

## Basin-Wide Effects of Game Harvest on Vertebrate Population Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal

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### ABSTRACT

Vertebrate responses to hunting are widely variable for target and nontarget species depending on the history of hunting and productivity of any given site and the life history traits of game species. We provide a comprehensive meta-analysis of changes in population density or other abundance estimates for 30 mid-sized to large mammal, bird and reptile species in 101 hunted and nonhunted, but otherwise undisturbed, Neotropical forest sites. The data set was analyzed using both an unnested approach, based on population density estimates, and a nested approach in which pairwise comparisons of abundance metrics were restricted to geographic groups of sites sharing similar habitat and soil conditions. This resulted in 25 geographic clusters of sites within which 1811 population abundance estimates were compared across different levels of hunting pressure. Average nested changes in abundance across increasingly greater levels of hunting pressure ranged from moderately positive to highly negative. Populations of all species combined declined across greater differences in hunting pressure by up to 74.8 percent from their numeric abundance in less intensively hunted sites, but harvest-sensitive species fared far worse. Of the 30 species examined, 22 declined significantly at high levels of hunting. Body size significantly affected the direction and magnitude of abundance changes, with large-bodied species declining faster in overhunted sites. Frugivorous species showed more marked declines in abundance in heavily hunted sites than seed predators and browsers, regardless of the effects of body size. The implications of hunting for seed dispersal are discussed in terms of community dynamics in semi-defaunated tropical forests.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>.

*Key words:* dispersal limitation; game harvest; hunting; large vertebrates; meta-analysis; population density; seed dispersal; tropical forests.

THE POPULATION DENSITY OF TROPICAL FOREST VERTEBRATES can range widely according to the baseline environmental heterogeneity affecting forest habitat quality. This may include the effects of soil fertility, elevation, hydrological cycles, floristic composition, total production and seasonality of edible fruit, and stand successional stage (Eisenberg 1980, Emmons 1984, Peres 1997, 1999a, Stevenson 2001, Naughton-Treves *et al.* 2003, Dunn 2004). The size of vertebrate populations and the strength of ecological interactions they provide are therefore expected to vary considerably across large spatial scales even in forest landscapes that have experienced a very limited recurrent history of anthropogenic habitat disturbance (Peres 2000a). These bottom-up determinants of vertebrate numbers are compounded by a number of top-down regulation mechanisms including natural predation and direct human exploitation via hunting and trapping, which disproportionately affects larger prey species with slower life histories (Peres 1990, Bodmer 1995). Yet the relative strengths of bottom-up versus top-down determinants of wildlife abundance in tropical ecosystems remain poorly understood. For instance, if the quality and amount of the local food supply are the principal regulators of consumer population size, then moderate changes in hunting pressure or natural predation may be overwhelmed by the impacts of bottom-up

forces, particularly for species that are relatively harvest-insensitive. Likewise, there is evidence to suggest that demographic resilience to hunting pressure is inextricably linked to forest habitat productivity (Peres 2000b, Peres & Dolman 2000, Bodmer *et al.* 2000) so that population densities in overhunted, high-productivity areas can be higher than in low-productivity, nonhunted areas (Peres 2000a). Large-scale comparisons of vertebrate population densities between areas subjected to different levels of hunting pressure can therefore be greatly confounded by forest primary productivity.

Protein acquisition by tropical forest dwellers relies heavily on meat from wild vertebrates (Redford & Robinson 1987, Jerzolinski & Peres 2003, Milner-Gulland *et al.* 2003). This off-take removes a large proportion of the game biomass in Amazonian and Guianan forests with profound consequences to the aggregate biomass and size structure of residual species assemblages (Peres 2000a, b). A conservative estimate indicates that as many as 23.5 million reptiles, birds, and mammals, corresponding to 164,692 tons of wild meat, are consumed each year by 2.22 million rural people in Brazilian Amazonia within households outside the wage-labor sector (Peres 2000a). Subsistence hunting is even more critical in unflooded (terra firme) forest areas where aquatic sources of alternative animal protein are often scarce. Annual harvest rates per unit area can be much higher in other tropical forest regions, including 23,500 tons of wild meat consumed in Sarawak

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(Bennett 2002), and 1–3.4 million tons in Central Africa (Fa & Peres 2001). The total demographic impact of hunting is far greater because many urban households are also subsidized by wild meat, and numbers of kills reported in rural households and urban bushmeat markets take no account of the hidden fraction of mortality contributed by lethally wounded animals that escape hunter retrieval. The total extent of partially defaunated, but otherwise “pristine” tropical forests, is often severely underestimated. For example, subsistence hunters have access to most areas of lowland Amazonia, affecting even the core of many relatively remote nature and indigenous reserves; only 1.6 percent of Brazilian Amazonia is both strictly protected on paper and inaccessible to game hunters (Peres & Lake 2003). In many respects, however, the pervasive effects of persistent overhunting in Neotropical forests lags behind those in more heavily settled parts of the African and Asian tropics, where many forests have already been defaunated to a much greater extent (Fa & Peres 2001, Corlett 2007).

Comparing abundances of game species between sites is a useful framework to evaluate local depletion from, and susceptibility of different species to, game harvest (Robinson & Redford 1994, Bodmer & Robinson 2004). However, differences in habitat quality, including forest structure, soil fertility, food supply, and density of nesting sites, may override the impact of hunting. Nevertheless, comparisons between slightly and persistently hunted sites 15–40 km apart in continuous forest landscapes sharing similar habitats suggest that game harvest has a major effect on game stocks, and differences in game abundance are correlated with key species life history traits, including intrinsic rate of increase, longevity, and generation time (*e.g.*, Bodmer *et al.* 1997, Peres & Nascimento 2006). These traits tend to be highly correlated with body size, a key variable in determining hunter preference in terms of both prey species and sex/age classes (Alvard 1993, Jerozolinski & Peres 2003). More vulnerable, large-bodied target species often provide low-redundancy, if not unique, ecological services, such as effective dispersal of large-seeded plants (Peres & Roosmalen 2002, Poulsen *et al.* 2002). Yet the scale of the impact of game hunting, both in terms of the arrays of species that are most affected and the extent to which their populations decline, is yet to be synthesized for any major tropical forest region. Additionally, the degree to which hunters depress population densities of key frugivorous vertebrates at different sites, thereby reducing the availability of whatever seed dispersal services they may provide, is yet to be assessed at large-spatial scales. Here we present a large-scale cross-site comparison of population abundances of game and nongame vertebrates in a large set of Neotropical forest sites as a function of the local history of subsistence hunting. In particular, we examine the degree to which hunting pressure either reduces or augments population densities of different species using both a nested and unnested comparative design in relation to site location and broad habitat type. We also discuss the implications of game harvest and different defaunation scenarios resulting in “half-empty” forests for the availability of seed dispersal services, particularly for large-seeded plants, in terms of tropical forest community dynamics.

## METHODS

**SURVEY SITES.**—We carried out a comprehensive compilation of the population density or any other abundance metric for all mid-sized to large forest vertebrate species censused by line-transect sampling at 101 Neotropical forest sites (Fig. 1). Most of these are in lowland Amazonia and the Guianan shields, but four additional sites are located in the Santa Cruz department of Bolivia (Rumiz *et al.* 2001) and eastern Paraguay (Hill *et al.* 1997). A total of 53 of these sites (52.5%) were surveyed by our own standardized, long-term program (1987–2005) of line-transect censuses of forest vertebrates conducted throughout lowland Amazonia (Peres 1997, 1999b, 2000a, b, Peres & Dolman 2000, Haugaasen & Peres 2005, Palacios & Peres 2005, Peres & Nascimento 2006; C. A. Peres, pers. obs.). Data for all other sites were updated from previous compilations (Peres 1999b, 2000a, b) on the basis of an exhaustive survey of published and unpublished reports of population densities (or other quantitative measures of abundance) of vertebrate species derived from line-transect censuses. However, we excluded from the final data base any survey based on a sampling effort of less than 100 km of line-transect census walks, which was considered to be insufficient.

Environmental perturbations that may or may not be independent from hunting pressure (hereafter, HP) such as selective logging, slash-and-burn agriculture, surface wildfires, and forest fragmentation can lead to marked changes in relative abundances of tropical forest vertebrates (*e.g.*, Barlow *et al.* 2005, Michalski & Peres 2005). This analysis is therefore restricted to survey sites consisting of continuous tracks of primary forest that may have been selectively

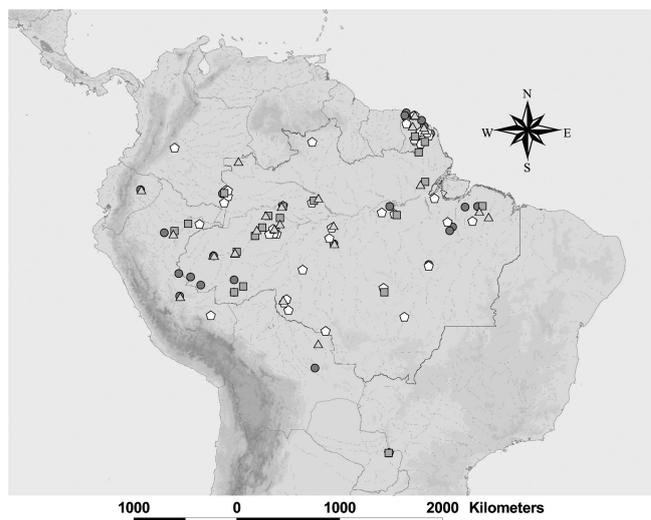


FIGURE 1. Geographic location of 101 Neotropical forest sites on which this analysis is based. Open pentagons indicate nonhunted sites; lightly, moderately, and heavily hunted sites are indicated by light, intermediate, and dark shaded triangles, squares and circles, respectively. Overlapping symbols represent more than one spatially independent site within the same geographic grouping.

hunted to a varying extent but otherwise had not been subjected to anthropogenic structural habitat disturbance. Even so, animal population densities in tropical forests can vary enormously between locations, reflecting baseline differences in habitat structure, forest composition, and primary productivity. In particular, soil fertility profoundly affects the aggregate biomass of vertebrate assemblages in lowland Amazonian forests (Peres & Dolman 2000, Peres 1999a, b in press). This analysis is, therefore, designed to at least partly take account of this spatial heterogeneity by restricting comparisons of hunting effect sizes to geographic clusters of forest sites that had been exposed to a different history of HP, but otherwise shared similar edaphic conditions and belonged to the same major forest type (e.g., terra firme forest on clay soils, terra firme forests on sandy soils, seasonally flooded forests in either black (igapó) or white-water (várzea) drainages).

All forest sites were either classed as nonhunted or assigned to one of three levels of HP—light, moderate and heavy—on the basis of: (1) semi-structured interviews with hunters who had lived at a given site for at least 2 years prior to surveys; (2) present and past human population density and distribution quantified on the basis of the number of households in each study area, as revealed by high-resolution (1:250,000) maps (RADAM 1973–1981); and (3) the number of shotgun blows heard during each census or any other *in situ* evidence left by hunters (e.g., “waiting” stations, spent shotgun shells). Interviews with hunters were unbiased with respect to fear of disclosing illegal hunting activities, since interviewees in such remote areas were unaware and unsuspecting of legality issues concerning game hunting. Supplementary information on other sites was obtained from different published or unpublished reports, or personal communication with individual investigators. To be conservative, this is the most refined resolution afforded by a common HP classification of all sites, given the large variation across studies in the level of details available describing the previous history of hunting, including the duration, intensity and periodicity of game harvest, numbers of hunters, size of catchment areas, hunting techniques and weapons, and prey species, sex and age-class selectivity of game hunters. Nonhunted sites are defined as those entirely uninhabited by Amerindians, detribalized Amazonians (*caboclos*, *riberieños*), and rubber-tappers at the time of surveys, and that offered no enduring evidence of past hunting activity (e.g., ax marks on core hardwoods along perennial streams; old scars on large commercially valuable latex trees). These sites could not be easily reached on foot by hunters, and access by our survey team to many of them was gained with helicopters and small aircraft. The term “nonhunted” as used here is therefore reserved for pristine forests of remote interfluvial basins and headwater regions of Amazonia, rather than areas only rarely visited by hunters (Peres & Lake 2003). Hunting at all hunted sites was carried out primarily with shotguns, because the rapid transition from traditional weapons to firearms has now reached even to some of the most remote parts of Amazonia (Jerozolinski & Peres 2003). More details on all but the most recently surveyed study areas (2001–2004), site classification according to levels of HP, and field procedures used during line-transect censuses and data analysis can be obtained elsewhere (Peres 1999c, 2000a, b and references therein) or from the author.

VERTEBRATE SPECIES SURVEYED.—This analysis focuses on a limited group of 30 forest game and nongame species, including primates from pygmy marmosets to large atelines, ungulates (one perisodactyl and four artiodactyls), large diurnal caviomorph rodents (agoutis and acouchis), cracids (piping guans, common guans, and curassows), small and large tinamids, trumpeters, woodquails, and tortoises (mean body mass = 10.8 kg, range = 0.15–160 kg; Table 2). For several reasons, there is considerable variation in the degree to which hunters exercise prey species selectivity across Amazonian forests (Redford & Robinson 1986, Fa & Peres 2001, Jerozolinski & Peres 2004), and not all game species are pursued by hunters at all sites. This analysis is, however, designed to provide a broad assessment of the magnitude of the effect of subsistence game hunting across a large number of otherwise undisturbed forest sites, subjected to varying histories of HP. Species are defined here in terms of either single taxonomic species occurring over broad geographic ranges, or functional groups of ecologically analogous congeners (often parapatric species) occurring at different sites (e.g., *Psophia* spp., *Dasyprocta* spp., *Saimiri* spp., *Lagothrix* spp.). Curassows (*Mitu tuberosa*, *Crax fasciolata*, and *Crax alector*), however, comprise the only functional group including species belonging to two closely related genera. Although the definition of seed dispersers and seed predators is often blurred (Norconk *et al.* 1998, Levey *et al.* 2002, Beck 2005), all species were assigned to just one of these two major classes of vertebrate seed interactions. Seed dispersers are defined as frugivores that consume primarily ripe fruit pulp (mesocarps, arils) and typically pass whole ingested seeds undamaged through their digestive tracts. On the other hand, seed predators such as pitheciine primates (Norconk *et al.* 1998, Peres & Roosmalen 2002), ungulates other than tapir (Bodmer 1991), and several tinamids and terrestrial cracids (Erard *et al.* 1991), are defined as primarily granivorous species that regularly destroy endosperms by crushing the seed testa or digesting embryos (Table 2), although some species may also occasionally disperse viable seeds.

UNNESTED AND NESTED ANALYSIS.—Meta-analysis is a combined quantitative synthesis of multiple independent studies using a set of summary statistics from each study (Hedges & Olkin 1985, Gurevitch *et al.* 2001). Mean abundance estimates derived from wildlife surveys conducted by many investigators at different sites have been expressed as a variety of metrics, including population density (individuals/km<sup>2</sup>), group density (groups/km<sup>2</sup>), and encounter rates of groups, subgroups or individuals; e.g., per 10 km of census effort, taking into account mean site-specific estimates of group or subgroup sizes. In an unnested analysis, we first consider the relationship between level of HP and population estimates across all sites, regardless of their location and habitat setting. In a meta-analysis, we subsequently extracted data on relative spatial changes in population abundance by calculating the ratios between the same measure of abundance (density estimates or encounter rates) obtained for any given species, almost always by the same survey team, at any two populations that had been subjected to different levels of HP, but were nested within the same geographic cluster of site localities sharing similar levels of forest productivity. For 30 mammal, bird, and reptile species censused across the 101

sites, this resulted in 113 sets of population abundance ratios ( $N = 1811$ ) between sites within 25 geographic clusters of forest types but subjected to different levels of HP (mean  $\pm$  SD number of nested sets of pairwise ratios per cluster =  $4.6 \pm 6.5$ , range = 1–30; mean  $\pm$  SD number of abundance ratios per site =  $15.7 \pm 5.7$ , range = 4–27). The degree of statistical independence in this analysis is further improved because these 113 sets of abundance ratios exclude 53.3 percent of the maximum number of 242 pairwise nested combinations of independent sites corresponding to those that had experienced the same level of HP. Because few wildlife surveys report the sampling variance around mean parameter estimates, it was not possible to take into account abundance estimate errors, which tend to be greater in surveys involving a small census effort, few detection events, and poor spatial replication within a given site (Buckland *et al.* 1993). Population abundance ratios (hereafter,  $R_d$ ) thus represent approximate “productivity-equivalent” pairwise comparisons of species-specific abundance estimates between any two populations exposed to different levels of HP.  $R_d$  values were first calculated between different levels of HP, and then  $\log_{10}$ -transformed (Table 1). Zero counts during surveys when a given species had once been unambiguously present at both paired sites were replaced by a small positive constant value (0.1) to allow log-transformations and geometric means to be calculated.

Log-transformed population density ratios for any given species are therefore positive ( $R_d > 0$ ) if abundance estimates were higher in the more intensively hunted of any pair of sites, and negative ( $R_d < 0$ ) if abundance estimates were higher in the less intensively hunted or nonhunted paired site. Density ratios close to zero ( $R_d \approx 0$ ) indicate little or no effect of HP. Negative  $R_d$  values between  $-1$  and  $-2$  indicate abundances at the less intensively hunted sites of between 10- and 100-fold greater than those found in the more intensively hunted site. Untransformed ratios describing pairwise changes in abundance could therefore range over more than three orders of magnitude.

This comparative approach is far more robust than traditional “vote-counting” analyses (which often consider only statistically significant changes in abundance), particularly because many valuable forest wildlife surveys that will be difficult to replicate involve relatively small sample sizes (*e.g.*, number of detection events), and

hence high sample variance and low statistical power (Hedges & Olkin 1985). This simple hierarchic meta-analysis thus considers basin-wide effect sizes of HP on changes in species abundance regardless of statistical significance, across all studies meeting a minimum sampling effort of 100 km of census effort. Beyond this cut-off point, however, we avoided weighting the outcome of each comparison by a correlate of sample size such as total census effort or number of independent detection events per species, because these data were not always reported and studies involving intermediate-to-high levels of census effort were considered to be equally valid. Mean effect sizes are considered significant when the 95 percent confidence intervals do not include zero.

## RESULTS

**UNNESTED CHANGES IN ABUNDANCE.**—Mean population density estimates in all nonhunted sites ranged from 0.60 individuals/km<sup>2</sup> ( $\pm 0.13$ ,  $N = 25$ ) in tapir to 24.7 individuals/km<sup>2</sup> ( $\pm 11.2$ ,  $N = 12$ ) in spider monkeys (Fig. 2). Compared to their mean baseline densities in nonhunted sites, these two large-bodied frugivores exhibited population densities 2.5- to 6.0-fold lower in light-to-moderately hunted sites, and 44- to 55-fold lower in heavily hunted sites. Other species showed mean population densities in nonhunted sites ranging from 0.3- to 11.5-fold greater than those in heavily hunted sites. In one extreme case, mean population densities of the large-herd living white-lipped peccary were 8.48, 1.65, and 0.26 individuals/km<sup>2</sup> in nonhunted, light-to-moderate, and heavily hunted sites, respectively, representing a 328-fold decline in mean densities from the least to the most hunted sites. In fact, white-lipped peccaries and several other harvest-sensitive species were often locally extinct in heavily hunted sites.

Considering all forest sites from any geographic grouping for which population density estimates (D, individuals/km<sup>2</sup>) were available, level of HP was a significant inverse correlate of this metric of abundance for exactly half of the 30 species examined. Conversely, densities of only two small-bodied primate species—represented by different functional groups of tamarins (*Saguinus* spp.)—were positively correlated with HP (Table 2). The coefficient of variation (CV) of all D estimates available for any given species was uncorrelated with a hunter preference score assigned to each species ( $r_s = 0.103$ ,  $N = 30$  species,  $P = 0.587$ , Table 2), but the highest CV values were obtained for the most preferred species. However, there was a significant correlation between body mass of vertebrate species and the direction and magnitude of density responses to level of HP as measured by Spearman correlations between D and HP ( $r_s = -0.501$ ,  $N = 30$ ,  $P = 0.029$ ). Density estimates for all large-bodied frugivores were strongly inversely correlated with level of HP (Table 2). The species-level rank correlation values summarizing the relationships between D and HP were significantly correlated with hunter preference (Table 2;  $r_s = -0.574$ ,  $N = 30$ ,  $P = 0.012$ ), but this score is not independent of prey body size. On the other hand, the relationships between D and HP were uncorrelated with trophic guilds ranked according to nutritional status of broad dietary classes (Table 2;  $r_s =$

TABLE 1. Possible nested pairwise comparisons of vertebrate abundance in Amazonian forest sites subjected to varying levels of hunting pressure (HP).  $R_d$  indicates how population abundance (or density) ratios were calculated;  $\Delta_{HP}$  are ranked scores describing step changes in HP.

Pairwise HP comparison	$R_d$ ratio	$\Delta_{HP}$
High:intermediate	$\log_{10}[(D_{\text{highHP}} + 0.1)/(D_{\text{mediumHP}} + 0.1)]$	1
Intermediate:low	$\log_{10}[(D_{\text{mediumHP}} + 0.1)/(D_{\text{lowHP}} + 0.1)]$	1
Low:none	$\log_{10}[(D_{\text{lowHP}} + 0.1)/(D_{\text{non-huntedHP}} + 0.1)]$	1
High:low	$\log_{10}[(D_{\text{highHP}} + 0.1)/(D_{\text{lowHP}} + 0.1)]$	2
Intermediate:none	$\log_{10}[(D_{\text{mediumHP}} + 0.1)/(D_{\text{non-huntedHP}} + 0.1)]$	2
High:none	$\log_{10}[(D_{\text{highHP}} + 0.1)/(D_{\text{non-huntedHP}} + 0.1)]$	3

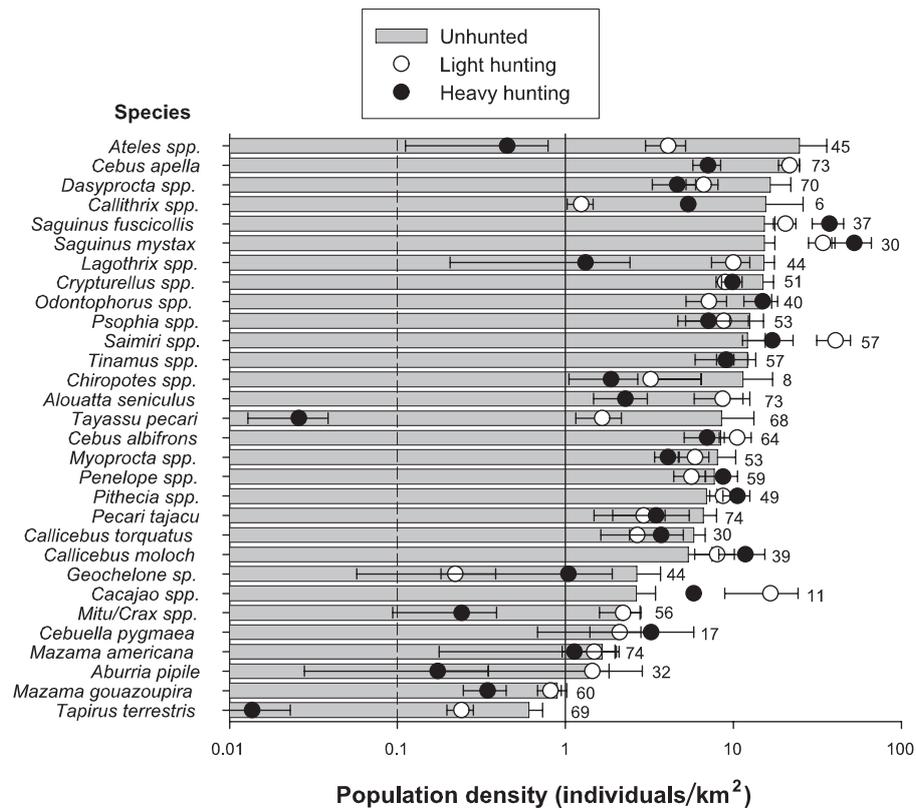


FIGURE 2. Mean  $\pm$  SE population density estimates for 30 Amazonian vertebrate species (or functional groups) in nonhunted (shaded bars) and hunted forest sites subjected to either light-to-moderate (open circles) or heavy hunting pressure (solid circles). Species are ranked according to their overall population density in nonhunted sites. Species for which hunted-site means are farthest to the left (along a log-transformed common scale of abundance) are most severely impacted by hunting. The total number of unpaired forest sites for which density estimates were available is shown for each species.

0.344,  $N = 30$ ,  $P = 0.379$ ), which in any case were inversely correlated with body size ( $r_s = -0.720$ ,  $N = 30$ ,  $P < 0.001$ ).

**NESTED CHANGES IN ABUNDANCE.**—Vertebrate population responses to pairwise differences in HP across sites sharing similar physiognomic conditions were widely variable. Considering the variation among species, population responses ranged from small-bodied primates that on average more than doubled their abundance at higher levels of HP, to large ungulates, mid-sized to large primates, gamebirds, and forest tortoises that declined to less than half their abundance in intensively hunted sites (Table 2). Considering all species pooled into higher vertebrate taxa (classes or orders), tortoises, most primates and gamebirds tended to show decreases in sites subjected to higher HP, whereas most ungulates and rodents showed slight increases. In particular, several key large-bodied game species in Amazonian forests such as woolly monkeys, spider monkeys, piping guans, curassows, white-lipped peccaries, tapirs, and forest tortoises were heavily impacted by hunting, showing highly negative paired changes in any metric of abundance ( $-54$  to  $-84\%$ ) in more intensively hunted compared to less hunted sites. In addition, 13 other species showed significantly negative correlations between paired changes in abundance and stepwise differences in HP (Table 2).

On average for all species,  $\log_{10}$ -transformed abundance ratios ( $R_d$ ) were  $-0.303 \pm 0.601$  and ranged from  $-2.52$  to  $1.51$  ( $N = 1811$ ), indicating a mean decline of 50.3 percent from paired abundance estimates in less-hunted sites. However, the overall distribution of  $R_d$  values clearly shifted on a log scale to more negative values with increasingly greater contrasts in HP ( $\Delta_{HP} = 1$ : mean  $\pm$  SD =  $-0.207 \pm 0.559$ ,  $N = 656$ ;  $\Delta_{HP} = 2$ : mean  $\pm$  SD =  $-0.269 \pm 0.565$ ,  $N = 844$ ;  $\Delta_{HP} = 3$ : mean  $\pm$  SD =  $-0.598 \pm 0.689$ ,  $N = 311$ ;  $F_{2,1808} = 49.742$ ,  $P < 0.001$ ; Fig. 3). Only the highest HP contrast ( $\Delta_{HP} = 3$ ) was associated with  $R_d$  values that were significantly lower from those across either one or two levels of HP (Tukey's HSD posthoc comparisons,  $P < 0.001$ ). In any case, this represents mean negative changes in population abundance of  $-37.9$  percent ( $\Delta_{HP} = 1$ ),  $-46.2$  percent ( $\Delta_{HP} = 2$ ),  $-74.8$  percent ( $\Delta_{HP} = 3$ ) in relation to overall abundance estimates in paired less intensively hunted sites. Including all pairwise comparisons, overall abundance ratios of 22 of the 30 species considered declined significantly ( $\pm 95\%$  CI less than zero) from a less hunted to a corresponding more hunted site (Fig. 4A). Excluding small differences in HP ( $\Delta_{HP} = 1$ ), 19 of the 30 species showed significant declines in abundance in more heavily hunted sites (Fig. 4B). This further reduced  $R_d$  values to a mean of  $-0.357 \pm 0.618$  ( $N = 1155$ ), equivalent to an average decline of 56.0 percent from abundance

TABLE 2. Population abundance changes for five groups of mid to large-bodied vertebrates from high to low levels of hunting pressure (HP) in Amazonian forests. Unpaired comparisons consider the relationship between abundance and HP but take no account of forest habitat type. Pairwise comparisons refer to population abundance changes across different levels of HP nested within groups of sites sharing a similar habitat and the same abundance metric. Correlation values for these sites represent the relationship between differences in abundance (abundance ratios or % change) and hunting regime ( $\Delta_{HP}$ ) across any two nested sites differing in HP ( $\Delta_{HP} > 0$ ), and those nested sites sharing more than a one-step change in HP ( $\Delta_{HP} > 1$ ). Correlation values in bold are significant ( $P < 0.05$ ). N indicates sample sizes.

Vertebrate taxon and species	Body mass (kg)	Game <sup>a</sup> preference	Trophic <sup>b</sup> guild	Unpaired effects <sup>c</sup>		Nested pairwise comparisons								
				$r_s$	N	percent change ( $\Delta_{HP} > 0$ )			percent change ( $\Delta_{HP} > 1$ )					
						$r_s$	Median	Mean	SE	N	Median	Mean	SE	N
PRIMATES														
<i>Cebuella pygmaea</i>	0.15	—	Ex/In	-0.206	17	0.338	39.55	45.72	43.65	6	79.75	79.75	133.95	2
<i>Callithrix</i> spp.	0.36	—	Fr/In	-0.455	6	<b>-0.725</b>	-82.30	29.5	75.6	9	-82.30	29.5	75.6	9
<i>Saguinus fuscicollis</i>	0.39	—	Fr/In	<b>0.395</b>	37	0.232	0.80	49.73	25.73	27	78.80	81.09	34.16	13
<i>Saguinus mystax/imperator/labiatus</i>	0.51	—	Fr/In	<b>0.572</b>	30	0.159	-4.95	63.59	20.14	66	40.10	80.89	22.78	45
<i>Saimiri</i> spp.	0.94	—	Fr/In	0.077	57	<b>-0.239</b>	-27.30	0.79	12.98	58	-37.65	-15.84	18.29	24
<i>Callicebus moloch/cupreus</i>	1.05	—	Fr/Fo	0.285	39	<b>-0.386</b>	18.20	267.03	97.59	39	-9.50	118.6	76.46	18
<i>Callicebus torquatus</i>	1.2	—	Fr/In	-0.296	30	0.03	-55.00	-1.12	37.69	20	-47.15	-58.48	8.89	10
<i>Pithecia</i> spp.	2.2	++	Sp/Fr	0.137	49	0.027	-2.30	42.43	28.27	54	-2.30	19.75	16.52	24
<i>Chiropotes</i> spp.	2.7	++	Sp/Fr	-0.472	8	<b>-0.054</b>	-64.80	-41.22	14.92	21	-68.10	-44.25	16.37	19
<i>Cacajao</i> spp.	3.16	+	Sp/Fr	0.335	11	<b>-0.577</b>	-48.00	-48.00	27.71	4	-96.00	-96.00	—	1
<i>Cebus apella</i>	2.91	++	Fr/Fa	<b>-0.423</b>	73	<b>-0.377</b>	-56.50	-33.78	5.73	108	-68.40	-41.87	7.35	70
<i>Cebus albifrons</i>	2.7	++	FR/Fa	-0.034	64	<b>-0.396</b>	-25.60	7.66	13.43	74	-39.45	-31.23	7.53	46
<i>Alouatta seniculus</i>	6.5	++	Fo/Fr	<b>-0.227</b>	73	<b>-0.201</b>	-57.40	-28.88	9.43	107	-63.50	-39.56	8.69	68
<i>Lagothrix</i> spp.	8.71	++	Fr/Fo	<b>-0.598</b>	44	<b>-0.405</b>	-97.90	-69.13	8.51	40	-93.90	-76.44	10.6	19
<i>Ateles</i> spp.	9.02	++	Fr	<b>-0.624</b>	45	<b>-0.360</b>	-78.10	-64.60	6.35	61	-85.60	-78.86	3.3	37
UNGULATES														
<i>Mazama gouazoubira</i>	18	++	Br	<b>-0.356</b>	60	<b>-0.159</b>	-20.60	25.74	27.34	83	-9.50	36.96	39.95	56
<i>Mazama americana</i>	28	++	Br	<b>-0.474</b>	74	<b>-0.188</b>	-22.70	10.65	13.37	103	-29.40	-12.02	9.6	66
<i>Pecari tajacu</i>	25	++	Sp/Fa	<b>-0.411</b>	74	-0.133	-47.60	-9.18	17.51	87	-51.20	-7.61	26.22	56
<i>Tayassu pecari</i>	32	++	Sp/Fa	<b>-0.640</b>	68	<b>-0.222</b>	-64.50	-59.10	4.62	81	-91.95	-60.99	6.36	46
<i>Tapirus terrestris</i>	160	++	Fr/Br	<b>-0.649</b>	69	<b>-0.477</b>	-47.40	-41.83	7.17	67	-75.00	-54.38	8.57	41
RODENTS														
<i>Myoprocta</i> spp.	0.75	+	Sp/Fr	-0.106	53	<b>-0.261</b>	7.20	45.09	26.18	77	2.95	18.81	10.93	54
<i>Dasyprocta</i> spp.	4	++	Sp/Fr	<b>-0.330</b>	70	-0.077	-10.20	64.56	34.15	105	6.30	74.13	47.04	71
BIRDS														
<i>Odontophorus</i> spp.	0.31	—	In/Fr	-0.259	40	0.120	-28.45	7.24	14.28	64	-15.40	22.27	19.23	45
<i>Crypturellus</i> spp.	0.42	+	In/Fr	-0.232	51	<b>-0.202</b>	-19.55	-9.36	6.99	84	-26.30	-20.00	7.24	57
<i>Tinamus</i> spp.	1.2	++	Sp/Fr/In	<b>-0.347</b>	57	-0.037	-29.40	12.32	13.45	85	-5.65	32.67	19.5	56
<i>Penelope</i> spp.	1.28	++	Fr/In	-0.080	59	-0.094	-20.65	-0.50	10.15	88	-25.40	-0.94	13.83	61
<i>Pipile cujubi</i> and <i>P. cumanensis</i>	1.2	++	Fr	<b>-0.662</b>	32	<b>-0.585</b>	-81.50	-73.34	8.55	14	-92.40	-85.97	4.3	11
<i>Mitu tuberosa/Crax</i> spp.	3	++	Sp/Fr	<b>-0.455</b>	56	<b>-0.234</b>	-65.60	-35.92	10.21	83	-65.90	-54.12	5.48	60
<i>Psophia</i> spp.	1.2	++	Fr/Fa	<b>-0.328</b>	53	<b>-0.494</b>	-37.90	-14.31	9.08	75	-53.15	-35.12	8.03	52
TORTOISES														
<i>Geochelone</i> spp.	4.58	++	Fr/Fa	<b>-0.507</b>	44	<b>-0.425</b>	-97.10	-81.40	5.52	21	-97.10	-84.04	6.02	18

a Refers to species that are (++) almost always targeted; (+) usually ignored; and (—) rarely if ever killed by game hunters.

b Trophic classes in order of importance: (Fr) frugivore; (Sp) seed predator; (Br) terrestrial browser; (Fo) arboreal folivore; (In) insectivore; (Fa) faunivore; (Ex) exudate feeder.

c Spearman correlations ( $r_s$ ) between level of HP and local abundance across all sites for which population density estimates (ind./km<sup>2</sup>) were available.

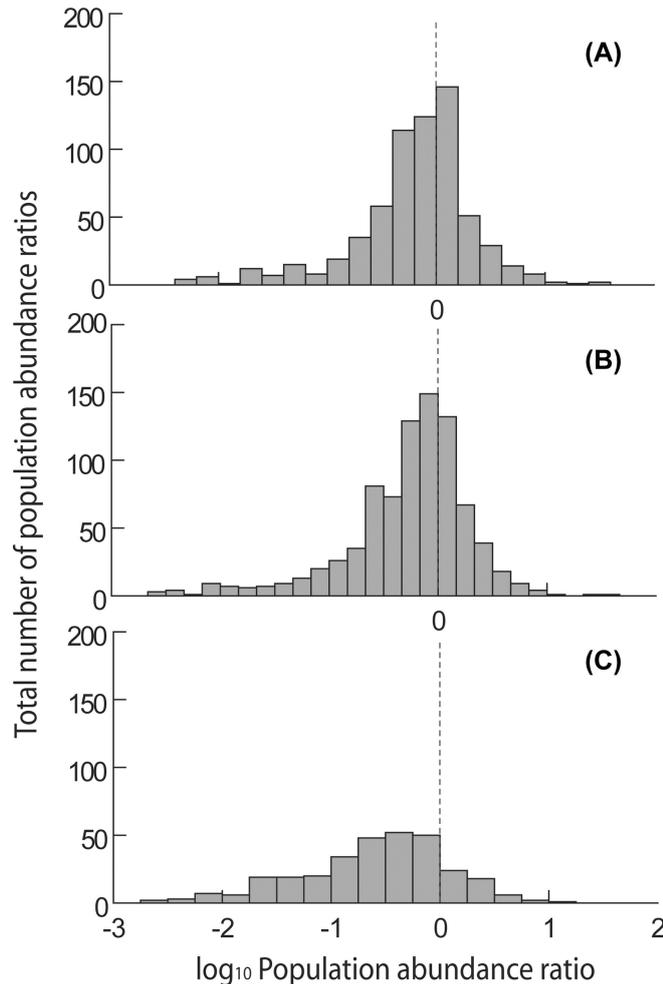


FIGURE 3. Overall distribution of abundance ratios between paired vertebrate populations exposed to increasing differences in hunting pressure (HP). Panels show step changes across (A) one, (B) two, and (C) three levels of hunting pressure ( $\Delta_{HP}$ ). Abundance ratios to the left of zero (dashed) lines represent negative changes in abundance in more intensively hunted sites.

estimates in forest sites at lower levels of HP. Again, this was particularly the case of species providing key seed-dispersal services such as large ateline primates, large cracids, and forest tortoises, whose population sizes at high levels of HP showed reductions in the order of 90–96 percent compared to those at low levels of HP.

Several generalist frugivores known to provide key endozoochorous seed dispersal services, exhibited considerably lower abundances in more intensively hunted sites, whereas some seed predators and/or scatterhoarders were actually more common where HP was more intensive. Considering nested comparisons across any difference in HP, seed predators of any species were on average 5.8 percent (SD = 17.8,  $N = 1006$ ) more abundant in more hunted sites, whereas seed dispersers were 2.4 percent (SD = 21.3,  $N = 805$ ) less abundant. However, both seed dispersers and seed predators declined by an average of 31.2 percent (SD = 16.5,  $N =$

151) and 34.1 percent (SD = 22.9,  $N = 160$ ), respectively, from nonhunted to heavily hunted sites (Fig. 5).

A generalized linear model explaining 23.6 percent of the overall variation in population abundance ratios showed that  $R_d$  values varied as a function of species body size, step changes in degree of HP, two levels of seed dispersal capacity (primarily frugivores or other trophic guilds), and the geographic grouping of survey sites (Table 3). Generalist frugivores that primarily consume mature fruit pulp exhibited more marked negative shifts in population abundance. However, these shifts in abundance for a number of site groupings were stronger at greater differences in HP as shown by a significant interaction between these variables. Major dietary class, in terms of five classes of diet assigned to different species, also had a significant effect on  $R_d$  values in an alternative model (in which dietary class replaced seed dispersal capacity), but this variable was highly correlated with body size.

Body size was the single most important determinant of overall abundance responses to hunting, explaining an appreciable amount of the variation across species in both the direction and magnitude of Spearman's correlations between: (1) population densities and HP ( $R^2 = 0.251$ ,  $F_{1,28} = 9.37$ ,  $P = 0.005$ ); and (2) nested abundance ratios and  $\Delta_{HP}$  ( $R^2 = 0.134$ ,  $F_{1,28} = 4.33$ ,  $P = 0.047$ ). Densities of small-bodied species were either unaltered or not detrimentally affected by hunting, regardless of their dietary or hunter preference status (Fig. 6). On the other hand, increasingly larger vertebrate species on average declined by up to 96 percent at higher levels of HP. Finally, those classed as primarily frugivorous declined even faster as a function of the most contrasting levels of HP ( $\Delta_{HP} = 2-3$ ; mean  $R_d = -0.379 \pm 0.663$ ,  $N = 805$ ) than those best defined as either seed predators or browsers (mean  $R_d = -0.243 \pm 0.540$ ,  $N = 1006$ ; ANCOVA,  $F_{1,1808} = 29.35$ ,  $P < 0.001$ ).

## DISCUSSION

This analysis corroborates the hypothesis that large-scale patterns of variation in the abundance of mid-sized to large vertebrates between hunted and nonhunted, *but otherwise comparable*, forest sites are primarily driven by HP, rather than other environmental gradients affecting habitat quality or other mechanisms of population regulation (Table 2, Fig. 4). Many tropical forest studies have attempted to compare wildlife population abundance, density, or biomass estimates across a smaller set of sites to quantitatively evaluate the effects of HP (*e.g.*, Freese *et al.* 1982, Glanz 1991, Oates 1996, Carrillo *et al.* 2000, Peres 2000a). These studies may acknowledge the importance of differences in habitat quality, including forest structure, floristic composition, and direct or indirect indicators of productivity, but are rarely adjusted to take account of their effects because of limited sample sizes, which may be further confounded by intercorrelated variables. In an ideal world, shifts in population abundance due to natural predation or game harvest should only be evaluated through a pseudoreplication-free design involving before-and-after comparisons between different levels of mortality within the same sites. However, spatially replicated temporal comparisons of this type are unrealistic because baseline data on hunted sites are rarely

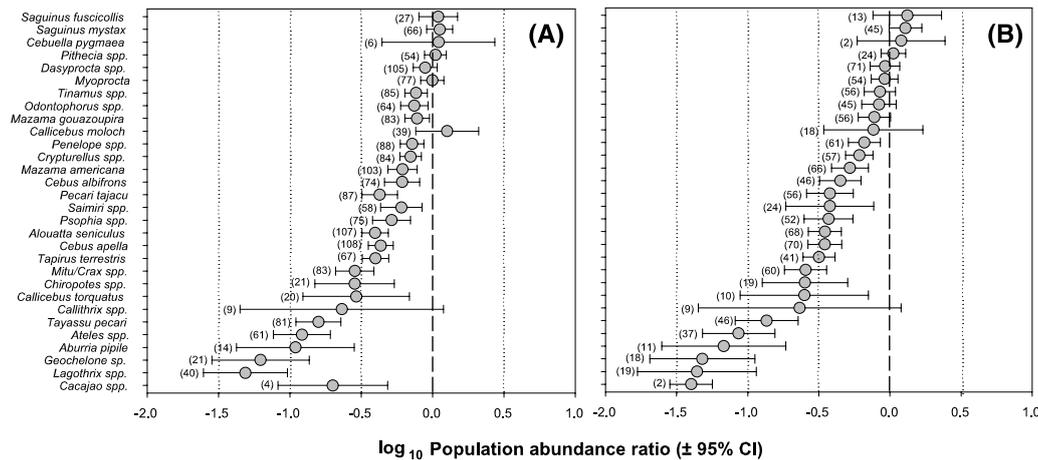


FIGURE 4. Mean hunting pressure (HP) effect size on the population abundance of Amazonian forest vertebrate species, considering (A) all pairwise comparisons, and (B) only comparisons between sites more than one level of HP apart ( $\Delta_{HP} > 1$ ). Species are ordered in the right panel in decreasing mean ratios along a  $\log_{10}$ -transformed scale so that a value of  $-1.0$  indicates a 90 percent reduction in abundance. Abundance declines are considered to be significant if 95 percent confidence intervals (error bars) do not include zero. Numbers of pairwise comparisons are indicated in parentheses.

available, and there are few feasible options for large-scale, long-term experiments that effectively manipulate HP in a large set of spatially independent sites. Alternatively, this meta-analysis pools together 101 structurally undisturbed forest sites under a wide range of environmental gradients, but broadly attempts to control for most habitat effects by nesting comparisons within 25 clusters of sites sampled by the same investigators and sharing similar geography, geochemistry, and forest types. Notwithstanding the multiple environmental gradients affecting closed-canopy forest sites throughout Amazonia, the large number of nested comparisons obtained for populations of most species should ensure a high signal-to-noise ratio, and a robust assessment of the basin-wide effects of hunting on game vertebrate abundance.

**HALF-EMPTY FORESTS.**—A growing proportion of remaining tropical forests worldwide has already succumbed to the “half-empty” forest syndrome (Redford & Feinsinger 2001), in which populations of key vertebrate species have been selectively depleted to varying degrees. Selective defaunation can be caused not only by local extinctions due to overhunting, but also by forest fragmentation or other forms of habitat deterioration, which often operate in concert with hunting (Peres 2001, Brashares *et al.* 2001, Michalski & Peres 2005, Barlow & Peres 2006). But few appreciate just how pervasive hunting is in the tropics. The rapid acceleration in tropical forest defaunation due to unsustainable hunting has already swept through many parts of the African, Asian, and American tropics, reflecting human demographics and reliance on wild meat by rural populations in different continents (Fa & Peres 2001, Milner-Gulland *et al.* 2003). Hunting rates are unsustainably high across large tracts of otherwise undisturbed tropical forests, averaging six times the maximum sustainable rate in Central Africa (Fa *et al.* 2001), and many Asian forests have already been silenced by a long history of severe wildlife exploitation (Corlett 2007). In Vietnam, for example, 12

species of large vertebrates have been extirpated over the last four decades, largely from overhunting (Bennett & Rao 2002).

Both the nested and unnested analyses presented here further confirm previous findings that subsistence game hunting profoundly affects the relative abundance and size structure of Amazonian vertebrate assemblages (Freese *et al.* 1982, Peres 1999b, 2000a, b, Peres & Dolman 2000). Considering the 12 most harvest-sensitive species, mean aggregate population densities were reduced sixfold from 115.3 individuals/km<sup>2</sup> in nonhunted sites to 60.7 individuals/km<sup>2</sup> in light-to-moderately hunted sites, to 19.4 individuals/km<sup>2</sup> in heavily hunted sites. The consequences in terms

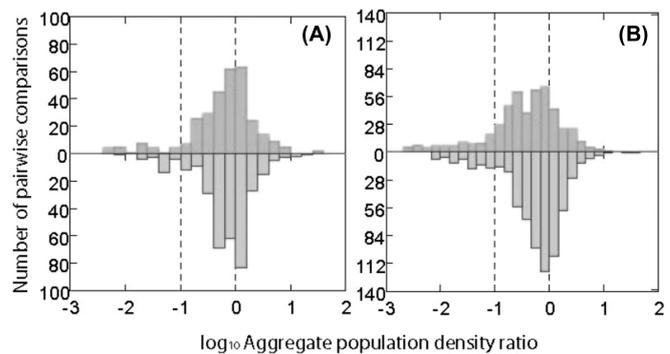


FIGURE 5. Distribution of  $R_d$  abundance ratios for species classed as either primarily frugivorous (shaded bars above zero) or otherwise (hashed bars below zero) considering (A) all “productivity-equivalent” pairwise comparisons between less intensively and more intensively hunted sites ( $N = 656$ ), and (B) those sites distinguished by at least two levels of hunting pressure ( $N = 1155$ ). Bars between the two vertical shaded lines represent declines of 0 to 90 percent of the abundance at the less intensively hunted site.

TABLE 3. Multifactorial ANCOVA from a generalized linear model (GLM<sup>1</sup>) explaining the log<sub>10</sub>-transformed ratio ( $R_d$ ) between the population abundance (or density) estimate of 30 forest vertebrate species at 101 Neotropical forests sites subjected to different levels of hunting pressure (HP).  $R_d$  values are calculated according to Table 1 across four levels of HP, yielding at most three possible step changes in HP ( $\Delta_{HP}$ ), entered as a nominal variable. Species were classed as either seed dispersers or otherwise based on current knowledge of their feeding ecology throughout Amazonian forests (see Table 2). Sites within the same geographic cluster shared the same forest type and similar edaphic conditions (see text).

Source	SS	df	MS	F	P
Corrected model	154.10	68	2.27	7.89	0.000
Intercept	5.01	1	5.01	17.46	0.000
log <sub>10</sub> Body mass	26.07	1	26.07	90.80	0.000
Seed dispersal capacity	4.61	1	4.61	16.06	0.000
Geographic cluster of forest sites	55.39	24	2.31	8.04	0.000
$\Delta_{HP}$	2.98		1.49	5.18	0.006
Seed dispersal capacity $\times$ Site cluster	11.77	24	0.49	1.71	0.018
Seed dispersal capacity $\times$ $\Delta_{HP}$	0.006	2	0.003	0.01	0.990
Site cluster $\times$ $\Delta_{HP}$	2.85	7	0.41	1.42	0.194
Seed dispersal capacity $\times$ Site cluster $\times$ $\Delta_{HP}$	4.58	7	0.65	2.28	0.026
Error	500.16	1742	0.29		
Total	820.56	1811			
Corrected Total	654.26	1810			

<sup>1</sup>GLM summary statistics:  $R^2 = 0.236$ ; Adj.  $R^2 = 0.206$

of aggregate biomass are even more insidious because hunters take a particularly heavy toll on the large-bodied component of tropical forest faunas (Fa & Peres 2001), which contributes a disproportionate fraction of the aggregate vertebrate biomass (Eisenberg 1980, Peres 1999a) and processes that regulate ecosystem dynamics (e.g., Terborgh 1992, Roldán & Simonetti 2001, Silman *et al.* 2003). Considering the same set of 12 species, mean aggregate population biomass was reduced almost 11-fold from 979.8 kg/km<sup>2</sup> in non-hunted sites to 392.9 kg/km<sup>2</sup> in light-to-moderately hunted sites, to only 89.2 kg/km<sup>2</sup> in heavily hunted sites. This is consistent with shifts in prey species profiles taken by hunters in Neotropical forests, which can be predicted on the basis of the local history of HP. For example, the age of village settlements and number of consumers per unit of hunting catchment area reduce both the size of individual kills and the degree of hunter selectivity in terms of the number of species harvested (Jerzolimski & Peres 2004). These patterns are consistent with results from a similar cross-site analysis of game harvest profiles obtained in west and central African forests (Fa *et al.* 2005).

DISPERSAL LIMITATION IN HALF-EMPTY FORESTS.—Frugivore populations are often severely depleted, if not extirpated, in persistently overhunted areas, and this may result in marked declines in the

availability and quality of seed dispersal services. Several studies in all major tropical land masses have shown that low densities of animal dispersal agents are likely to eventually depress plant recruitment in certain guilds (Ganzhorn *et al.* 1999, Webb & Peart 2001, Peres & Roosmalen 2002, Cordeiro & Howe 2003, McConkey & Drake 2006, Terborgh & Nunez-Iturri 2006). Plant species that formerly relied on large-bodied vertebrates as seed vectors may succumb to low rates of dispersal and thereby suffer increased density dependent seed or seedling mortality (Jansen & Zuidema 2001, Wright 2003). The tropical forest literature is beginning to amass a considerable body of evidence of countless seeds and seedlings that would not have been able to arrive and recruit at a given site well beyond the crowns of the nearest conspecific adults without the aid of vertebrate dispersers (e.g., Webb & Peart 2001, Indonesian Borneo, Terborgh & Nunez-Iturri 2006, Peru, Wang *et al.* 2007, Cameroon). Seed deposition patterns and seedling communities are thus likely to become substantially impoverished in the absence of mutualistic seed transport. Such changes may alter plant community composition, leading to declines in the recruitment of animal-dispersed plants and compensatory increases in abiotically dispersed species (Tabarelli *et al.* 1999, Jansen & Zuidema 2001, Cordeiro & Howe 2003, Wright *et al.* 2007). Loss or decline of dispersers should amount to a wide range of consequences to patterns of seed dispersal and seedling recruitment, especially large-seeded, gut-dispersed plants that rarely recruit underneath parents (Chapman & Onderdonk 1998, Peres & Roosmalen 2002, Nunez-Iturri & Howe 2007, Wright *et al.* 2007). For example, two genera of large-bodied primates—woolly monkeys (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.)—are often driven to local extinction in overhunted forests across Amazonia and the Guianan shields (Peres 1990, 1999b). Many large-seeded tree and liana species producing indehiscent, hard-husked fruits that are rarely or never handled by other frugivores rely on these prehensile-tailed primates for dispersal, and a number of these require gut passage to stimulate germination. A simulation study based on field data suggests that many large-seeded plants will suffer a 40–50 percent reduction in the probability of effective gut dispersal in overhunted forests (Peres & Roosmalen 2002). Moreover, because dietary overlap between different guilds of frugivores can be very low (Gautier-Hion *et al.* 1985, Poulsen *et al.* 2002), a drastic decline of a particular guild of frugivores can lead to a collapse of seed dispersal services for dependent plant species.

The abundance of potential seed dispersal agents was drastically reduced in many moderately to persistently hunted sites. For example, 12 of the 15 harvest-sensitive vertebrate species (pairwise changes of –62% or lower; Fig. 4B) are frugivores (*sensu stricto*) that habitually consume mature mesocarps or other ripe pulp material but pass whole seeds intact. For example, a nonhunted population of woolly monkeys in central Amazonia (mean density = 19.3 individuals/km<sup>2</sup>) on average moves  $23.2 \pm 6.8$  kg of seeds per group per day across home ranges as large as 1300 ha (Peres 1994). Of over 225 plant food species consumed throughout the year by a single group, 193 consisted of fruits. On the basis of the mean basin-wide rates of decline in woolly monkeys due to hunting and assuming a linear relationship between frugivore abundance and quantitative

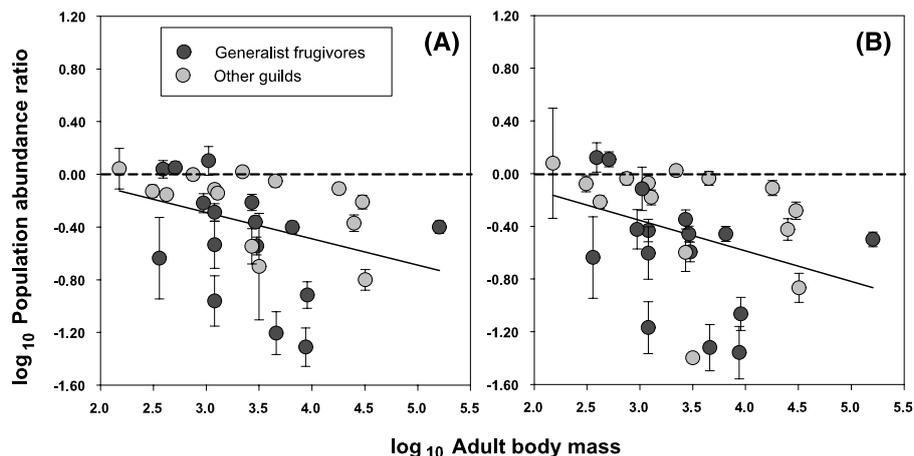


FIGURE 6. Mean  $\pm$  SE population density ratios for forest vertebrate species in Amazonian forests occurring at sites subjected to different levels of hunting pressure, but were otherwise structurally undisturbed. Population ratios are based on (A) all possible pairwise comparisons; and (B) comparisons between moderately to heavily hunted sites against nonhunted sites. Dark and light-shaded circles represent species classed as either primarily frugivorous or other trophic guilds including arboreal and terrestrial browsers and seed predators.

seed removal, daily rates of seed deposition generated by *Lagothrix* in Amazonian terra firme forests are expected to be reduced from 9.51 kg of seeds/km<sup>2</sup> in nonhunted sites to only 2.94 kg/km<sup>2</sup> in any hunted site, and to 2.24 kg/km<sup>2</sup> in moderately to heavily hunted sites. However, woolly monkeys are often driven to local extinction by hunters (Peres 1990, 1999b), resulting in a complete collapse of their dispersal services. Even species operating primarily as seed predators, such as caviomorph rodents (Peres *et al.* 1997, Jansen & Forget 2001), pitheciine primates (Norconk *et al.* 1998) and pecararies (Beck 2005), either gut disperse or scatterhoard many plant species, and thereby have a positive role in plant community dynamics. The spatial structure of the overall seed rain is also expected to become less diffuse both qualitatively and quantitatively because of weaker and greatly simplified fruit–frugivore matrices, in which the strength of single pairwise interactions decline as an unknown function of reduced disperser density and meager seed removal. Rarified populations of key dispersers of large-seeded plants may play limited ecological roles in terms of both the species profile and numbers of seeds transported, but this depends on the relationship between frugivore population size and the per capita rates of seed dispersal (Redford & Feinsinger 2001). In social species, the quality of seed dispersal services delivered after fruit feeding bouts is often affected by group sizes and group density, both of which can be affected by hunting. For example, gregarious flying foxes in a Pacific archipelago cease to be effective seed dispersers long before they become rare (McConkey & Drake 2006). Hence, many plant species may persist in overhunted tropical forests for decades or centuries, but are unlikely to contribute to future generations once populations of their seed dispersers are reduced to small numbers or driven to ecological extinction.

Frugivore body size is directly related to the size spectrum of ingested seeds that are passed through intact (Janson 1992, Wheelwright 1985, Peres & Roosmalen 2002), and for several reasons hunting has a disproportionate effect on large-bodied species

that are most likely to disperse large-seeded plants. Most partial defaunation scenarios in structurally undisturbed forests will continue to retain many small-bodied vertebrates that are not targeted by hunters, including nongame birds, bats, small primates, and didelphid marsupials. These are also important dispersers and may exhibit positive density compensation as a response to reduced densities of large-bodied frugivores (Peres & Dolman 2000). However, smaller-bodied frugivores inescapably ingest and disperse a much narrower seed size spectrum (*e.g.*, Knogge & Heymann 2003) and cannot functionally compensate for the loss of larger counterparts. Loss or reduction of specialized seed dispersal services could therefore affect a considerable guild of gut dispersed, large-seeded plants that cannot usually recruit underneath parent trees and lianas.

The extent of “half-empty” tropical forests now far exceeds all forms of structural tropical forest disturbance, which vary enormously in the degree to which they can be detected at large spatial scales. Hunting is one of the least detectable forms of anthropogenic perturbation (Peres & Lake 2003) and many apparently unaltered close-canopy forests mask an advanced stage of failed or moribund ecological interactions with potentially perverse consequences to ecosystem dynamics. Several studies are beginning to show that selective defaunation can have pervasive, long-term effects on forests, but much is still unknown. Whereas many remaining forests will suffer severe defaunation, others will be only partially defaunated, and the fate of these “half-empty” forests remains uncertain (Redford & Feinsinger 2001). More conclusive evidence is therefore required before the role of animal-mediated dispersal limitation (under reduced availability or failure of effective animal dispersal services) in accelerating losses in plant diversity can be properly understood.

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