hunters were hired to meet the needs of the hungry mining camp, with resulting declines in large vertebrate abundance in the immediate area.

While the permanent mining settlement was abandoned and later repurposed with the designation of the land as a conservation concession, ephemeral artisanal mining persists, scattered along the river. In July of 2011, Los Amigos station managers called in the help of state police to evict illegally squatting miners. Nonetheless, the problem persists. Adding to these pressures is the government designation of a portion of the concession grounds for selective timber harvesting. Currently, the concession is managed both for conservation purposes and as a source of timber, two uses which are not entirely compatible.

Despite these pressures, the Los Amigos forest is in a state of recovery. Vertebrate densities – particularly for large-bodied game species – are believed to be substantially lower than “natural” levels, but may be increasing. Overall, the Los Amigos site represents a forest under mid-level disturbance.

iii) Site 3: The Tambopata Research Center

The Tambopata Research Center (TRC; 69°36'59"W, 13°7'9"S) is an eco-lodge and research facility located within the 275,000 hectare Tambopata National Reserve, and adjacent to the million-

hectare Bahuaja-Sonene National Park. The facilities are managed by the eco-tourism company Rainforest Expeditions, while the majority of the land is managed for strict conservation by the Peruvian government.

Past and current pressures

The Tambopata-Candamo Reserved Zone was established by the Peruvian government in August 1990. The initial boundaries of this zone were used to establish the Bahuaja-Sonene National Park as a strict conservation zone in 1996, and in 2000 the Park boundaries were expanded and the adjacent Tambopata National Reserve was designated. Prior to the 1990 establishment of the reserve zone, gold mining operations were present in the region, with activity tapering off after designation of the reserve and as a likely result of mining overexploitation in the region. Despite an administrative ban on the entry of large-scale mechanized dredges, small-scale individual mining may persist in the area (ParksWatch 2002). Nonetheless, the scale of human disturbance is small. Potential hunting pressure may have existed in the vicinity of the Tambopata Research Center in the past, though currently the site is well-protected. TRC is considered a faunally intact forest.

Methods

i) Documenting vertebrate abundance

I followed transect protocol as described in the distance analysis literature specific to tropical forest surveys of primates (Peres 1999a; Marshall *et al.* 2008; Buckland *et al.* 2010), with minor modifications to account for site-specific circumstances. I implemented line transects of 1m width and varying length (from 750m to 1500m, according to terrain conditions and station layout) at each site, with trail heads located no fewer than 500m from the station base. To reduce bias to the greatest extent possible, existing trails were used only when a) they were no larger than 1m in width, and b) they were little used by researchers, and unused by tourists. As such, existing trails were often overgrown and in some cases required additional clearing of vegetation. In cases where existing trails were absent or distributed in such a manner so as to preclude their use in a distance survey (trails which were not representative of mature forest, too short, too close together, overlapping or in a perpendicular orientation, etc.), I cut additional transects and left them to rest for at least 1 day prior to data collection. I flagged transects every 50m and georeferenced them using a GPS device (see Figures 3-5).

Reserva Amazonica: Transects and Surroundings

Cooper Rosin; Duke University; June-August, 2011

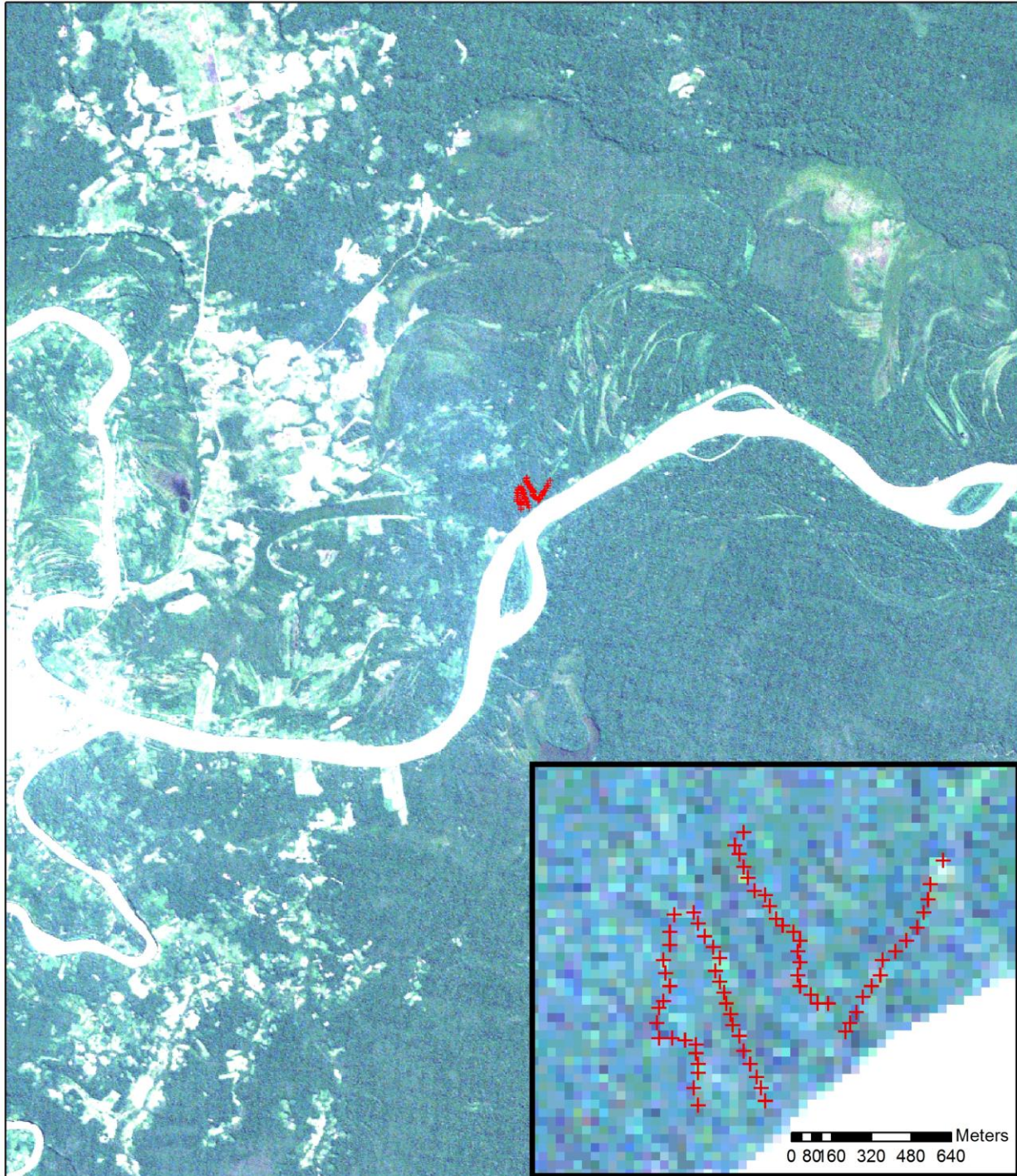
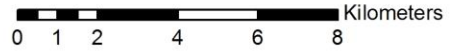


Figure 3: Reserva Amazonica georeferenced transects and surroundings (Landsat TM5 imagery). Note high density of human disturbance in the form of land clearing for agriculture, roads, settlements, etc., though this disturbance does not always translate directly to hunting pressure.

Los Amigos Biological Station (CICRA): Transects and Surroundings

Cooper Rosin; Duke University; June-August, 2011

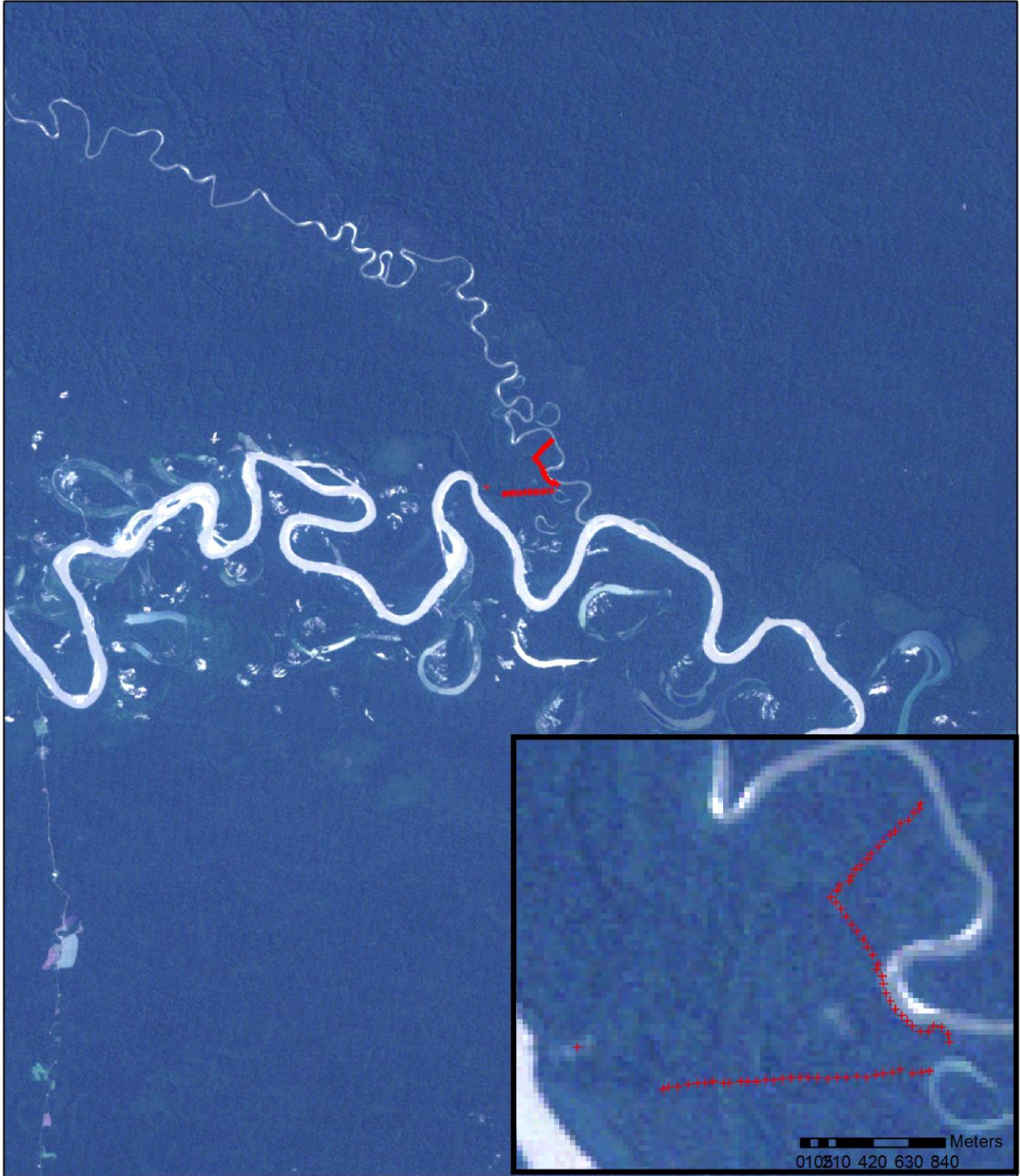
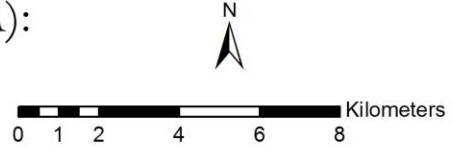


Figure 4: Los Amigos georeferenced transects and surroundings (Landsat TM5 imagery). Note presence of a road and land clearing in SW corner, and high density of small ponds resulting from mining activities surrounding the river course.

Tambopata Research Center: Transects and Surroundings

Cooper Rosin; Duke University; June-August, 2011



0 1 2 4 6 8 Kilometers

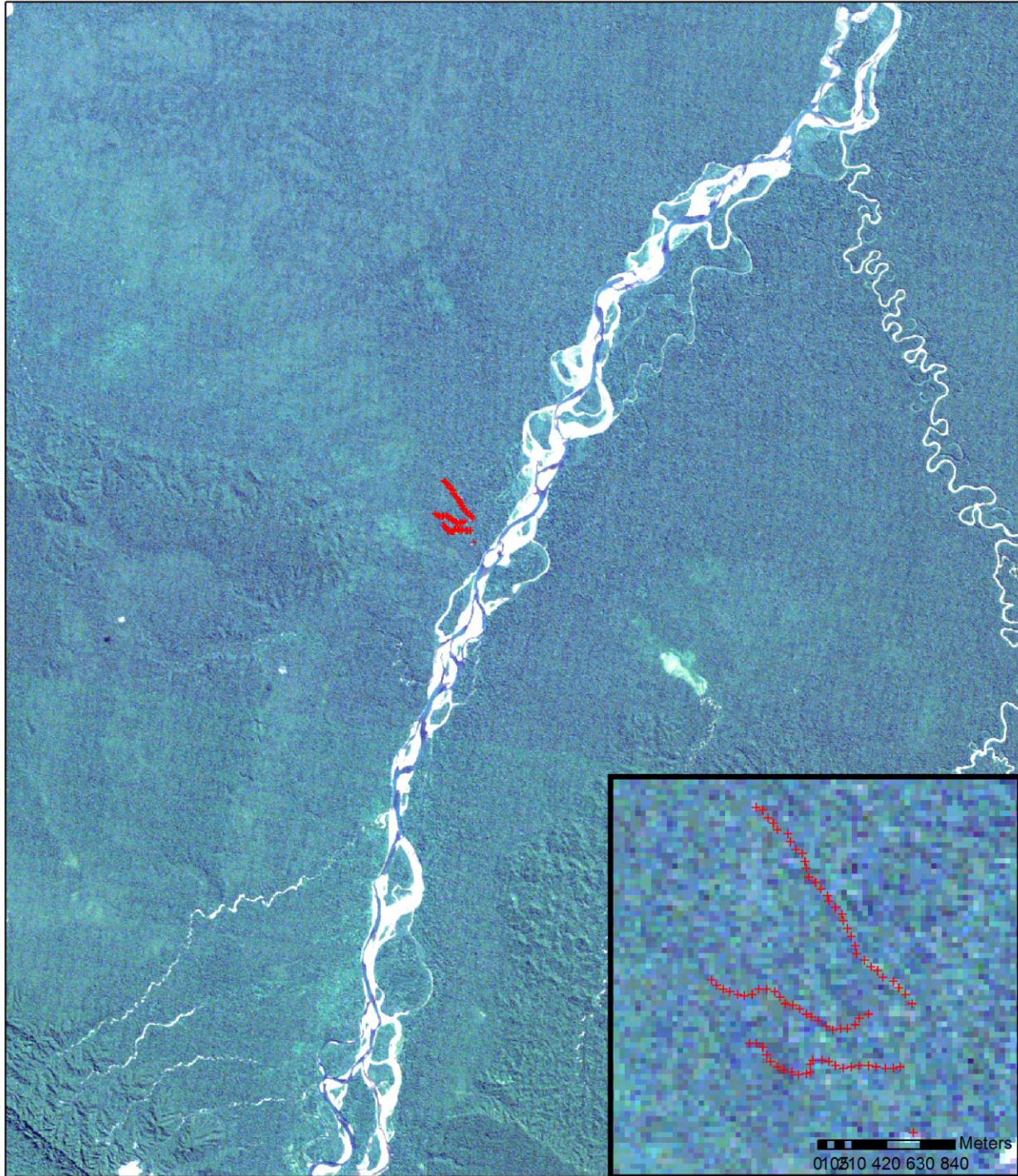


Figure 5: Tambopata Research Center georeferenced transects and surroundings (Landsat TM5 imagery). Note lack of broad-scale human-induced disturbance.

Transects were surveyed in sequence, during two daily periods corresponding to peak activity of diurnal vertebrate subjects: in the morning (0630-1100 h) and afternoon (1300-1730 h). Given that rainfall both alters subject behavior and hinders auditory detection, no transects were surveyed under such conditions. To survey each transect, I walked quietly at a mean pace of ~1.5km/hour, listening for detection cues and scanning the transect line and surrounding forest. I stopped approximately every 100m to pause for a very short period and listen for any additional cues. For each animal sighting, several data were recorded: time of day, species, number of individuals, perpendicular distance from transect (“PD”, in meters), detection mode (visual or acoustic), and group diameter (m) for species found in groups. Distance data were measured via pacing, with regular re-calibration to ensure accuracy. Data collection was limited to primates, large frugivorous and granivorous birds, rodents, and ungulates (Table 1).

Table 1: Body mass and hunter preference of focal species.

Common Name	Latin Name	Body Mass (kg)	Hunter Preference*
Primates			
Spider monkey	<i>Ateles chamek</i>	9.0	4
Red howler monkey	<i>Alouatta seniculus</i>	6.5	3
Brown capuchin	<i>Cebus apella</i>	2.9	3
White-fronted capuchin	<i>Cebus albifrons</i>	2.7	2
Monk saki	<i>Pithecia monachus</i>	2.2	2
Dusky titi	<i>Callicebus brunneus</i>	1.1	0
Squirrel monkey	<i>Saimiri boliviensis</i>	0.9	0
Saddleback tamarin	<i>Saguinus fuscicollis</i>	0.4	0
Emperor tamarin	<i>Saguinus imperator</i>	0.4	0
Birds			
Razor-billed currawong	<i>Mitrospingus canescens</i>	3.0	4
Spix's guan	<i>Penelope jacquacu</i>	1.3	3
Blue-throated piping guan	<i>Pipile cumanensis</i>	1.2	3
Pale-winged trumpeter	<i>Psophia leucoptera</i>	1.2	2
Great tinamou	<i>Tinamus major</i>	1.2	3
Small tinamous	<i>Crypturellus spp.</i>	0.4	1
Rodents			
Brown agouti	<i>Dasyprocta variegata</i>	4.0	3
Southern Amazon red squirrel	<i>Sciurus spadiceus</i>	0.6	1
Bolivian squirrel	<i>Sciurus ignitus</i>	0.2	0
Amazon dwarf squirrel	<i>Microsciurus flaviventer</i>	0.1	0
Ungulates			
White-lipped peccary	<i>Tayassu pecari</i>	32.0	4
Collared peccary	<i>Tayassu tajacu</i>	25.0	4
Red/gray brocket deer	<i>Mazama spp.</i>	25.0	4

* Degree of hunter preference on a scale of 0 (always ignored) to 4 (never ignored), from Peres & Lake (2003)

ii) Analyzing transect data

Field data notated by hand was entered and organized using Microsoft Excel. For each species surveyed, an individual encounter rate was calculated per every 10km surveyed. Vertebrate transect data was further modeled using the program *Distance v. 6.0*, a Windows-based computational package, to generate site-specific population density estimates for each focal species (Buckland 2001). Density, D , is estimated by

$$D = \frac{n}{2\mu L}$$

where n is the number of animal “objects” detected along the transect, L is the transect length and μ is the effective strip half-width. Effective strip half-width, μ , is a measure of the distance from the transect line for which as many objects are detected beyond μ as are missed within μ of the line. Program *Distance* generates species-specific μ values and detection functions, based on the distribution of perpendicular detections along the transect line, with the assumption that detection probability decreases with increasing distance from the line (Figure 6). *Distance* allows for selection among several models for best-fit, and produces an overall estimate of density (number of individuals per unit area). Here, the Hazard-rate model with a Cosine adjustment offered the best density estimator for forest primates and other species, as determined by the minimum Akaike information criterion (see Peres 1997; Buckland *et al.* 2001). All data were truncated to exclude the largest 5% of perpendicular distance values, which further benefitted model fit.

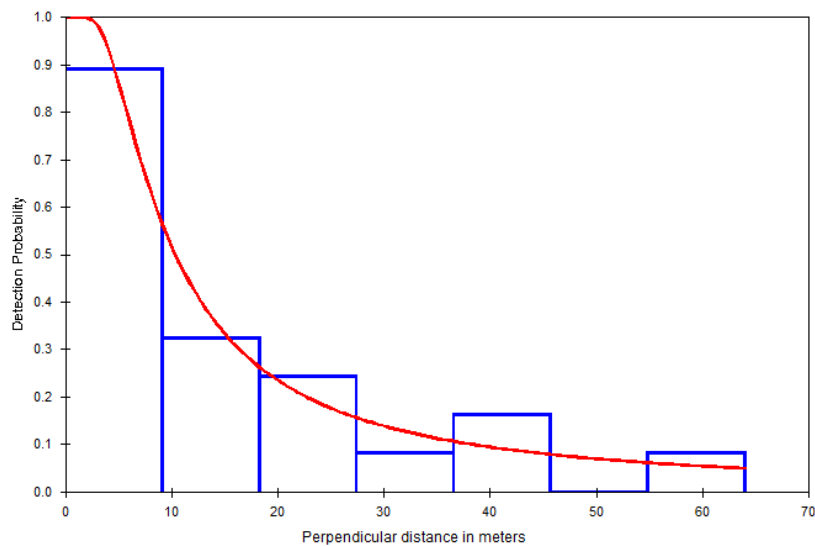


Figure 6: A *Distance*-generated detection function for *Cebus spp.* modeling decreasing detection probability with increasing perpendicular distance (PD) from the transect line.

Results

Data was collected over a total of 304.95km of transect survey effort, with 100.15km at Reserva Amazónica, 102.3km at Los Amigos, and 102.5km at Tambopata Research Center. The total number of recorded individual animal observations was 101 at RA, 139 at LA, and 163 at TRC, with the majority of detections (55%) owing to an initial auditory cue (35% were detected initially by sight, and the remaining 10% were “flushed,” essentially a combination of both sight and sound). An encounter rate (individuals/km) was calculated for each focal species at each site (Table 2).

Table 2: Encounter rates (individuals sighted per km of transect surveyed) of focal species at three sites.

Common Name	Latin Name	Encounter Rate (ind./km)		
		RA	LA	TRC
Primates				
Spider monkey	<i>Ateles chamek</i>	–	0.14	0.68
Red howler monkey	<i>Alouatta seniculus</i>	–	0.03	0.22
Brown capuchin	<i>Cebus apella</i>	0.10	0.79	0.62
White-fronted capuchin	<i>Cebus albifrons</i>	0.04	0.28	–
Monk saki	<i>Pithecia monachus</i>	–	0.07	–
Dusky titi	<i>Callicebus brunneus</i>	–	–	–
Squirrel monkey	<i>Saimiri boliviensis</i>	–	0.61	0.27
Saddleback tamarin	<i>Saguinas fuscicollis</i>	0.95	0.54	0.28
Emperor tamarin	<i>Saguinas imperator</i>	–	0.03	–
Birds				
Razor-billed curassow	<i>Mitu tuberosum</i>	–	–	0.04
Spix's guan	<i>Penelope jacquacu</i>	0.14	0.42	0.30
Blue-throated piping guan	<i>Pipile cumanensis</i>	–	–	0.02
Pale-winged trumpeter	<i>Psophia leucoptera</i>	0.30	0.37	1.51
Great tinamou	<i>Tinamus major</i>	0.10	0.22	0.17
Small tinamou	<i>Crypturellus spp.</i>	0.20	0.28	0.20
Rodents				
Brown agouti	<i>Dasyprocta variegata</i>	0.09	–	0.19
Southern Amazon red squirrel	<i>Sciurus spadiceus</i>	0.12	0.16	0.05
Bolivian squirrel	<i>Sciurus ignitus</i>	0.02	–	–
Amazon dwarf squirrel	<i>Microsciurus flaviventer</i>	–	0.01	–
Ungulates				
White-lipped peccary	<i>Tayassu pecari</i>	0.71	0.59	3.15
Collared peccary	<i>Tayassu tajacu</i>	–	0.08	0.11
Red/gray brocket deer	<i>Mazama spp.</i>	–	–	–

Observed *Distance*-derived density estimates reflect both hunter preference and the degree of hunting pressure at each site. At heavily-hunted Reserva Amazónica, large primates are completely absent, with low densities of large frugivorous birds and mid-sized primates, and high densities of both small primates and small granivorous birds (Table 3). Conversely, at the intact Tambopata Research

Center, large primates and large frugivorous birds abound, while small primates and granivorous birds occur at lower densities. Los Amigos, representing a site under moderate hunting pressure, exhibits mid-level densities for most species, with a notable abundance of mid-sized primates.

Table 3: Distance-generated density estimates of focal species and population-level effects of hunting at three sites.

Functional Group	Density (ind./km ²)			Result of hunting pressure
	RA	LA	TRC	
Primates				
<u>Large Folivorous</u>				
<i>Alouatta seniculus</i>	NA	0.3	2.1	Large primates decline
<u>Large Frugivorous</u>				
<i>Ateles chamek</i>	NA	3.9	15.9	
<u>Mid-Sized</u>				
<i>Cebus spp.</i>	3.7	19.8	11.1	Mid-sized primates fill niche space
<u>Small</u>				
<i>Saguinas spp.</i>	37.6	24.6	7.4	Small primates increase
<i>Saimiri boliviensis</i>				
<i>Pithecia monachus</i>	NA		NA	
Birds				
<u>Large Frugivorous</u>				
<i>Penelope j./Pipile c.</i>	8.0	18.2	44.0	Large frugivorous birds decline
<i>Psophia leucoptera</i>				
<u>Large Granivorous</u>				
<i>Mitu tuberosum</i>	NA	NA		Large granivorous birds decline slightly
<i>Tinamus major</i>	6.2	11.9	12.4	
<u>Small Granivorous</u>				
<i>Crypturellus spp.</i>	20.4	18.3	15.1	Small granivorous birds increase slightly

Discussion

i) Density modeling

Modeling transect data to generate density estimates provides a comparable and interpretable metric for analysis. While estimates of density allow for more inference than simple transect or encounter rate data, in-depth modeling also introduces the risk of distorting real wildlife population responses to hunting. Still, population-level trends in modeled densities should mirror the initial encounter rate, as they are both measures of the same variable: abundance. While encounter rate was calculated on an individual species basis and densities were generated based on functional groups, the two metrics unequivocally reflect common trends (Tables 2 and 3).

The extent to which individual results can be compared with similar results across broad spatial scales depends upon the level of standardization of field approach, data collection methods, and model parameters of *Distance* analysis. The three sites examined in this analysis meet these standards, given that

all were carried out by the same individuals following the same protocol. Comparability with other such studies, however, depends upon the assumption that these standards have been met. Assuming as much, the results of this analysis can be viewed within the framework of studies from across the basin.

Terborgh *et al.* (2008) provided density estimates for large frugivores at Boca Manu, a heavily hunted site at the edge of Manu National Park, while Endo *et al.* (2010) thoroughly documented the intact forest at Cocha Cashu Biological Station. Tallying all five sites allows for the examination of large frugivore populations across a continuum of hunting pressures, from near-complete defaunation to an essentially “natural” state (Table 4). In both primates and birds, human hunting pressure reduces populations of the largest-bodied species to an extreme degree. In the case of large primates in particular, populations may be extremely slow to recover, as evidenced by the higher population density at Cocha Cashu versus TRC (Table 4; further discussion below).

Table 4: Basin-wide density estimates of large frugivores.

Functional Group	Density (ind./km ²)				
	BM ¹	RA	LA	TRC	CC ²
Large Frugivorous Primates	0.0	0.0	3.9	15.9	37.5
Large Frugivorous Birds	2.1	8.0	18.2	44.0	29.2

1: Boca Manu, heavily defaunated. Terborgh *et al.* (2008)

2: Cocha Cashu, intact. Endo *et al.* (2010)

Despite the desire to compare population density estimates across multiple sites and time periods – and the potential value garnered therein – such examinations may introduce error, given variability in field methods or the specifics of analysis. A comparison of primate density estimates from four separate studies conducted at the Los Amigos Biological Station (Table 5) supports this assertion. At face value, one might interpret these results as an indication of real population trends over the 13 year time period. However, variability in sample size, field personnel and methods, and *Distance* analysis parameters may preclude making any meaningful conclusions. Peres (1999a) notes the critical importance of field observer proficiency, both in detection of subtle cues and the identification of individual species. Standardization of proficiency is simply impossible, which creates a likely source of variability between studies. Additionally, site-specific factors such as edaphic conditions, forest composition and structure, and disturbance history can contribute to uncertainty in the analysis. Natural behavioral variation in the animal subjects themselves can substantially influence density estimation; aggregation of primates at a major fruiting tree located on or near the surveyed transect can artificially raise density estimates in the short-term, as animal objects are no longer randomly distributed in space. Such behaviors may be the source of the extreme divergence seen in *Ateles* estimates from different studies at Los Amigos (Table 5). Minor alteration of *Distance* parameters can also potentially generate substantially different density

estimates. Even with appropriate standardization, population change of less than 10-30% may not be detected in visual sighting surveys (Plumptre 2000).

Table 5: Density estimates of two primate species at the Los Amigos Biological Station.

Species	Density (ind./km ²)			
	Kirby (1998)	Guzmán (2007)	ACCA (2005-2008)	Rosin (2011)
<i>Ateles chamek</i>	8.2	5.9	14.8	3.9
<i>Cebus apella</i>	10.6	12.0	15.5	13.9

Small sample sizes further confound meaningful inference and comparability between studies. The baseline recommendation is to exceed 40 independent detection events per species, though many fewer sightings may suffice given a favorable distribution of data (Peres 1999a). Such standards may be unreasonable in tropical forest sites where target species naturally occur at low densities. When hunting effects contribute further to the rarity of detection for a given species, *Distance* modeling becomes problematic. Even with substantial survey effort, the frequency and distribution of detection events for species occurring at very low densities will almost certainly not be favorable enough to generate robust density estimates.

One partial solution to overcome data insufficiencies is to pool data across sites. This allows *Distance* to generate a single “global” detection function for a given species, and apply it separately to that species’ data from each site. The advantage of this is a functional increase in sample size, with greater comparability between sites. However, this approach may not be appropriate in cases where sites vary by habitat type or other conditions. In particular, hunting pressure may induce behavioral responses which alter the detectability of a given species, such as the avoidance of trails or transects, the reduction of vocal cue frequency or volume, or the alteration of typical escape maneuvers. In such cases, pooling data may be inappropriate given uneven detectability, with hunting pressure potentially distorting density modeling. However, without statistical support of this differential detectability, pooling remains a viable option. In the case of distance analysis surveys, statistical support comes in the form of a significant Analysis of Variance (ANOVA) result in comparing PD values across sites; a significant ANOVA result (i.e. $p < .05$) indicates greater variance in PD values between sites than within sites, supporting differential detectability. ANOVA results from this study (see Appendix) were almost entirely insignificant ($p > .05$), with the exception of small primates and large frugivorous birds, for which further ANOVA of a subset of the data indicated that pooling was appropriate across two – rather than all three – sites (RA and LA for small primates; LA and TRC for large frugivorous birds). In all other cases, data were pooled across the three sites surveyed in order to effectively raise sample size and add robustness to the analysis.

Despite the use of analysis methods that can account for human disturbance factors, some natural behaviors associated with group-living species may yet complicate *Distance* analysis. Measuring group size and PD can be difficult given large non-cohesive groups, especially since individuals closer to the transect line are more detectable than those farther away. Perpendicular distance can be measured either to the estimated center of the group, or extrapolated from its overall spread and the PD to the edge of the group. Neither method is without bias, however, nor is group spread necessarily constant across season or time of day (Plumptre 2000; Marshall *et al.* 2008). The shape of social groups rarely conforms to any geometric standard such as a circle, further confounding data collection. Distance to group center must be measured as accurately as possible to comply with modeling assumptions (Buckland *et al.* 2010), but no degree of accuracy can overcome error inherent in the estimation of group spread or location on which this measurement is based. In extreme cases, as with large groups of peccaries (*Tayassu pecari* in particular), peripheral individuals are detected and sampled, but the core of the group may remain undetected or simply immeasurable. *Distance* analysis based on these necessarily poor estimates will never provide meaningful results. For such species, a simple encounter rate (Table 2) may be preferable to bias-prone density modeling.

Statistical inference with these data can be limited, given small sample sizes and variability in model parameters. Indeed most published analyses fail to report any form of statistical support for their density figures. This may be due partly to the aforementioned difficulty in comparing results (including statistical results) between studies, as well as a result of the inherent statistical uncertainty (in the form of large confidence intervals, provided by *Distance*) in such analyses. Confidence intervals for each density value estimated here are included in the Appendix.

ii) Hunting: Direct Effects

Hunting most dramatically affects large-bodied vertebrates – those greater than 5kg – which comprise the largest component (65-78%) of animal biomass at nonhunted sites (Peres 1990; Peres 2000). In primate communities specifically, population declines of the three ateline genera represent the main effect of hunting (Peres 1990; Peres 1999b). Such declines are the result of both hunter preference and large vertebrate life histories (see below). Large frugivorous primates, *Ateles* in particular, are both abundant and highly conspicuous at nonhunted sites. Given high densities, gregarious social structure, and physical size, *Ateles* are prized prey species for human hunters, providing easy detectability and a large meat payoff. Hunter preference can vary based on several of these factors, as well as cultural taboos (da Silva *et al.* 2005), but the strongest determinant of preference is large body size (see Table 1). Given this size selectivity, large game vertebrates may be drastically reduced at hunted sites while undesirable species

are left untouched. Indeed the results presented here support this assertion, with a complete absence of large primates at the most heavily hunted site (Table 3).

Drastic reductions of dominant species such as *Ateles* are not without consequences to the broader faunal assemblage. The dynamics of inter-specific competition for resources and space can govern wildlife populations, and in cases of large vertebrate defaunation, smaller vertebrates may exhibit a compensatory response from competitive release. Density compensation refers to an increase in abundance of smaller-bodied vertebrate populations in response to declines in their larger counterparts (MacArthur *et al.* 1972), though the underpinnings of this phenomenon have been debated (see review by Faeth 1984). Density compensation may occur in Amazonian primate communities, with increased abundance of mid-sized primates (and to a lesser degree, small primates) in response to intensive hunting of their larger counterparts (Peres & Dolman 2000).

Results from this study support a compensatory response of smaller-bodied game vertebrates at hunted sites (Table 3). Small primates increased under hunting pressure, with the greatest densities at the most heavily hunted site, Reserva Amazónica. At this site, the predominant small primate was the saddleback tamarin, *Saguinus fuscicollis*. Normally subordinate to larger primates, *S. fuscicollis* is subject to frequent agonistic displacement at fruiting trees (Terborgh 1983). In the absence of large primates this does not occur, freeing space, time, and resources previously unavailable due to inter-specific competition. Indeed *S. fuscicollis* may well be considered “hyperabundant” at Reserva Amazónica, given high densities and supergroups as large as 17 individuals – well above estimates of typical mean group size (5 individuals per group; Terborgh 1983) and range (2-12 individuals per group; Emmons 1997). Mid-sized primates (*Cebus*) also increased at hunted versus nonhunted sites, but reached their greatest abundance under mid-level, rather than intense, hunting pressure. This is likely owing to two factors: a) under mid-level hunting, mid-sized primates are avoided, while intense hunting pressure may result in them being taken, and b) *Cebus* may respond to the presence of sympatric primates, both large and small, reaching peak densities when neither small nor large primates are particularly abundant.

Game birds mirrored population trends seen among primates. Large frugivorous birds in particular (*Penelope*, *Pipile*, and *Psophia*) suffered drastic reductions in density under increasing hunting pressure. Small granivorous birds increased under hunting pressure, reflecting trends seen among small primates. While large granivorous birds apparently declined under hunting, the data were not as compelling as with their frugivorous counterparts. This may be due simply to an insufficient quantity of data, or may reflect real responses to hunting. Frugivorous species decline more severely at hunted sites than both granivorous and folivorous species, regardless of body size (Peres & Palacios 2007), which may account for the lack of distinct population trends of granivorous vertebrates specifically.

Ungulates surveyed also reflected clear trends across the hunting gradient. Though neither species of *Mazama* deer was encountered at any site, peccaries had a strong presence in transect observations and were often readily detectable. White-lipped peccaries (*Tayassu pecari*) in particular form tremendously large groups, with herds of more than 200 individuals exceeding 4.8 tons in total biomass (Sowls 1984). Peccaries are also highly desirable to hunters and can be severely reduced by hunting pressure (Peres 1996). Though peccary density estimates were not calculated here for reasons described above, encounter rates reveal strong population-level effects of hunting pressure (Table 2). Indeed *Tayassu pecari* was by far the most frequently encountered and conspicuous of any species at the intact Tambopata Research Center. Conversely, populations surveyed at the two hunted sites were rare and highly wary of human presence.

In intact forests, collective biomass of large vertebrates (*Ateles* and *Tayassu* in particular) is hugely greater than that of small ones. In the absence of anthropogenic effects, the largest species are dominant, conspicuous, and highly abundant. Given hunting pressure, these ecological mainstays are increasingly replaced by their smaller counterparts. As ecological impact is commensurate with biomass, not just abundance, targeted hunting of the largest species can be devastating to both the faunal assemblage and ecosystem as a whole.

iii) Hunting: Effects on Forest Dynamics

In addition to altering vertebrate population structure, hunting can have broader effects to the forest community as a whole. In particular, the loss of large frugivorous vertebrates may dramatically alter forest processes such as dispersal and recruitment; as important seed dispersers under the Janzen-Connell model, these species are crucial in maintaining biodiversity and associated dynamics. Larger-bodied frugivores are inherently capable of ingesting a wider range of fruit sizes, as well as a greater quantity of fruit than smaller-bodied frugivores (Peres & van Roosmalen 2002; Knogge & Heymann 2003). Thus smaller-bodied species, even with increased abundance, cannot replace the dispersal function of larger ones. Indeed, for plant species in hunted forests, diaspore size is negatively correlated with vertebrate dispersal success (Stoner *et al.* 2007). Under hunting pressure, tree species most reliant on large frugivores will likely suffer severe recruitment limitation as a result of decreased dispersal.

Studies from the Madre de Dios region suggest that these broader impacts of hunting are already being seen. Initial results from Swamy (unpublished data) highlight the strong dispersal limitation that results from hunting pressure. Comparing seedfall trap contents from Reserva Amazónica and Cocha Cashu (an intact site of similar composition to TRC, located within Manu National Park; see Figure 2), Swamy documented a difference in the farthest apparent dispersal distance of 27m for the primate-

dispersed *Pseudolmedia laevis* between the two sites. Visualizing these seedfall results spatially, it is clear that in the absence of large vertebrate dispersers, seeds simply are not being dispersed away from the parent tree, instead clumping in very high densities close to their source (Figure 7). As predicted by Janzen-Connell dynamics, this limited spatial dispersal will drastically reduce recruitment due to the localized presence of host-specific natural enemies.

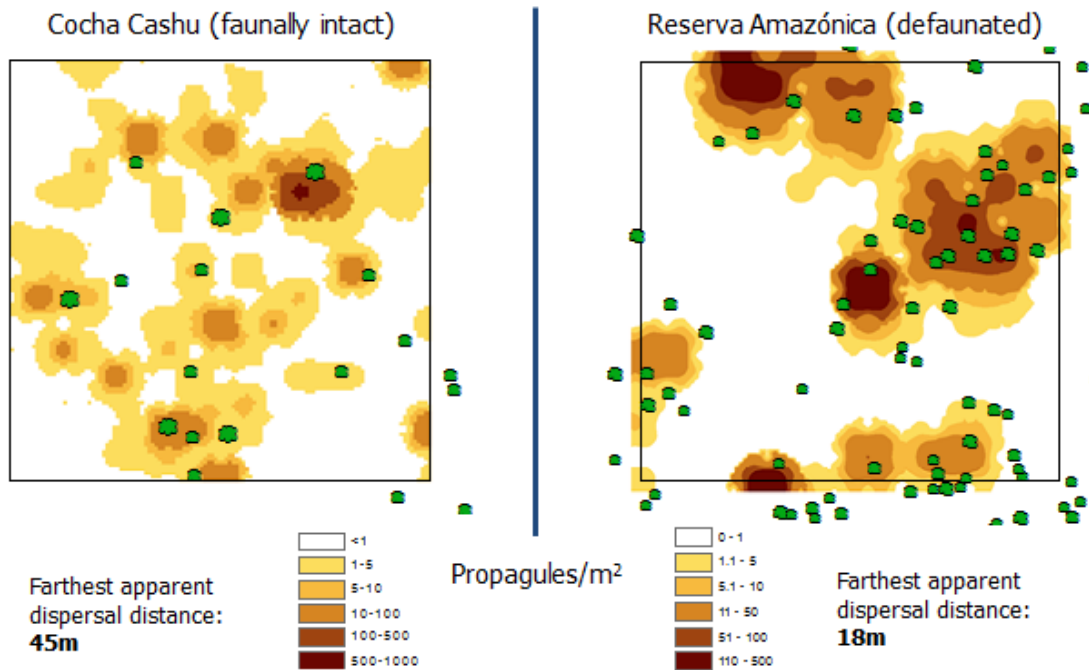


Figure 7: Seedfall distribution of *Pseudolmedia laevis* at two sites; note high density clumping of seeds near their parent trees (in green) at defaunated Reserva Amazónica vs. spatially dispersed seedfall at intact Cocha Cashu (Varun Swamy, unpublished data).

Terborgh *et al.* (2008), in another Madre de Dios study comparing heavily hunted Boca Manu with intact Cocha Cashu, noted a variety of effects of hunting on the forest community. These effects included an altered relative abundance of tree species, reduced overall sapling recruitment, and increased recruitment of species dispersed by abiotic means such as wind. As above, large-seeded species were especially affected with decreased recruitment. Hunting thus alters tree community composition, with decreased biodiversity and shifts toward otherwise relatively rare species not reliant on animal dispersers.

iv) Conservation Implications

Hunting universally accompanies forest exploitation, with direct and indirect effects. Unlike dramatic anthropogenic impacts such as deforestation, hunting is relatively insidious; its impacts cannot be detected or mapped remotely, instead requiring intensive field study to quantify (see Peres *et al.* 2006; Wilkie *et al.* 2011). Such studies are inherently limited in scale, and in many cases the results themselves are difficult to separate from natural factors that regulate game vertebrate populations.

Wild game can be a major source of dietary calories for subsistence hunters in the Amazon. In tropical forest localities, the estimated carrying capacity for humans dependent exclusively on wildlife for protein may be as low as 1 person/km² (Robinson & Bennett 2000), though population densities exceed this nearly everywhere across the tropics. Additionally, widespread habitat fragmentation synergistically increases the effects of hunting on game vertebrates (Peres 2001). Subsistence hunting is thus almost certainly unsustainable wherever it occurs.

Even limited hunting pressure may be problematic, as large vertebrate dispersers need not be completely eliminated for hunting to have secondary impacts. Species in “half-empty forests” (Redford & Feinsinger 2001) may be sufficiently reduced that they cease to function as seed dispersers before they become rare (McConkey & Drake 2006). Given the rapid and dramatic loss of preferred game species in forests subject to hunting pressure, even mild or short-lived hunting may have long-term effects. Many large game vertebrates are additionally vulnerable to major population declines, given their long life histories and low reproductive capacity. *Ateles* monkeys in particular take several years to reach reproductive age, and then are subject to long interbirth intervals and extended nursing periods (Milton 1981).

Evidence from Cocha Cashu suggests that even in forests now considered intact, *Ateles* populations may still be in recovery from past disturbances. Symington (1988), in a complete census of the local *Ateles* population, documented the total presence of 77 individuals. In a follow-up census 19 years later, Gibson (2005) found that the same population had grown to 119 individuals. While this notable increase may be due to several factors, it is likely that these populations were still recovering from local hunting pressure during the rubber boom, nearly 70 years prior. This may explain differences seen in population densities between other sites in the basin as well. *Ateles* populations in TRC (less isolated and more recently protected than Manu) are in general lower than those seen at Cocha Cashu (Table 4). Despite confounding factors, this suggests that the TRC populations may be in a state of growth as well. The fact that populations of game vertebrates such as *Ateles* can be so slow to recover from disturbance does not bode well for conservation.

In order to reduce the deleterious effects of hunting, conservation measures must focus on some combination of formal government protection and personal incentives to shift hunting pressures away from large vertebrate dispersers. One possible approach involves the implementation of education initiatives, in order to a) improve domestic animal husbandry practices to reduce reliance on wild game, and b) raise awareness for the ecosystem-level effects of hunting large frugivores. Targeted hunting of large frugivorous vertebrates such as *Ateles* will effectively reduce the future persistence of large-fruited trees, which may themselves be important to the diets of local people. Rare-to-occasional hunting of

Ateles may be sustainable in localized areas, given the influx of immigrating animals from non-hunted populations nearby (da Silva *et al.* 2005), though there is currently no impetus for local populations to reduce hunting to this level. Shifts toward more highly fecund species such as capybara and peccaries may also lift some of the burden away from hunted primates. However, hunting of these species may have broader negative effects of their own. Peccaries in particular are important ecosystem engineers (Keuroghlian & Eaton 2009; Beck *et al.* 2010), and in most cases are already subject to hunting pressure.

Formal protection through designated conservation areas may be the best approach in limiting hunting impacts. Both primate density and biomass are positively correlated with degree of protection from hunting (Freese *et al.* 1982). However, in many cases protected areas are small, insufficiently supported, or poorly designed, offering little or no real protection. In a recent geospatial analysis, Peres & Lake (2003) concluded that only 1.2% of the Brazilian Amazon is both designated as “protected” and reasonably inaccessible to hunters (>9km from the nearest access point). This highlights the need for large conservation zones with protected core areas. This may be possible only through the creation of a network of megareserves, each greater than 1 million hectares in area (Peres 2005; Laurance 2005). New protected areas could be created – and existing ones modified – which enhance passive defensibility by encompassing entire watersheds, and thus naturally reducing hunters’ access by rivers and roads (Peres & Terborgh 1995).

Hunting which targets large frugivorous vertebrates has broad long-term consequences. Many populations are slow to recover from hunting pressures, and even minor disturbances may have deleterious effects. Large frugivores consume a variety and quantity of fruit unmatched by their smaller counterparts, and function as critical seed dispersers for many tropical plant species. In the absence of these actors, trees reliant on animal-mediated dispersal suffer from spatially limited seedfall and reduced overall recruitment. Such losses result in expansive changes to tropical forest community composition and biodiversity. Without effective conservation action, unabated hunting pressures will undoubtedly continue to diminish the integrity and wonder of tropical forests now and into the foreseeable future.

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Appendix

i) PD ANOVA Results

Table A1: Large frugivorous primates (*Ateles chamek*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
LA	4	170.	42.5	2,241.66667		
TRC	19	485.	25.52632	816.26316		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	952.00229	1	952.00229	0.93343	0.34497	4.32479
Within Groups	21,417.73684	21	1,019.89223			
Total	22,369.73913	22				

Table A2: Mid-sized primates (*Cebus spp.*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	4	54.	13.5	33.		
LA	23	396.	17.21739	308.17787		
TRC	16	365.	22.8125	149.7625		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	426.55643	2	213.27822	0.93488	0.40104	3.23173
Within Groups	9,125.35054	40	228.13376			
Total	9,551.90698	42				

Table A3: Small primates (*Pithecia monachus*, *Saguinas spp.*, *Saimiri boliviensis*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	17	119.	7.	46.625		
LA	19	115.	6.05263	28.27485		
TRC	7	138.	19.71429	275.2381		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	1,031.3915	2	515.69575	7.09744	0.0023	3.23173
Within Groups	2,906.37594	40	72.6594			
Total	3,937.76744	42				

Table A4: Small primates (*Pithecia monachus*, *Saguinus spp.*, *Saimiri boliviensis*) subset PD ANOVA results: RA, LA.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	17	119.	7.	46.625		
LA	19	115.	6.05263	28.27485		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	8.05263	1	8.05263	0.21817	0.64342	4.13002
Within Groups	1,254.94737	34	36.91022			
Total	1,263.	35				

Table A5: Large frugivorous birds (*Penelope jacquacu*, *Pipile cumanensis*, *Psophia leucoptera*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	21	119.	5.66667	26.63333		
LA	28	327.	11.67857	149.04101		
TRC	42	581.	13.83333	96.38618		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	939.96429	2	469.98214	4.86078	0.00995	3.10007
Within Groups	8,508.60714	88	96.68872			
Total	9,448.57143	90				

Table A6: Large frugivorous birds (*Penelope jacquacu*, *Pipile cumanensis*, *Psophia leucoptera*) subset PD ANOVA results: LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
LA	28	327.	11.67857	149.04101		
TRC	42	581.	13.83333	96.38618		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	78.00238	1	78.00238	0.66502	0.41764	3.9819
Within Groups	7,975.94048	68	117.29324			
Total	8,053.94286	69				

Table A7: Large granivorous birds (*Tinamus major*, *Mitu tuberosum*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	9	30.	3.33333	8.		
LA	20	126.	6.3	116.53684		
TRC	18	155.	8.61111	69.4281		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	170.62861	2	85.3143	1.0854	0.34664	3.20928
Within Groups	3,458.47778	44	78.60177			
Total	3,629.10638	46				

Table A8: Small granivorous birds (*Crypturellus spp.*) PD ANOVA results: RA, LA, TRC.

Analysis of Variance (One-Way)						
Summary						
Groups	Sample size	Sum	Mean	Variance		
RA	17	51.	3.	5.375		
LA	25	107.	4.28	10.21		
TRC	20	89.	4.45	9.52368		
ANOVA						
Source of Variation	SS	df	MS	F	p-level	F crit
Between Groups	22.99387	2	11.49694	1.32487	0.27363	3.15312
Within Groups	511.99	59	8.6778			
Total	534.98387	61				

ii) Density Estimate Associated Values: Observational Information, Densities, Confidence Intervals (95%), and Effective Strip Widths (ESWs)

Table A9: Observational information and Distance-generated density estimate associated values.

Functional Group	Number of Observations (# of groups sighted)			Encounter Rate (individuals sighted per 1km)			Density (ind./km ²)			Density 95% CI			ESW (m)		
	RA	LA	TRC	RA	LA	TRC	RA	LA	TRC	RA	LA	TRC	RA	LA	TRC
Primates															
<u>Large Folivores</u>															
<i>Alouatta seniculus</i>		1	5		0.03	0.22		0.3	2.1		(0.2, 3.1)	(0.7, 6.2)			55.0
<u>Large Frugivores</u>															
<i>Ateles chamek</i>		4	19		0.14	0.68		3.9	15.9		(0.1, 116.1)	(5.2, 48.9)			21.5
<u>Mid-Sized Frugivores</u>															
<i>Cebus albifrons</i>	1	6		0.04	0.28		3.7	19.8	11.1	0.6, 22.4)	(8.1, 48.3)	(5.2, 23.9)	24.4		
<i>Cebus apella</i>	4	17	16	0.08	0.66	0.62									
<u>Small Frugivores</u>															
<i>Pithecia monachus</i>		3			0.07		37.6	24.6	7.4 (unpooled)	(11.4, 124.4)	(9.5, 63.4)	(0.4, 13.9)	10.9 20.7		
<i>Saguinus fuscicollis</i>	17	11	6	0.95	0.54	0.28									
<i>Saguinus imperator</i>		1			0.03										
<i>Saimiri boliviensis</i>		3	1		0.61	0.27									
Birds															
<u>Large Frugivores</u>															
<i>Penelope jacquacu</i>	9	18	19	0.14	0.42	0.30	8.0 (unpooled)	18.2	44.0	(3.2, 20.0)	(11.3, 29.3)	(24.7, 78.3)	13.0 21.5		
<i>Pipile cumanensis</i>			2			0.02									
<i>Psophia leucoptera</i>	12	10	21	0.30	0.37	1.51									
<u>Large Granivores</u>															
<i>Mitu tuberosum</i>			3			0.04	6.2	11.9	12.4	(1.9, 20.0)	(0.5, 295.1)	(7.0, 22.0)	8.2		
<i>Tinamus major</i>	9	20	15	0.10	0.22	0.17									
<u>Small Granivores</u>															
<i>Crypturellus spp.</i>	17	25	20	0.20	0.28	0.20	13.9	18.3	15.1	(5.1, 38.0)	(7.5, 44.3)	(8.1, 28.5)	6.7		