

## Game Vertebrate Densities in Hunted and Nonhunted Forest Sites in Manu National Park, Peru

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### ABSTRACT

Manu National Park of southern Peru is one of the most renowned protected areas in the world, yet large-bodied vertebrate surveys conducted to date have been restricted to Cocha Cashu Biological Station, a research station covering < 0.06 percent of the 1.7 Mha park. Manu Park is occupied by > 460 settled Matsigenka Amerindians, 300–400 isolated Matsigenka, and several, little-known groups of isolated hunter–gatherers, yet the impact of these native Amazonians on game vertebrate populations within the park remains poorly understood. On the basis of 1495 km of standardized line-transect censuses, we present density and biomass estimates for 23 mammal, bird, and reptile species for seven lowland and upland forest sites in Manu Park, including Cocha Cashu. We compare these estimates between hunted and nonhunted sites within Manu Park, and with other Neotropical forest sites. Manu Park safeguards some of the most species-rich and highest biomass assemblages of arboreal and terrestrial mammals ever recorded in Neotropical forests, most likely because of its direct Andean influence and high levels of soil fertility. Relative to Barro Colorado Island, seed predators and arboreal folivores in Manu are rare, and generalist frugivores specializing on mature fruit pulp are abundant. The impact of such a qualitative shift in the vertebrate community on the dynamics of plant regeneration, and therefore, on our understanding of tropical plant ecology, must be profound. Despite a number of external threats, Manu Park continues to serve as a baseline against which other Neotropical forests can be gauged.

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

*Key words:* bushmeat; defaunation; distance sampling; forest vertebrates; hunting; indigenous people; Manu National Park; trophic cascade.

THE LONG-TERM OCCUPATION OF TROPICAL FOREST reserves by indigenous peoples has fuelled a vigorous debate between those who view indigenous peoples as conservation allies and those who see them as a threat to the long-term viability of wildlife populations (Harmon 1987, Redford 1991, Alcorn 1993, Redford & Stearman 1993, Robinson 1993, Peres 1994, Zimmerman *et al.* 2001, Shepard 2002, Terborgh & Peres 2002, da Silva *et al.* 2005, Nepstad *et al.* 2006, Ohl-Schacherer *et al.* 2007, Shepard *et al.* in press). A well-known skirmish appeared in the pages of *Conservation Biology*, triggered by Terborgh's (1999) warning that the Westernizing and fast-growing Matsigenka indigenous population within Peru's Manu National Park, located in the southeastern Peruvian Amazon, will eventually degrade Manu's biological integrity unless some way is found to promote voluntary resettlement outside the park (Redford & Sanderson 2000, Schwartzman *et al.* 2000, Terborgh 2000, Peres & Zimmerman 2001).

Since its creation in 1973, Manu Park has been considered one of the world's most important tropical protected areas. It constitutes the core area of a UNESCO Biosphere Reserve, is located in one of the most species-rich biodiversity hotspots, and is a World Heritage Site. Manu Park is remarkable not only for its high level of biological diversity, including a wide array of different habitats with

distinct faunal and floral compositions, but also for the apparently high abundance of many species that are threatened or rare elsewhere, probably because of its soil nutrient-rich eutrophic forests, arguably some of the most fertile in the Neotropics (Foster 1990, Ohl *et al.* 2007). The 1.7 Mha Manu Park covers the watershed of the Manu River, including large stretches of lowland tropical rainforest. Over most of the park, the vegetation is characterized by a mosaic of different types of tropical lowland rainforest on both recently formed, inundated alluvial floodplains (lowland forest) and older, elevated, and hilly terraces (upland or terra firme forest) (see Terborgh 1990, Terborgh *et al.* 1996, Shepard *et al.* 2001), although the southwestern portion of the park includes an Andean elevational gradient (*ca* 340–3450 m asl), ranging from montane rain forest through cloud forest, the mossy, low canopy *elfin forest*, and Andean grassland (*puna*).

The core of Manu Park is officially considered as an 'untouchable area', where only nonintrusive activities such as research are permitted. But when the park was established in 1973, Peruvian law did not yet recognize the indigenous populations that were known to be present. In the years following park establishment, however, several laws granted ancestral populations the right to remain within protected areas, provided that their traditional subsistence activities did not interfere with the park's conservation goals. Thus, in a legal contradiction, the Manu Park core area is inhabited by a considerable indigenous population. As of late 2007, there

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were > 460 Matsigenka people settled mostly in two state-recognized communities inside Manu Park's core area, growing at an annual rate of *ca* 4 percent or more (Fig. 1). The Tayakome settlement was founded by missionaries in the early 1960s, and the Yomybato settlement dates from the late 1970s. Three to four hundred more isolated Matsigenka reside in remote settlements in the Manu headwaters, and there are unknown numbers of uncontacted hunter-gatherers, in total almost certainly surpassing 1000 people (see also Shepard *et al.* in press). The Matsigenka populations engage in swidden agriculture, growing manioc, bananas, maize, and diverse minor crops (Ohl *et al.* 2007). They fish with traditional and modern technology, but due to park gun restrictions and the high cost, they hunt mainly with bow-and-arrow (Ohl-Schacherer *et al.* 2007). Three to four hundred more isolated Matsigenka reside in remote settlements in the Manu headwaters, mostly > 600 m asl. There are at least two small groups of elusive, nomadic foragers in Manu Park of unknown population size: a Mashco-Piro population in the headwaters of the Pinquen River that has been sighted occasionally on the southern bank of the lower Manu for decades (Kaplan & Hill 1984), and another group, possibly also Mashco-Piro, that has migrated more recently towards the north bank tributaries of the middle and upper Manu, apparently fleeing petrochemical companies and loggers who moved into the adjacent Rio de las Piedras in the mid-1990s (Shepard *et al.* in press). Both of these groups have actively avoided and rejected all contact, both with outsiders and with local indigenous groups, perhaps fearful of the toll of introduced diseases.

At present, the main biodiversity threat posed by humans is the reduction in large-bodied vertebrate game populations caused by overhunting (Terborgh 1999, Shepard *et al.* in press). Yet Manu Park retains a full complement of large mammal (Terborgh 1983, Janson & Emmons 1990) and gamebird species (Terborgh *et al.* 1990) and most of the Park area has been subjected to light or no hunting pressure (Ohl-Schacherer *et al.* 2007).

Efforts to resolve people-park conflicts in Manu begin with reliable estimates of terrestrial vertebrate abundances, especially game species. However, most research on vertebrate populations in Manu Park has been concentrated at a single lowland forest site, Cocha Cashu Biological Station (11.88826° S, 71.40756° W), which is situated at the edge of an oxbow lake in an alluvial plain inside a mature lowland forest. It is unclear to what extent faunal density estimates obtained within the 10 km<sup>2</sup> study area of Cocha Cashu Biological Station (accounting for < 0.06% of the park area) can be extrapolated to the entire park or even just to areas < 600 m, which are primarily comprised of upland forest. Tropical forest vertebrate surveys across the Amazon basin and elsewhere reveal great spatial variability in population abundance and community composition. Some of this variability can be explained by baseline environmental variables, such as geomorphology and soil fertility (Barnes & Lahm 1997; Peres 2000, 2008), some by biogeography (Ayres & Clutton-Brock 1991, Primack & Corlett 2005), and an increasing amount by anthropogenic disturbance, including hunting (Peres & Palacios 2007).

In this study, we used standardized line-transect surveys to characterize the mid- and large-bodied terrestrial vertebrate assemblage (including all major game species) at seven forest sites within Manu Park. Two sites are heavily hunted by Matsigenka native communities, and five have not been subjected to hunting for at least 35 yr. Surprisingly, given the long research history of Cocha Cashu (Gentry 1990), the large vertebrate assemblage at this site has never been censused systematically using this technique, although diurnal primates were censused along the main trail system by Janson and Terborgh (1980) in July 1974. This study therefore presents the first estimates of large vertebrate abundances in Manu Park that allow us to (1) compare the two major forest types < 600 m asl; (2) compare against previous abundance estimates at Cocha Cashu, which were based on a variety of census techniques; (3) compare against forest sites elsewhere in the Neotropics; and

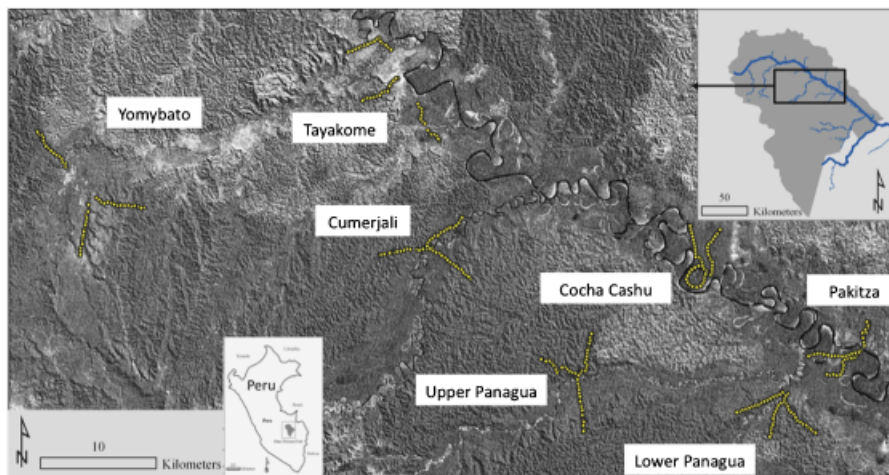


FIGURE 1. Map of the seven census sites in Manu National Park. Dotted lines are the individual line transects. The Tayakome and Yomybato sites are the two Matsigenka villages. At the villages, the censuses started at the perimeter of the inhabited areas, accounting for the space between the trailheads. Light-color forests (upper left and upper-right corners) are dominated by either bamboo (*Guadua* spp.) or *Cecropia sciadophylla*. Upper inset, map of Manu Park; Lower inset, Peru, showing the location of Manu Park.

finally (4) quantify the effects of Matsigenka subsistence hunting on vertebrate species composition and population abundance.

## METHODS

**STUDY SITES.**—The study was conducted at seven locations inside Manu Park, at altitudes of 340–420 m asl (Table S1; Fig. 1). Pairwise distances between the census sites (measured from the central campsites) ranged from 8 to 70 km (mean  $\pm$  SD distance between sites =  $32 \pm 17$  km). Annual rainfall averages 2000–2600 mm, with a dry season between May and September/October. Away from the high-elevation, Andean portion of the park, the mean temperature is fairly constant, but in the dry season, there can be several-day cold fronts (*frijajes*) that reach as low as 9°C, thereby reducing animal activity.

The two major Matsigenka settlements, Tayakome and Yomybato, are located on upland terraces, 10–50 m above the Manu River (Fig. 1; Shepard *et al.* 2001). About 200 people live in each of these two permanent communities. The rest of the population is found in smaller, less stable satellite settlements. The five nonhunted census sites are 15–70 km from any Matsigenka settlement. The Cumerjali tributary is occasionally visited by hunters on long-distance forays, but the Upper and Lower Panagua sites have not been visited by Matsigenka hunters within at least the last two generations (although we cannot completely rule out transient forays by uncontacted indigenous people), and both Cocha Cashu Biological Station and the Pakitza guard post have been protected from hunting since at least the Park's founding in 1973.

The Cocha Cashu and Pakitza census sites were exceptions in two ways. Firstly, these were the only two sites located exclusively in lowland forest. Secondly, at Cocha Cashu, one transect circled the oxbow lake rather than radiating outward. At Pakitza, the third, northern transect (Fig. 1) was abandoned after the presence of an uncontacted indigenous group was detected, which also prevented us from conducting censuses upriver of Tayakome or near the mouth of the Manu River.

All census transects were 1 m wide, marked every 50 m, georeferenced with a Garmin GPS60 (Garmin International Inc., Olathe, KS, U.S.A.) with external antenna, and mapped in relation to forest topography (Fig. 1). In most sites, we censused three, non-spatially independent transects radiating outwards from the central campsite or Matsigenka settlement. The transects in the two Matsigenka settlements were deliberately placed within the zones of high Matsigenka hunting effort (Fig. 1; see Ohl-Schacherer *et al.* 2007 for further site descriptions).

Excluding one transect at Tayakome and three at Cocha Cashu, all trails were opened specifically for this study, minimizing possible bias caused by previous human interference in the area. In total, 20 transects, totaling 90 km, were censused. All cut transects were left to rest for at least a day before being censused.

There is no way that we can correct statistically or otherwise for the local hunting pressure exerted by nomadic indigenous foragers such as the Mashco Piro. For ethical and safety reasons, we cancelled census efforts, where their presence was evident, also effectively minimizing any transitory impacts of their hunting ac-

tivities on our census data. The extremely high abundance of vertebrate game species recorded in our 'nonhunted' sites, in contrast to the noted reductions in abundance around sedentary indigenous settlements, further attests to the ephemeral and minimal impact of hunting by nomadic peoples.

**LINE-TRANSECT SURVEYS.**—Our line-transect censuses focused on medium to large-bodied diurnal vertebrates because these species can be detected visually and/or acoustically, are the preferred game species among indigenous hunters (Ohl-Schacherer *et al.* 2007), and represent a disproportionate fraction of the total vertebrate biomass in tropical forests (Terborgh 1983, Peres 1999a). For each animal sighting, we recorded the time, species, perpendicular distance from the transect (PD), group size, detection mode (*e.g.*, visual or acoustic), group diameter for large, uncohesive groups or subgroups (as often occurs in large group-living primates), and distance along the transect. Detection rates naturally decline with PD, but given a sufficient number of independent observations, the PD distribution can be modeled to calculate an 'effective strip width' using the program Distance v. 4.1 (Buckland *et al.* 1993), which is then used to generate a group or population density estimate based on the number of group or single-animal encounters.

Censuses were conducted from January to July 2006, thus, in the late rainy and early dry season. No census was conducted in May, the month with the highest frequency of *frijajes*, when animal activity can be atypically low. Trails were walked on rainless days during the morning (0630–1030 h) and afternoon (1300–1700 h) by two observers (a wildlife biologist and a local Matsigenka hunter) at a mean velocity of 1.2 km/h. All trailheads were placed > 400 m from campsites or from any Matsigenka houses. Each transect in five of our seven sites were surveyed for *ca* 10 d, usually within a 21-day period (for a detailed description of our census procedures, see Peres 1999b). However, Cocha Cashu, and Pakitza were censused over multiple days interspersed between February and July (Table S1), making comparisons with historical abundance estimates at these sites more reliable. Seasonal changes may affect the detectability or even the spatial distribution of some species (Haugaasen & Peres 2007), so to partially control for this effect with respect to the nonhunted vs. hunted comparison, one Matsigenka settlement was censused in the rainy season (Yomybato), and one in the dry season (Tayakome; Table S1).

**TAXONOMIC TREATMENT.**—Mammal species nomenclature follows Solari *et al.* (2006), with some adjustments made by the authors. Unfortunately, due to the rapidly changing nature of mammalian alpha-taxonomy, in some places the Latin and common names differ from those used in previous publications from the area (including Janson & Emmons 1990, Ohl-Schacherer *et al.* 2007). To facilitate comparison with previous publications, we provide both current and older Latin names in Tables 1 and S2 or in the text. Bird nomenclature follows Walker *et al.* (2006) and is consistent with Ohl-Schacherer *et al.* (2007).

**SPECIES ABUNDANCE ESTIMATES ANALYSIS.**—For each species surveyed, we calculated the encounter rate (per 10 km walked, ER). We also

TABLE 1. Abridged table of population density estimates at the different sites censused in Manu National Park.  $D_{ind}$ , density of individuals ( $/km^2$ ); U, upland, terra firme forest; L, lowland, floodplain forest. Densities not calculated for species with low sample sizes (see text). Tayakome and Yomybato are the two hunted sites. White-lipped peccary population density estimates derived on the basis of a global model stratified by site-specific encounter rates, in which sampling units are defined as small clusters of peccaries ( $N = 93$ ) sighted from the transect. See Table S2 for a complete version, including explanations for footnotes.

Taxa	Yomybato, hunted, U	Tayakome, hunted, U	Upper Panagua, U	Lower Panagua, U	Pakitza, L	Cumerjali, U	Cocha Cashu, L
	$D_{ind}$	$D_{ind}$	$D_{ind}$	$D_{ind}$	$D_{ind}$	$D_{ind}$	$D_{ind}$
<b>Primates</b>							
<i>Saimiri boliviensis</i>	–	4	10.8	29.3	47.9	15.8	49.7
<i>Saguinus fuscicollis</i>	37	5.3	37.8	53.3	29.9	43	12.7
<i>Saguinus imperator</i>	–	1.6	–	–	–	–	6
<i>Callicebus brunneus</i> <sup>3</sup>	7.8	5.2	18.6	20.2	4.3	12.3	5.8
<i>Pithecia irrorata</i> <sup>5</sup>	4.8	1.9	–	–	–	2.3	1.1
<i>Cebus apella</i>	11.2	6	15.5	30.1	30.2	17.1	28.2
<i>Cebus albifrons</i>	1.8	2.5	11.9	10.1	22.8	7.4	22.5
<i>Alouatta sara</i> <sup>1</sup>	0.7	8.3	12.2	11.4	6.3	17	8.6
<i>Lagothrix cana</i> <sup>4</sup>	7.6	9.7	13.2	39.1	48.5	34.1	1.2
<i>Ateles chamek</i> <sup>2</sup>	2.3	7.8	45.9	41.7	14	49	36.3
<b>Ungulates</b>							
<i>Mazama spp.</i> <sup>6</sup>	1	2.7	3.21	1.45	1.68	4.68	2.49
<i>Pecari tajacu</i> <sup>7</sup>	7.8	3.78	8.2	5.17	2.25	5.8	8.03
<i>Tayassu pecari</i>	1.1	5.8	9.2	21.7	43.8	32.4	15
<b>Rodentia</b>							
<i>Dasyprocta variegata</i>	–	1.64	0.99	1.88	1.826	1.722	3.47
<i>Myoprocta pratti</i>	0.5	0.53	2.2	0.53	0.55	1.65	1.14
<i>Sciurus spp.</i> <sup>8</sup>	2.49	15	39.7	16.4	11.61	14.77	9.72
<b>Birds</b>							
<i>Crypturellus spp.</i> <sup>10</sup>	17.72	12.8	16.1	15.9	29.51	15.28	16.03
<i>Tinamus spp.</i> <sup>11</sup>	5.52	8.27	6.46	7.32	12.36	26.92	11.59
<i>Mitu tuberosum</i>	0.62	2.12	5.9	8.9	12.18	7.89	2.73
<i>Odontophorus gujanensis</i>	89.3	69.1	50.2	48.6	13.64	86.8	15.47
<i>Penelope jacquacu</i>	34.74	12.6	20.2	13.7	2.24	29.34	4.58
<i>Pipile cumanensis</i>	–	1.55	0.53	1.55	0.25	1.07	0.74
<i>Psophia leucoptera</i>	5.42	13.7	52.7	37.4	14.95	20.39	23.89

calculated group ( $D_{grp}$ ) and population (individual) densities ( $D_{ind}$ ) when a sufficient number of independent detection events was available across all the sites, or, in the case of the emperor tamarin (*Saguinus imperator*), when we could apply the detection functions derived from the more abundant saddle-back tamarin, (*S. fuscicollis*). Only encounter rates are presented for rare species (e.g., felids, coatis, tayras), here defined as those detected fewer than 39 times, with a few exceptions: brown agouti (*Dasyprocta variegata*;  $N_{sightings} = 38$ ), brocket deer (*Mazama spp.*, 37), green acouchy (*Myoprocta pratti*, 13), blue-throated piping guan (*Pipile cumanensis*, 16), and gray-monk saki (*Pithecia irrorata*, 16), for which available data still allowed us to construct more error-prone but reasonable detection curves. On a site-by-site basis, data obtained during afternoon census walks were included in the analysis only when density estimates for any given species including both the morning and afternoon data did not differ by > 20 percent from estimates based on morning census data only. This is because while

several diurnal species exhibit an activity peak during early- to mid-morning hours, others exhibit a more markedly bimodal distribution of activity (Hill et al. 1997, Peres 1999b).

Analysis of Variance (ANOVA) tests revealed that species-specific PD distributions were not significantly different across sites, once a handful of outlier observations were removed from the dataset (typically, acoustic records of vocally conspicuous primate groups > 50 m from the transect). This allowed us to pool the PD values across census sites and thereby obtain a single, more robust probability distribution of encounter distances for each species. Following Buckland et al. (1993), density estimates were derived by always choosing the best-fit models as judged by the lowest number of parameters and coefficients of variation, series expansions, and AIC values. Extreme PD values were also truncated whenever necessary to improve model convergence and avoid including outliers that could bias model estimators, especially vocally conspicuous group living species. Further details are given in Appendix S1.

For each species, mean (sub)group sizes were calculated using the mean values of all (sub)group counts obtained from transects within a site, thus considering each site as an independent group of values. For primate species foraging in large, uncohesive groups for which whole-group counts tend to be incomplete, we recorded multiple observations, sizes, and PDs of each subgroup (cluster) encountered along the same transect walks, even if they were < 500 m apart and likely belonged to the same social group (or 'community' in the case of spider monkeys). This sampling approach reduces the variance in cluster size, need not assume complete spatial independence between neighboring clusters or feeding parties, and has the advantage of boosting sample sizes and overall model fitness (S. Buckland, pers. comm.). For some large group-living primate species (e.g., gray woolly monkeys *Lagothrix cana* and Peruvian spider monkeys *Ateles chamek*), which can move in fairly uncohesive groups, we also considered the cluster spread in the analysis, thereby minimizing density overestimates (Peres 1997a). Thus, the cluster density,  $D_{\text{clt}}$ , is

$$D_{\text{clt}} = \frac{N}{2L\left(ESW + \frac{CSp}{3}\right)}$$

where  $N$  = number of cluster detections,  $L$  = km walked,  $ESW$  = effective strip width, and  $CSp$  = cluster spread, i.e., mean diameter of the cluster. Individual population density  $D_{\text{ind}}$  is calculated by multiplying  $D_{\text{clt}}$  against the mean cluster size for that site.

**BIOMASS ESTIMATES.**—Population biomass densities were calculated by multiplying the individual population density ( $D_{\text{ind}}$ ), if available, against 80 percent of each species' mean adult body mass estimated from whole carcasses weighed in the Matsigenka communities, using a hunter offtake dataset consisting of 2089 kills and 102,397 consumer-days sampled between October 2004 and September 2005 (Ohl-Schacherer *et al.* 2007). However, for those primate species that are markedly sex dimorphic, we calculated the mean body mass as the mean of adult female and adult male weights, using a dataset from Peres (1999a). Also, for both genera of tinamous (*Tinamus* and *Crypturellus*), the mean body mass was calculated at the level of genus from a Cocha Cashu dataset (Terborgh *et al.* 1990).

For white-lipped peccaries (*Tayassu pecari*), which can form large, uncohesive herds of well over 600 individuals that often move rapidly across the landscape, we were unable to derive a reliable population density estimate ( $D_{\text{ind}}$ ; Tables 1 and S2). However, we conservatively estimate the density and biomass of clusters detected from all transects, which were then multiplied against the mean cluster size ( $D_{\text{clt}}$ ; Tables 1 and S2) based on reliable subgroup counts. Subgroups are merely defined as a cluster of individuals observed simultaneously within 50 m of the transect (range = 1–23). These clusters of animals were, however, but a small part of much larger herds which could be heard up to 400 m from the transects. In total, we detected 93 clusters of white-lipped peccaries belonging to at least 22 different herds at the seven sites. Population biomass was then calculated by multiplying density estimates by 80 percent of the mean body weight of animals harvested by Matsigenka hunt-

ers (Ohl-Schacherer *et al.* 2007). Silman *et al.* (2003) report that minimum group counts numbered between 90 and 138 in 1978, just before they disappeared, and after their reappearance in 1990 and subsequent population recovery, and herd sizes considerably larger than 100 individuals have been regularly observed near Cocha Cashu Biological Station.

**COMMUNITY ANALYSIS.**—Constrained correspondence analysis (CCA) was performed on the community-wide population density dataset (Tables 1 and S2) using the function *cca* from the package *vegan* 1.13-2 (Oksanen *et al.* 2007) in the statistical program R 2.7.2 (R Development Core Team 2007). We used 21 species, omitting the patchily distributed and rare primate species *Saguinus imperator* and *Pithecia irrorata*, but otherwise using all species for which sightings were sufficient to be able to estimate a population density  $D_{\text{ind}}$  in at least one site, setting  $D_{\text{ind}} = 0$  in the rest of the sites for that species (Tables 1 and S2). The evidence for an effect of each of two categorical factors Hunting (Hunted vs. Nonhunted) and Forest type (Lowland vs. Upland) was assessed by a mock ANOVA permutation test on each factor, separately (Oksanen *et al.* 2007). We were unable to test a model with both factors because of strong collinearity (both hunted sites are in upland forest). Note, however, that the statistical power in these tests is weak, because of low sample size. The pairwise, quantitative Jaccard distance metric,  $J = \frac{2B}{1+B}$ , where  $B$  (Bray–Curtis dissimilarity) is  $\sum_i \frac{|x_{ij} - x_{ik}|}{(x_{ij} + x_{ik})}$ , where  $x = D_{\text{ind}}$ , was used over  $i = 23$  species and communities  $j$  and  $k$ . We repeated the above analyses with a biomass dataset, using the same 21 species.

## RESULTS

**DENSITY ESTIMATES.**—Overall, 1495 km of census walks were conducted over the seven forest sites (mean  $\pm$  SD = 213.6  $\pm$  33.9 km/site), resulting in observations of 37 mammal, 17 large bodied bird, and one reptile species, all of which were partly or entirely diurnal. Of these 55 species, 23 (including white-lipped peccaries) had a sufficient number of observations to allow estimation of population density estimates,  $D_{\text{ind}}$  (Tables 1 and S2). Primates were by far the most abundant species encountered, totaling 1575 groups or 59.9 percent of all single animal or group encounters.

Although we were unable to obtain complete counts of white-lipped peccary herds, we can confirm that this species has rebounded from an almost complete regional absence that lasted from approximately 1978 to 1990 (Silman *et al.* 2003, Ohl-Schacherer *et al.* 2007), and our censuses suggest population densities of 3.4  $\pm$  2.3 SE ind/km<sup>2</sup> in hunted sites and 24.4  $\pm$  6.2 ind/km<sup>2</sup> in nonhunted sites (Tables 1 and S2).

The following diurnal, nocturnal, or cathemeral species were detected in low numbers, at very few sites, and primarily by indirect signs (e.g., tracks, scats, active dens, fresh scratches) or vocalizations: giant armadillo (*Priodontes maximus*), South American tapir (*Tapirus terrestris*), paca (*Agouti paca*), black-headed night monkey (*Aotus nigriceps*), pygmy marmoset (*Cebuella pygmaea*), ocelot (*Leopardus pardalis*), jaguar (*Panthera onca*), puma/cougar (*Puma concolor*), kinkajou (*Potos flavus*), Allen's olingo (*Bassaricyon alleni*), and rufous-

vented ground cuckoo (*Neomorphus geoffroyi*). Both forest canids (bush dog *Speothos venaticus* and short-eared dog *Atelocynus microtis*), which are very rare, were visually detected. Despite the low number of direct sightings, we recorded unambiguous evidence of jaguars and/or pumas (vocalizations, tracks or scratches) at all sites, including the two hunting catchments close to Matsigenka settlements.

In addition, some typically (semi)aquatic species that were not expected to be detected from the forest transects, were observed during surveys: giant otter (*Pteronura brasiliensis*), muscovy duck (*Cairina moschata*), and horned screamer (*Anhima cornuta*). The remaining diurnal species of midsized to large vertebrates known to occur in the lowland areas of Manu Park, such as the smaller cats *Felis wiedii* and *Puma yagouaroundi*, the mustelids *Galictis vittata* and *Mustela africana*, the small primate *Callimico goeldii* and a few other animals (see Solari *et al.* 2006), were not detected due to their secretive behavior, patchy distributions, and/or low local densities.

Species abundances were generally higher in nonhunted areas than in the two hunted sites, Yomybato and Tayakome (Tables 1, 2 and S2). However, several species did not show clear decreases in abundance or were more abundant in one or both hunted sites: brocket deer (*Mazama* spp., mainly *M. americana*), saddle-back tamarin (*Saguinus fuscicollis*), gray monk saki (*Pithecia irrorata*), collared peccary (*Pecari tajacu*), Spix's guan (*Penelope jacquacu*), marbled wood quail (*Odontophorus gujanensis*), and small tinamous (*Crypturellus* spp.). Finally, we report a minor range extension. Emperor tamarins (*Saguinus imperator*), which were previously known only from sites on the north (left) bank of the Manu River, also occur on the south (right) bank of the Manu River, at Tayakome.

**BIOMASS ESTIMATES.**—We first examine the five nonhunted sites and derive a conservative total biomass estimate for each site by excluding white-lipped peccaries, for which our abundance estimates are less reliable (Table 2). In the five sites, primates account for a mean of 69 percent (range = 61–79%) of this conservative total, showing their disproportionate biomass contribution to the overall diurnal vertebrate community. Large-bodied ateline primates alone (*i.e.*, woolly monkeys and spider monkeys) were particularly strongly represented in several nonhunted sites, accounting for a mean of 48 percent (range = 36–55%) of the total biomass estimate across all sites. The highest total primate biomass estimates recorded were in the nonhunted Lower Panagua and Cumerjali sites, with a total of 779.9 and 774.9 kg/km<sup>2</sup>, respectively.

Unexpectedly, and despite enjoying a reputation as having one of the highest recorded biomass densities in Neotropical forests (Janson & Emmons 1990), our conservative estimate of Cocha Cashu's vertebrate biomass (759.1 kg/km<sup>2</sup> without white-lipped peccaries) is lower than all four of the other nonhunted sites (Upper and Lower Panagua, Pakitza, and Cumerjali). In fact, both of the nonhunted lowland sites (Cocha Cashu and Pakitza) exhibited a lower aggregate biomass than did the three nonhunted upland sites. We emphasize, however, that our abundance and biomass estimates do not apply to higher elevations of Manu Park (> 600 m asl) nor to the extensive areas of low-phytomass bamboo forests that lie toward the north of the Manu River (*e.g.*, light areas in the upper left of Fig. 1), where we expect the arboreal mammal biomass to be lower.

The inclusion of white-lipped peccaries raises the total vertebrate biomass estimates in the nonhunted sites by an additional 25–141 percent (Table 2). We can only speculate as to the reasons for the recent population recovery (and the original disappearance), but Matsigenka informants have reported that white-lipped peccaries almost completely disappeared from the environs of Yomybato and Tayakome starting in the late 1970s to the early 1980s, and began to return in 1988–1990 (G. Shepard, unpubl. data), although some hunters did manage to kill a few in 1988–1989 (Ohl-Schacherer *et al.* 2007). These dates fit those reported from Cocha Cashu and along the Alto Madre de Dios River (Silman *et al.* 2003). A widespread, simultaneous population decline seems consistent with a hypothesis of epidemic disease and eventual recovery (Fragoso 2004). In support of the disease hypothesis, Matsigenka recall a sudden but more temporary die-back of tapirs in the early 1980s, when seven or more sick individuals or carcasses were found in the forest over the course of several months without any obvious signs of human or animal predation; during about the same time, a number of weak or ill collared peccaries were observed, although their numbers did not decline appreciably (G. Shepard, unpubl. data; Ohl-Schacherer *et al.* 2007). However the Matsigenka observed no such sick individuals or inexplicable carcasses for white-lipped peccaries at the time. Thus the alternative hypothesis of a massive, long-distance migration of white-lipped peccaries is also possible.

**LARGE VERTEBRATE RESPONSES TO HUNTING AND FOREST TYPES.**—A CCA of the species density dataset produced a roughly L-shaped distribution of survey sites (Fig. S1A). Community composition differed significantly (mock ANOVA test,  $P = 0.015$ ) between lowland and upland forest types, with lowland forests characterized by especially higher densities of squirrel monkeys (saimboli), white-fronted capuchins (cebualbi), white-lipped peccaries (tayapeca), brown agoutis (dasyvari), razor-billed curassows (mitutube), and brown (aka tufted) capuchins (cebuapel) (Fig. S1A). The community composition of the two hunted sites (Tayakome and Yomybato) was not formally significantly different from the nonhunted census sites ( $P = 0.098$ ), but did contain higher densities of woodquails (odontoph, 184% = mean hunted/mean nonhunted density), and Spix's Guan (penejacq, 169%) (as well as gray monk sakis [pithirro, 421%]; Tables 1 and S2; although this species was not included in the dataset; see 'Methods').

CCA of the biomass dataset produced a more T-shaped distribution of survey sites (Fig. S1B). Community biomass composition was not formally significantly different between hunted and nonhunted sites ( $P = 0.16$ ) nor between lowland and upland forest sites ( $P = 0.36$ ). Nonetheless, there were clear effects of hunting on overall biomass. The total censused vertebrate biomass at Yomybato and Tayakome, including white-lipped peccaries, amounted to only 25.8 and 36.2 percent of the average total censused biomass of the nonhunted sites, respectively (Table 2). The higher abundance of white-lipped peccaries in Tayakome accounted for most of the difference between the two Matsigenka settlements (Table 2). Interestingly, some species were more abundant in the hunted sites, especially in Yomybato (Fig. S1B).

TABLE 2. Vertebrate biomass estimates calculated for those species with reliable  $D_{ind}$  values (Table 1) and for white-lipped peccaries (*Tayassu pecari*; see 'Methods'). The 'Cocha Cashu JET' column lists biomass estimates from Janson and Emmons (1990) for mammals and Terborgh et al. (1990) for birds, and the 'BCI' column lists density and biomass estimates from Barro Colorado Island, Panama (Leigh 1999: Appendix 7.2). The 'CC/CCJET' and 'CC/BCI' columns calculate the ratios of the respective columns.

Species	Biomass (kg/km <sup>2</sup> )							Cocha Cashu JET	BCI (ind/km <sup>2</sup> )	CC/CCJET (%)	CC/BCI (%)	Equivalent BCI Species
	Yomybato, hunted	Tayakome, hunted	Upper Panagua	Lower Panagua	Pakitza	Cumerjali	Cocha Cashu					
Primates												
<i>Alouatta sara</i>	3.6	43.2	63.4	59.3	32.8	88.4	44.6	156.0	440 (80)	29	10	<i>Alouatta palliata</i>
<i>Ateles chamek</i>	16.6	56.3	331.2	300.8	100.7	353.6	262.3	180.4	5 (1)	145	5246	<i>Ateles geoffroyi</i>
<i>Callicebus brunneus</i>	6.6	4.4	15.7	17.0	3.6	10.3	4.9	20.2	–	24		
<i>Cebus albifrons</i>	3.9	5.4	25.7	21.8	49.2	16.0	48.6	75.6	52 (20)	64	94	<i>Cebus capucinus</i>
<i>Cebus apella</i>	26.1	13.9	36.0	70.0	70.2	39.7	65.7	93.1		71		
<i>Lagothrix cana</i>	53.0	67.6	92.0	272.4	337.6	237.6	8.4	7.0	–	120		
<i>Pithecia irrorata</i>	4.8	3.3	0.0	0.0	0.0	4.0	0.8	1.8	–	43		
<i>Saguinus fuscicollis</i>	11.5	1.7	11.8	16.6	9.3	13.4	3.9	5.0	2.1 (3)	79	188	<i>Saguinus geoffroyi</i>
<i>Saguinus imperator</i>	0.0	0.7	0.0	0.0	0.0	0.0	2.4	4.9		50		
<i>Saimiri boliviensis</i>	0.0	3.0	8.1	22.0	36.0	11.9	37.4	45.1	–	83		
Ungulates												
Mazama spp. <sup>a</sup>	24.1	66.5	79.1	35.7	41.4	115.3	61.4	78	45 (3)	79	136	<i>Mazama americana</i>
<i>Pecari tajacu</i>	135.4	65.6	142.4	89.8	39.1	100.7	139.4	140	230 (10)	100	61	<i>Pecari tajacu</i>
<i>Tayassu pecari</i>	28.6	150.4	239.2	564.4	1137.7	842.8	389.6	105.5 <sup>b</sup>	–	369		
Rodentia												
<i>Dasyprocta variegata</i>	0	4.5	2.7	5.1	5.0	4.7	9.4	20.8	280 (100)	45	3	<i>Dasyprocta punctata</i>
<i>Myoprocta pratti</i>	0.3	0.3	1.4	0.3	0.4	1.1	0.7	7.95	–	9		
<i>Sciurus spadiceus</i>	1.4	8.4	22.2	9.2	6.5	8.3	5.4	5	45 (180)	109	12	<i>Sciurus granatensis</i>
Birds												
<i>Crypturellus spp.</i>	5.3	3.8	4.8	4.7	8.8	4.6	4.8	15.5		31		
Tinamus spp.	5.5	8.3	6.5	7.4	12.4	27.1	11.7	22.7		51		
<i>Mitu tuberosum</i>	1.5	5.3	14.6	22.1	30.2	19.6	6.8	15.5		44		
<i>Odontoph. gujanensis</i>	35.7	27.6	20.1	19.4	5.5	34.7	6.2	16		39		
<i>Penelope jacquacu</i>	36.1	13.1	21.0	14.2	2.3	30.5	4.8	2.6		183		
<i>Pipile cumanensis</i>	0.0	1.7	0.6	1.7	0.3	1.2	0.8	7		12		
<i>Psophia leucoptera</i>	6.5	16.4	63.2	44.9	17.9	24.5	28.7	13.5		212		
Primate biomass	126.0	199.3	583.8	779.9	639.5	774.9	479.0	589.0		81		
Total biomass without <i>T. pecari</i>	378.0	421.0	962.5	1034.5	809.3	1147.1	759.1	933.6		81		
Total biomass with <i>T. pecari</i>	406.6	571.4	1201.7	1598.9	1946.9	1989.9	1148.7	1039.1		111		

<sup>a</sup>Mainly *Mazama americana*, but including an unknown small number of *M. gouazoubira* sightings,

<sup>b</sup>Corrected from the original typographical error, '105. < 5.'

## DISCUSSION

This study represents the first fully standardized, large-scale series of line-transect surveys of medium- to large-bodied terrestrial vertebrates in Manu Park. The Manu Park ecosystem contains a full complement of forest vertebrate species and, roughly > 85 percent

of the park area < 600 m asl (13,851 km<sup>2</sup>) has been largely free of persistent hunting for three decades or more. In fact, of all Neotropical forest sites investigated to date, Cocha Cashu Biological Station has been repeatedly portrayed as a prime example of a pristine lowland forest embedded within vast tracts of continuous wilderness areas, and complete with all harvest- and area-sensitive



large-bodied vertebrates (Terborgh 1988). This has exposed a debate over the representativeness of a number of ecological processes uncovered at less extensive, more accessible, and more human-modified Neotropical forest sites where several species of large-bodied mammals are locally extinct (*e.g.*, Barro Colorado Island: Wright *et al.* 1994). In the two Panagua census sites (far even from the migration routes of the nomadic Mashco Piro), it is possible that no hunting had taken place for half a century or more before the surveys, even by historical indigenous populations. This provides both an opportunity to characterize an intact vertebrate community and to gauge the effects of subsistence hunting by the two major Matsigenka settlements. Additionally, our standard line-transect census technique allows us to verify previous density estimates at the Cocha Cashu Biological Station.

COCHA CASHU.—A variety of census techniques have been used at Cocha Cashu to estimate the population densities of birds (Robinson & Terborgh 1990, Terborgh *et al.* 1990) and mammals (Terborgh 1983, Janson & Emmons 1990), including live-trapping, nocturnal and diurnal censuses, and intensive single-species observations such as spot-mapping of avian vocalizations and full-day follows of habituated primate groups. Also, most studies at Cashu were restricted to the 600-ha trail system of the main study area and, more specifically, around the permanent research station and the lake (Terborgh *et al.* 1990), whereas our transects covered a much broader area (Fig. 1). The supra-annually inundated mature and young floodplain forest encompassed by this study area may be atypically productive, compared with other parts of Manu Park, for reasons related to water stress during the dry season and soil fertility (Mazer 1996). For example, population densities of howler monkeys and other arboreal folivores across Amazonia decline nonlinearly with distance to rivers and alluvial floodplains (Peres 1997b), a pattern that runs against what would be expected if howler densities were primarily driven by hunting pressure. Previous density estimates at Cashu (Saavedra 1984) might therefore be expected to differ from those reported here. The most obvious disparities between this study and the historical estimates at Cashu are the lower biomass estimates for red howler monkey (*Alouatta sara*) and brown titi monkey (*Callicebus brunneus*), for which previous estimates are 3.5 and 4.1 times higher, respectively (Table 2). Likely explanations are that brown titi monkeys are small and secretive and that howler monkeys are often inactive and high in the canopy. They may therefore be easily overlooked during strip censuses, but can be counted when groups are followed individually. Otherwise, there is good overall correspondence between our density estimates and those obtained previously at Cocha Cashu. Omitting only white-lipped peccaries, the Pearson correlation coefficient between our biomass results and those of Janson and Emmons (1990) is 0.86 ( $P < 0.001$ ; Table 2).

As already stated, despite the fact that lowland forest soils, such as at the Cocha Cashu site, are more fertile (Mazer 1996, Ohl *et al.* 2007), our results showed a lower aggregate biomass in Cocha Cashu and Pakitza than in the nonhunted upland sites, suggesting that most of the core area of Manu Park, which is primarily comprised of upland forest, has a vertebrate biomass density similar to or higher than that of Cocha Cashu.

MANU VS. OTHER AREAS.—Manu Park safeguards some of the most species-rich and highest biomass of mid- to large-bodied forest vertebrate assemblages in any Neotropical forest, confirming and even surpassing earlier surveys based on a much smaller sampling effort restricted to Cocha Cashu (Emmons 1984b). This is clearly the case for both terrestrial and arboreal mammals in nonhunted portions of Manu Park that are well beyond the hunting catchment areas of the two major Matsigenka settlements. For example, the five nonhunted mature floodplain and upland forests surveyed (Cumerjali, Lower Panagua, Upper Panagua, and Pakitza) were within the top 10 aggregate primate biomass estimates for any of 148 forest sites surveyed to date throughout lowland Amazonia and the Guianan Shields (C.A. Peres, unpubl. data); even the lowest estimate obtained from these five sites is above the 95th percentile (based on an empirical distribution function of all Amazonian primate surveys). Furthermore, Lower Panagua, Cumerjali, and Pakitza had the highest primate biomass levels recorded to date, except for a seasonally flooded Pleistocene *várzea* forest along the Rio Juruá, Brazil, that is also subjected to little or no hunting (Boa Esperança: Peres 1997a).

Studies have indicated a strong correlation between soil fertility and vertebrate abundance in Amazonian forests (Peres 2000, 2008). Oligotrophic forests, such as those found in much of Central Amazonia and the Guianan Shield region tend to support a low density of large vertebrates, but not necessarily a lower species richness. However, lower population densities increase the probability that any given species will be overlooked for a given amount of census effort. That we repeatedly recorded 12 of the 14 primate species known to occur in Manu (all except the rare Goeldi's monkey and the secretive pygmy marmoset, both of which are extreme forest habitat specialists), is a good example of the contrast between Manu Park and less nutrient-rich Amazonian forests. The exceptionally high habitat productivity of Manu Park for arboreal mammals is underscored by the fact that both of the largest primate species (woolly and spider monkeys) were frequently represented in large numbers, co-occurred microsympatrically, and were often observed in relatively stable mixed-species groups. This is highly unusual at other Amazonian sites where these genera co-occur (Iwanaga & Ferrari 2002; C.A. Peres, unpubl. data).

We also revise previous faunal density comparisons between Manu (Cocha Cashu Biological Station) and Barro Colorado Island in Panama (Terborgh 1988, Wright *et al.* 1994, Leigh 1999). Compared with Manu, Barro Colorado Island has a much lower biomass of spider monkeys (and large mammals with large spatial requirements such as, woolly monkeys and white-lipped peccaries), but a much higher biomass of large rodents (*Dasyprocta* and *Agouti*), howler monkeys (*Alouatta*), and sloths (*Bradypus* and *Choloepus*) (Table 2; Leigh 1999: Appendix 7.2). In fact, both sloth genera, the largest contributors to mammal biomass at Barro Colorado Island (1490 kg/km<sup>2</sup> for *Bradypus variegatus* alone), were never recorded in our censuses, nor was a single individual detected on any other occasion inside Manu Park during the entire fieldwork period, which is unexpected, even considering the difficulty of detecting sloths in the forest (sub)canopy. This is consistent with a hunting study carried out inside the Manu Park (Ohl-Schacherer



*et al.* 2007), where no sloths were recorded in a list of 2089 animals killed during a 1-yr period by Matsigenka hunters. Yet this list included many prey items (birds and mammals) smaller than either of the two sloth species occurring in Manu Park. The apparent low abundance of sloths in both upland and lowland forest sites is in marked contrast with Amazonian seasonally inundated (*várzea*) forests with a sustained annual flood pulse, where sloths represent a major part of the arboreal mammal biomass (Peres 1999a). In short, Barro Colorado Island is characterized by high abundances of seed predators and arboreal folivores (Eisenberg & Thorington 1973) and relatively low abundances of generalist frugivores that specialize on mature fruit pulp. Given that both small and large predators were detected regularly in all Manu census transects (see also Emmons 1984a, Janson & Emmons 1990), it is tempting to explain these differences, which were consistent across both non-hunted and hunted sites, by invoking stronger top-down control (Terborgh *et al.* 2001). However, bottom-up mechanisms are also likely important, considering the high production of fruits and seeds in Manu (Terborgh 1983) and other significant differences in the resource base available to vertebrate consumers at these forest sites.

**EFFECTS OF HUNTING.**—The aggregate large vertebrate biomass was considerably higher in nonhunted forest sites, compared with the sites within the core hunting catchment of the two main Matsigenka settlements in Manu Park. This is consistent with comparisons of hunted and nonhunted sites within and outside forest catchments harvested by a wide range of subsistence hunters in Amazonia (*e.g.*, Hill *et al.* 1997, Mena *et al.* 2000, Peres 2000; see meta-analysis in Peres & Palacios 2007). Moreover, these results are unlikely to be largely driven by differences in forest productivity because nonhunted, upland forest sites sustained an aggregate game vertebrate biomass 2–4+ -fold higher than that of the hunted sites, which are also located in upland forest areas (Fig. 1). For key harvest-sensitive game species, such as spider monkeys, population densities in hunted sites were up to 21 times lower in hunted sites compared with nonhunted sites of the same forest type. A recent analysis of game offtake by the Matsigenka using the Robinson and Redford production index (Ohl-Schacherer *et al.* 2007), which is known to flag up only severe cases of overhunting (Milner-Gulland & Akçakaya 2001), estimated that five mammal and gamebird species were being exploited unsustainably within the hunting zones of these two settlements: spider monkeys, woolly monkeys, razor-billed curassows, Spix's guan, and white-lipped peccaries. Nonetheless, populations of all five species still occur within both hunting zones, and Spix's guan exhibits abundances that exceed those in nonhunted areas (Tables 1, 2 and S2). Recent analyses (Levi *et al.* 2009) find that because Matsigenka hunters use bow-and-arrow technology, there has not been enough time since settlement founding to extirpate the large-primate populations within the settlements' 10 km-radius hunting zones, which are also being supplemented by immigration from nonhunted source areas (Ohl-Schacherer *et al.* 2007).

In addition, a few vertebrate species were more abundant in one or both of the hunted sites, including Spix's guan (*P. jacquacu*),

marbled wood quail (*O. gujanensis*), collared peccary (*P. tajacu*), saddle-back tamarin (*S. fuscicollis*), and tinamous (primarily *Crypturellus* spp.) or did not show clear decreases (*e.g.*, red brocket deer, *M. americana*) (Tables 1, 2 and S2; Fig. S1A and B). One possible explanation is that these species have been released from competition or predation by species that are directly or indirectly suppressed in hunted sites, thereby exhibiting partial density compensation (Peres & Dolman 2000). It is also possible that the habitat matrix created by slash-and-burn agriculture near the Matsigenka settlements (Ohl *et al.* 2007) favors one or more of these species. For instance, increased abundance of Spix's guan has also been reported by Racz-Luna (2001) around the Piro settlement of Diamante, just outside Manu Park. Such species have been referred to as 'anthropogenic fauna' (Naughton-Treves *et al.* 2003) and are typically characterized by high intrinsic population growth rates (Bodmer *et al.* 1997). A final reason that would explain the higher densities of some of those species in the Matsigenka catchments is their low importance in the 'hunter's menu' (Jerzolimski & Peres 2003), especially considering the high abundance of more desirable target species. This is the case of at least several species < 1 kg, including *Saguinus* spp., *O. gujanensis*, and *Crypturellus* spp.

In summary, our extensive line-transect surveys document that Manu National Park contains some of the highest densities of mid-to large-bodied terrestrial vertebrates ever recorded in Neotropical forests, confirming and even surpassing previous estimates made at Cocha Cashu Biological Station. We detect the effects of hunting by Matsigenka indigenous people only in the hunting zones surrounding Matsigenka settlements (as predicted in Levi *et al.* 2009). Manu Park's vertebrate assemblage therefore provides a snapshot of how a nutrient-rich Neotropical forest 'should be'. Compared with the intensively studied, artificially created Barro Colorado Island research site, midsized seed predators and arboreal folivores in Manu are relatively rare, and arboreal frugivores specializing on mature fruit pulp are abundant. The impact of such a qualitative shift in the vertebrate community on the dynamics of plant regeneration, and therefore, on our understanding of tropical plant ecology, must be profound.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Details of census sites and transects.*

TABLE S2. Species, sighting rates, and population density estimates at the different sites censused in Manu National Park. ER: Encounter rate (group sightings/10 km walked);  $D_{ind}$ : Density of individuals ( $/km^2$ );  $D_{cl}$  = Density of clusters ( $/km^2$ ); CV = coefficient of variance of estimates; U = upland, terra firme forest; L = lowland, floodplain forest. Densities not calculated for species with low sample sizes (see text). Tayakome and Yomybato are the two hunted sites. White-lipped peccary population density estimates derived on the basis of a global model stratified by site-specific encounter rates, in which sampling units are defined as small clusters of peccaries (N = 93) sighted from the transect.

FIGURE S1. Constrained correspondence analysis of animal species (A) density and (B) biomass estimates in the seven forest sites censused.

FIGURE S2. Example frequency distribution of perpendicular distances and the best-fit detection function selected, based on the data obtained for razor-billed curassow in Manu National Park, Peru.

APPENDIX S1. (A) Description of the Perpendicular Distance (PD) estimation procedure; (B) Pre-ANOVAS; (C) Minimum number of detections.

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