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## Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity

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**Abstract** Density compensation is a community-level phenomenon in which increases in the abundance of some species may offset the population decline, extirpation, or absence of other potentially interacting competitors. In this paper we examine the evidence for density compensation in neotropical primate assemblages using data from 56 hunted and nonhunted, but otherwise undisturbed, forest sites of Amazonia and the Guianan shields from which population density estimates are available for all diurnal primate species. We found good evidence of density compensation of the residual assemblage of nonhunted mid-sized species where the large-bodied (ateline) species had been severely reduced in numbers or driven to local extinction by subsistence hunters. Only weak evidence for density compensation, however, was detected in small-bodied species. These conclusions are based on the effects of ordinal measures of hunting pressure on the aggregate primate biomass across different size classes after controlling for the effects of forest type and productivity. These results are interpreted primarily in relation to patterns of niche partitioning between different primate functional groups or ecospecies. This study suggests that while overhunting drastically reduces the average body size in multi-species assemblages of forest vertebrates, depletion of large-bodied species is only partially offset (i.e. undercompensated) by smaller taxa.

**Key words** Density compensation · Competitive release · Primate community · Primate biomass · Forest productivity

### Introduction

Density compensation is a community-level phenomenon in which increases in the abundance of some species neutralize the population decline, extirpation, or absence of other potentially interacting species (MacArthur et al. 1972). The summed population densities (or biomass) of communities in species-poor sites may thus be equivalent to or greater than (in the case of excess density compensation) that of species-rich sites. Mechanisms of density or niche-breadth compensation may include expansions in foraging substrates, diet and habitat types (Diamond 1970; Cody 1975), all of which may result in greater average population densities for species released from competition provided that a sufficiently long response time is allowed. Partial rather than complete density compensation may be expected following severe population collapses or local extinctions of some species if the remaining species in the community are able to use only some of the additional resources, or all of the additional resources less efficiently, than the species which had previously sequestered them (Cody 1975).

The evidence for and against density compensation in vertebrates has been largely derived from studies of insular avifaunas (Crowell 1962; Grant 1966; Diamond 1970; Morse 1977; Wright 1980; George 1987), and remains largely inconclusive (see Faeth 1984 for a review). For example, comparisons between primate populations on small islands that have a reduced primate species pool, and those of congeners in more diverse mainland assemblages, provide some tentative evidence for competitive release, such as substantially higher densities or habitat breadth expansion in island populations in southeast Asia (e.g. *Macaca* spp.: Sugardjito et al. 1989) and Africa (e.g. *Procolobus kirkii*: Struhsaker and Siex 1996). While density compensation on islands does appear to take place (Wright 1980), it remains unclear whether most cases are due to competitive release (MacArthur 1972; Diamond 1978), predator release (Case 1975; Morse 1977), reduced dispersal (the so-called

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fence effect) (Krebs et al. 1969; Emlen 1978), or are artifacts arising from differences in other environmental variables including habitat types (Abbott 1980) and climatic conditions (Case 1975).

Despite the early enthusiasm for island studies of density compensation (Crowell 1962; MacArthur 1972; MacArthur et al. 1972), field tests of similar numerical responses in continental faunal assemblages have been conducted far less frequently (but see Eltringham 1974; Hairston 1981; Davidson et al. 1984; Tonn 1985; Schmitt and Holbrook 1990; Sinclair 1995). Density compensation in continental assemblages may be examined by comparing the composition and density of species between sites that differ in the density of potential competitors, particularly competitive dominants. However, variation in the density of dominants may be caused by unrecognized environmental differences between areas that confound interpretation of any "response". Clearly, experimental manipulation is desirable. For example, evidence of competitive release has been provided from monitoring the effects of individual perturbations on East African herbivore communities, with an increase in ungulate populations following the removal of a dominant large herbivore (see Eltringham 1974 and review in Sinclair 1995). Despite these few opportunistic studies, large-scale replicated field manipulations of competitor density are difficult to conduct. Previous implicit tests of density compensation in continental primate assemblages (as opposed to mainland-island comparisons) are inconclusive, as they rely on comparing censuses conducted before and after hunting at a single unreplicated site (Sussman and Phillips-Conroy 1995), or on comparisons between a small number of sites that differ in either hunting pressure (Emmons 1984,  $n=7$ ) or in the residual primate assemblage within forest fragments (Struhsaker 1978,  $n=6$ ) where confounding area and edge effects may occur.

The selective depletion or extirpation of large-bodied game species by hunters provides an opportunity to test for potential density compensation, in the release of smaller guild members from either exploitation or interference competition. Such responses have been suggested (but not tested for) in bird communities in hunted but otherwise undisturbed forests of French Guiana (Thiollay 1988). Subsistence hunting by Amazonian forest dwellers is a widespread phenomenon that selectively targets the large-bodied component of the vertebrate fauna but ignores most of the smaller- and medium-sized species (Redford and Robinson 1987; Peres 1990; Bodmer 1995). This is particularly the case of the species-rich, size-graded primate communities of lowland Amazonia and the Guianan Shields in which only species exceeding 3 kg in body weight are consistently harvested by subsistence hunters (Peres 1999a, 1999b). These species include primarily the three prehensile-tailed ateline genera (*Alouatta*, *Ateles* and *Lagothrix*) and the capuchin monkeys (*Cebus*), which can be severely affected by hunting pressure throughout their range (Peres 1990, 1999a, 1999b; Ráez-Luna 1995).

Most species in Amazonian primate assemblages rely heavily on ripe fruit pulp whenever this become available (Terborgh 1983; Peres 1994a). Co-occurring primates thus comprise a functionally loose but taxonomically restricted ecological community, as a group of trophically similar, sympatric species that actually or potentially compete for the same resources (Tokeshi 1993). Release from exploitation competition within this broad trophic class may, therefore, provide at least one mechanism for density compensation. In nonhunted forests, large-bodied species account for a disproportionate contribution to the total primate community biomass (Peres 1999a, in press), and consume a large proportion of the fruit crops shared by smaller species (Terborgh 1983; Peres 1994b; Stevenson in press). Small and medium-sized primate species could thus show competitive release in response to reduced exploitation competition following the reduction in density or extirpation of large-bodied species by subsistence hunters. In addition, interference competition between sympatric primates in the form of agonistic displacements of subordinate, small-bodied species by larger counterparts is frequent at both large and small-crowned fruiting trees (Terborgh 1983; Wright 1985; Stevenson in press). This could operate as an additional mechanism suppressing the densities of small-bodied species. However, we hypothesize that compensatory releases should be stronger in mid-sized than in small-bodied species because the former are more likely to share critical resources with large-bodied species during periods of resource scarcity (Terborgh 1983; Peres 1994a).

A standardized series of vertebrate surveys conducted throughout the Amazon basin has shown that severe population declines or local extinction of large-bodied species, particularly of the three ateline genera, comprise the main shift in primate community structure in overhunted forests (Peres 1990, 1999a). In general, as hunting pressure increases there is a gradual but drastic decline in the contribution of large-bodied species to the total primate community biomass. Although the relative biomass contribution of small and medium-bodied species increases substantially in overhunted sites (Peres 1999a), this could be entirely due to depression of large-bodied species without any subsequent density compensation. Rather, tests of density compensation should consider responses in the absolute abundance of small and medium-bodied species. In addition, previous analyses of the response of Amazonian primate assemblages to hunting have failed to control for the important and confounding effects of forest productivity and structure.

In this paper, we analyse a comprehensive data set on the structure of 56 primate communities of northern South America, derived primarily from a large-scale series of line transect surveys, that provides a replicated experiment to examine the evidence for compensatory release. We examine relationships between the population biomass of different size classes of diurnal primates, and hunting pressure. We consider possible compensatory increases of nonhunted medium-bodied and small-

bodied species, in response to declines in hunted medium-bodied and large-bodied species. The analyses control for forest types. This takes into account other nested environmental variables such as forest structure and soil fertility, which have a large effect on the species composition and total biomass of primate communities (Peres 1997, 1999a, 1999c).

## Materials and methods

### The data set

Data on forest type, degree of hunting pressure and the composition and population density of all co-occurring diurnal primate species were available from 56 forest sites in Brazil, Peru, Bolivia, Guyana, Surinam and French Guiana. This data set includes 20 sites from western Amazonian white-water river catchments that are discussed in detail in Peres (1997), extended to include a further 36 sites available from the literature, and distributed throughout the Amazon basin and the Guianan shields (Peres 1999a). These include 41 sites from central-western Amazonia (west of the Negro and Madeira Rivers), 9 sites from eastern Amazonia (east of the Madeira River) and 6 sites from the Guianan shields (north of the Amazon and east of the Negro River). Forest sites considered here differed in the degree to which they had been hunted, but otherwise consisted of entirely undisturbed primary forest. The location and characteristics of each site are shown in Appendix 1; sources of the primate composition and abundance data may be found in Peres (1999a).

Primate density estimates for 26 of the 56 forest sites were obtained from a standardized series of diurnal line-transect surveys, using census methodology described in Peres (1997, 1999a). This excludes only a single nocturnal primate species (night monkeys, *Aotus* spp.) which occurred at most sites. Most of the additional data were compiled from similar line-transect censuses sharing a robust sampling effort, and in a few cases from more intensive synecological studies reporting the densities of all primate species co-occurring at a single site on the basis of group follows. In all cases, the spatial scale at which censuses were conducted was equivalent for all sympatric species, thus avoiding systematic distortions in abundance-body size relationships (Blackburn and Gaston 1996). In addition, we excluded from the analysis any survey failing to consider the full complement of diurnal primate species occurring at a given site, or consisting of a relatively small sampling effort, which presumably provided less reliable density estimates.

In order to calculate population biomass, we used the mean weight of individuals of each species, defined as 80% of the average body mass of adult males and females in different Amazonian populations (see Ford and Davies 1992; Peres 1999a and references therein).

### Ecospecies classification

This study is concerned with the functional composition of primate communities. In a number of cases, ecologically similar, congeneric species present a parapatric distribution with species substitution at sharp range boundaries. To remove such biogeographic effects from between-site comparisons, functionally equivalent primate species were aggregated within discrete ecological groups (hereafter, ecospecies). The ecospecies classification follows that derived by Peres (1997, 1999a) based on extensive information on species morphology, behavioral ecology, patterns of resource use and geographic distribution. For the purposes of analysing primate community structure, biomass data were aggregated within three size categories: (1) small-bodied (<1.5 kg); (2) medium-bodied (1.5–4 kg); and (3) large-bodied (>4 kg). Ecospecies within each of these size classes tend to share a more similar feeding ecology than those across classes (Mittermeier and

Roosmalen 1981; Terborgh 1983; Soini 1986; Peres 1994a). The classification of primate taxa across ecospecies and size classes is shown in Table 1.

Although all large-bodied ecospecies are selectively hunted (Peres 1990), only some medium-bodied ecospecies are consistently taken (*Cebus apella*, *C. albifrons*, *Chiropotes*), while others (*Pithecia*, *Cacajao*) are largely ignored by subsistence hunters (Redford and Robinson 1987; Peres 1990). As compensatory responses are more likely to occur within groups of ecologically similar species, responses to hunting were investigated separately for hunted and nonhunted medium-bodied ecospecies.

Within the group of selectively hunted medium-sized ecospecies, *Cebus apella* and *C. albifrons* are generalist omnivores, relying heavily on mature fruit pulp (Terborgh 1983; Peres 1994a), whereas *Chiropotes* are specialized seed predators (van Roosmalen et al. 1988). On the other hand, both of the nonhunted medium-sized (pitheciine) ecospecies are seed specialists (*Cacajao*: Ayres 1986; *Pithecia*: Peres 1993a). The two nonhunted pitheciine genera (ecospecies), *Pithecia* and *Cacajao*, co-occur at a broad geographical scale, however, their habitat distribution is largely mutually exclusive, with *Pithecia* occurring in both flooded and unflooded forests whereas *Cacajao* is largely restricted to flooded forests (Ayres 1986; Peres 1997). The geographic distribution of the selectively hunted *Chiropotes* and the mostly nonhunted *Cacajao* is also largely mutually exclusive, so that only one or the other of these ecospecies occurs within a given site, reducing the opportunity for compensatory effects between these two ecospecies. However, the selectively hunted capuchin monkeys (*Cebus* spp.) are ubiquitous and co-occur with either of the nonhunted pitheciines. We therefore examine the data for evidence for compensatory release, as *Pithecia* may respond to the hunting of *Chiropotes*, while a weaker response of both *Pithecia* and *Cacajao* may occur to hunting of *Cebus* spp.

### Hunting pressure

The level of hunting pressure imposed on the primate community of each forest site was determined independently of biotic data collection. For the 26 sites surveyed by Peres (1989, 1990, 1997, 1999a), hunting pressure was categorized on the basis of (1) semi-structured interviews with at least two independent long-term resident hunters per site; (2) the frequency at which direct evidence of hunting was found (e.g. shotguns sounds heard; hunting trails; "waiting" stations; old campsites) during census work; and (3) present and past human population densities quantified on the basis of the number of households in each area during the 1960s and 1970s (derived from 1:250,000 maps: RADAM 1973–1981). For all additional sites surveyed by other investigators, hunting pressure was determined from information explicitly provided within each published or unpublished data source, or through personal communications to C.A. Peres. Hunting pressure was categorized according to four levels:

1. *None*. "Pristine" sites entirely uninhabited by forest dwellers and showing no enduring evidence of hunting activity (see Peres, in press). These sites had not been accessible to hunters for at least 50 years at the time of surveys by virtue of either geographic isolation or strict protection. In the case of remote upland forests, access for census work was achieved using helicopters subcontracted to the Brazilian Oil Company (Petrobrás).
2. *Light*. Forest sites located in areas with a low density of human residents (<0.2 person km<sup>-2</sup>) and only sporadically visited by hunters during at least 50 years prior to censuses.
3. *Moderate*. Forest sites sustaining moderate human densities of 0.2–1.0 person km<sup>-2</sup>, and characterized by intermediate frequencies at which they were visited by hunters over at least 100 years prior to censuses.
4. *Heavy*. Forest sites subjected to continuous, persistent hunting pressure for at least 100 years prior to censuses, and sustaining a high human population density (>1.0 person km<sup>-2</sup>).

Hunting at all sites was primarily practised for subsistence purposes and with the aid of firearms (i.e. shotguns), rather than traditional weapons. Because of the long-term history of hunting at

**Table 1** Aggregation of taxonomic species into ecospecies and size classes

Ecospecies	Ecospecies English name	Taxonomic species grouped <sup>a</sup>	Mean body mass (kg)
Small-bodied species (<1.5 kg)			
<i>Cebuella</i>	Pygmy marmosets	<i>Cebuella pygmaea</i>	0.15
<i>Callithrix</i>	Marmosets	<i>Callithrix</i> (all congeners)	0.36
<i>S. fuscicollis</i>	Saddle-back tamarins	<i>Saguinus fuscicollis</i> , <i>S. nigricollis</i>	0.39
<i>S. mystax</i>	Moustached, red-bellied, emperor and midas tamarins	<i>Saguinus mystax</i> , <i>S. labiatus</i> , <i>S. imperator</i> , <i>S. midas</i>	0.51
<i>Callimico</i>	Goeldi's monkeys	<i>Callimico goeldii</i>	0.59
<i>Saimiri</i>	Squirrel monkeys	<i>Saimiri</i> (all congeners)	0.94
<i>C. cupreus</i>	Red and dusky titi monkeys	<i>Callicebus</i> (all congeners except <i>C. torquatus</i> )	1.05
<i>C. torquatus</i>	Collared titi monkeys	<i>Callicebus torquatus</i>	1.20
Medium-bodied species (1.5–4.0 kg)			
Selectively hunted			
<i>Chiropotes</i>	Bearded saki monkeys	<i>Chiropotes satanas</i> , <i>C. albinasus</i>	2.70
<i>C. apella</i>	Brown capuchins	<i>Cebus apella</i>	2.91
<i>C. albifrons</i>	White-fronted and other non- <i>apella</i> capuchins	<i>Cebus albifrons</i> , <i>C. olivaceus</i> , <i>C. kaapori</i>	2.70
Nonhunted			
<i>Pithecia</i>	Saki monkeys	<i>Pithecia</i> (all congeners)	1.80
<i>Cacajao</i>	Uakaries	<i>Cacajao calvus</i> , <i>C. melanocephalus</i>	3.17
Large-bodied species (>4 kg)			
<i>Alouatta</i>	Howler monkeys	<i>Alouatta seniculus</i> , <i>A. belzebul</i>	6.50
<i>Lagothrix</i>	Woolly monkeys	<i>Lagothrix lagotricha</i>	8.71
<i>Ateles</i>	Spider monkeys	<i>Ateles paniscus</i> , <i>A. chamek</i> , <i>A. marginatus</i> , <i>A. belzebuth</i>	9.02

<sup>a</sup> Includes only those diurnal species occurring at the 56 forest sites considered here

moderately or heavily hunted sites, their large-bodied primate populations had long been depressed or driven to extinction, thus presumably allowing a sufficient time lag for any potential density compensation of the residual species to occur.

#### Forest types

The composition and biomass of primate communities was related to the intensity of subsistence hunting while controlling for differences in forest type. Different forest types of lowland Amazonia and the Guianan shields vary considerably in soil fertility, hydrological regime, primary productivity, forest structure, resource seasonality and spatio-temporal heterogeneity (Peres, in press). As these variables are highly intercorrelated, and largely nested within forest types, it is not appropriate to attempt to control for each of them independently. Rather, forest types are included as a single ordinal variable according to the following four categories:

1. *Oligotrophic terra firme forests (OTF)*. Unflooded forest located on oligotrophic soils in remote interfluvial regions of the Amazon and the Guianan shields. Oligotrophic soils are typically characterized by a closed nutrient cycling, and have been largely deprived of sedimentation since Pre-Cambrian days.
2. *Mesotrophic terra firme forest (MTF)*. Unflooded forests atypically sustained by nutrient-rich upland soils, or located immediately adjacent to white-water floodplains, or alluvial headwater forests. These areas have probably received more recent deposition of mineral nutrients than those in remote interfluvial areas, resulting in mesotrophic soils.
3. *Alluvial forests (ALL)*. Floodplain forests under the direct influence of white-water tributaries (or subtributaries) of the Amazon, which are typically subjected to supra-annual flash floods (every 4–8 years) of relatively short duration (a few days to several weeks).

4. *Várzea forests (VAR)*. Seasonally inundated forests partially immersed into the broadened meandering channels of suspension-rich white-water rivers for as long as half of the year. These sites include both Pleistocene or Holocene flooded forests and are characterized by a sustained annual influx of alluvial deposits of Andean origin, high soil fertility and high primary productivity.

#### Data analysis

The structure of the data set is summarized in Table 2. Of the total set of 56 sites considered here, 20 were drawn from OTF, 24 from MTF and 12 from floodplain forests (ALL and VAR). In relation to the level of hunting pressure, 29 sites were categorized as either nonhunted or only lightly hunted, while 27 received either moderate or heavy hunting pressure. Pristine sites with no hunting occurred primarily in remote and inaccessible interfluvial areas, thus the majority of sites in this category are in OTF forests (9 of 11 OTF sites).

The entire matrix of 56 sites by 16 ecospecies, weighed according to the density estimate of each ecospecies at each site, was analysed by canonical correspondence analysis (CCA), performed using CANOCO version 3.11.5 (ter Braak 1987–1992). CCA is a technique that relates community composition to known variation in underlying environmental gradients to which all species respond. Ecospecies data were related to both forest type and hunting pressure, entered as environmental variables. The choice of coefficients in constructing the environmental axes is that which maximizes the dispersion of the species scores, so that variation in the species data may be directly related to the environmental variables (Jongman et al. 1995). CCA can be used in combination with de-trended correspondence analysis (DCA) to infer whether the measured environmental variables can account for a large variation in the species data.

**Table 2** Summary of the primate community data set

Level of hunting pressure	Forest types				
	Oligotrophic terra firme (OTF)	Mesotrophic terra firme (MTF)	Alluvial forest (ALL)	Várzea forest (VAR)	
1 None	9	1	1	0	11
2 Light	3	9	3	3	18
3 Moderate	4	5	1	4	14
4 Heavy	4	9	0	0	13
Total number of sites	20	24	5	7	56

Additional analyses of the biomass density of each primate size class were conducted to examine hunting and possible compensatory effects while controlling for forest type. These analyses were carried out separately for inundated (ALL and VAR) and terra firme forests (OTF and MTF), for the following reasons: the range of hunting pressure recorded differed between these two forest categories (1–3 for inundated, 1–4 for terra firme); forest productivity is much greater in inundated forests due to sediment supply and this may influence the strength and importance of competition and compensatory effects; inundated forests, particularly VAR, typically have a simplified understorey structure with consequences for food resources and primate community structure. The hunting pressure variable is ordinal, with four increasing levels, suggesting the use of non-parametric statistical tests. However parametric analyses were considered preferable because these have greater statistical power. Consequently, hunting pressure levels 1 (no hunting) and 2 (light hunting) were merged to reduce the number of levels of this ordinal variable. As no inundated sites received heavy hunting pressure, the hunting variable for these forest types becomes a two-state categorical variable that can be analysed by *t*-tests or as a factor within analyses of variance that control for forest type. For terra firme forests all four levels of hunting pressure were represented; merging categories 1 and 2 thus results in three levels of hunting pressure that were considered within a single categorical variable by analyses of variance. Where effects of hunting were significant within analysis of variance, differences between different levels of hunting pressure were examined by a Tukey multiple comparison test on group means. Means and standard errors presented here are of untransformed data, however, all analyses of variance were conducted on  $\log(1+x)$  transformed biomass data to satisfy the condition of homoscedasticity.

### Biogeography

Sites from central-western Amazonia (coded as group 1) tend to have higher species richness than those in the Guianan shields and eastern Amazonia (coded as group 2). All but one of the inundated sites were obtained from biogeographical region 1, thus it was not possible to include biogeography within the CCA analysis of primate community composition. Terra firme sites are drawn from both biogeographic regions (region 1,  $n=30$ ; region 2,  $n=14$ ), thus potentially confounding effects of biogeography were controlled for within analyses of variance.

## Results

The number of ecospecies present in the primate assemblage of a particular site varies considerably (mean=7.7, SD=2.7, range 2–12,  $n=56$ ). In part this reflects differences in the species assemblages of different forest types. In particular, várzea sites support significantly fewer ecospecies ( $4.86\pm 1.35$ ,  $n=7$ ) than alluvial

( $6.80\pm 3.27$ ,  $n=5$ ), MTF ( $8.58\pm 2.32$ ,  $n=24$ ) or OTF forests ( $7.75\pm 2.77$ ,  $n=20$ ) (ANOVA,  $F_{3, 52}=4.25$ ,  $P=0.009$ , Tukey multiple comparison test; várzea differs from all other groups  $P<0.05$ , all other groups homogenous  $P>0.05$ ). However, the variation in ecospecies richness also reflects the biogeography of successive interfluvial regions, with a greater  $\alpha$ -diversity occurring towards western Amazonia (Ayres and Clutton-Brock 1992; Peres and Janson 1999). Between-site differences in species richness within an assemblage of trophically similar species may affect species packing, realized niche and the degree of compensatory responses. However, within the data set there was no correlation between ecospecies richness and hunting pressure (all terra firme forests combined,  $r_s=-0.068$ ,  $P=0.658$ ,  $n=44$ ; all floodplain forests combined,  $r_s=0.043$ ,  $P=0.886$ ,  $n=12$ ). Thus variation in ecospecies richness will not result in systematic bias in tests for compensatory responses to hunting.

### Canonical ordination of primate communities in relation to forest type and hunting pressure

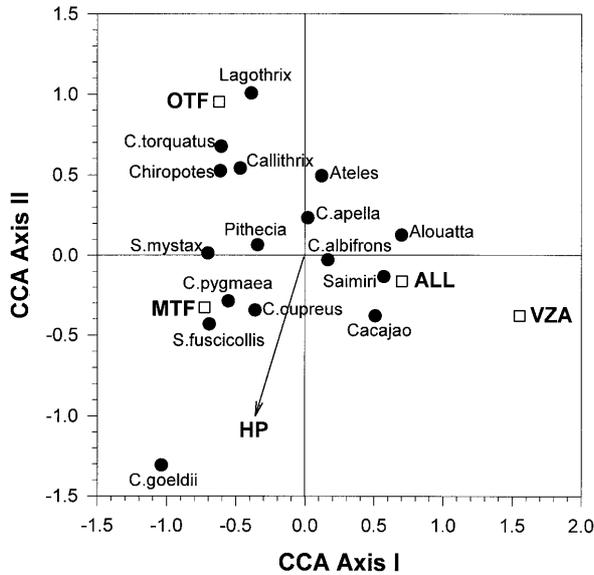
The first two axes of this CCA explained 26.0% of the variance within the ecospecies data (sum of all eigenvalues=1.500,  $\lambda_1=0.294$ ,  $\lambda_2=0.096$ ); this is the cumulative variance in the ecospecies matrix explained by linear combinations of the forest type and hunting pressure variables. The next two axes of the CCA explained only a further 2.5% of the variance in the ecospecies data, and were thus discarded. The figure of 26.0% of variance explained by the first two CCA axes compares favourably with that of 39.5% explained by the first two axes of an unconstrained ordination of the ecospecies data, independently of environmental variables, using DCA (sum of all eigenvalues =1.500,  $\lambda_1=0.397$ ,  $\lambda_2=0.195$ ).

The species-environment correlation, the correlation between the site scores that are weighted averages of the species scores and the site scores that are a linear combination of the soil variables, is 0.878 for the first axis and 0.742 for the second. Both the first axis and the overall CCA were significant at  $P<0.0001$  (Monte Carlo test; 9999 random permutations).

One sample was identified as having an extreme environment space influence (Cahuana Island, Peru); excluding this site increased the explanatory power of the ordination only slightly, so that the first two axes explained

**Table 3** Canonical correspondence analysis (CCA): inter-set correlations of forest type and hunting pressure variables with the first two species axes of CCA, and the canonical coefficients and associated *t*-values (in parentheses) of each environmental variable with each of the first two axes

Variable	Inter-set correlations		Canonical coefficients ( <i>t</i> -values)	
	Axis 1	Axis 2	Axis 1	Axis 2
OTF	-0.317	0.409	-0.996 (10.384)	0.398 (2.503)
MTF	-0.522	-0.198	-1.062 (10.833)	0.208 (1.280)
ALL	0.216	-0.042	-0.322 (3.636)	-0.124 (0.842)
VAR	0.764	-0.157	0.000 (0)	0.000 (0)
HP	-0.287	-0.674	-0.271 (3.245)	-0.912 (6.577)



**Fig. 1** Canonical correlation analysis (CCA) species ordination showing the location of each ecospecies in relation to CCA axes I and II. Identities of ecospecies are given in Table 1. The effects of the environmental variables are indicated by the centroids corresponding to each forest type and by a vector for the bi-plot score of the quantitative variable HP, hunting pressure

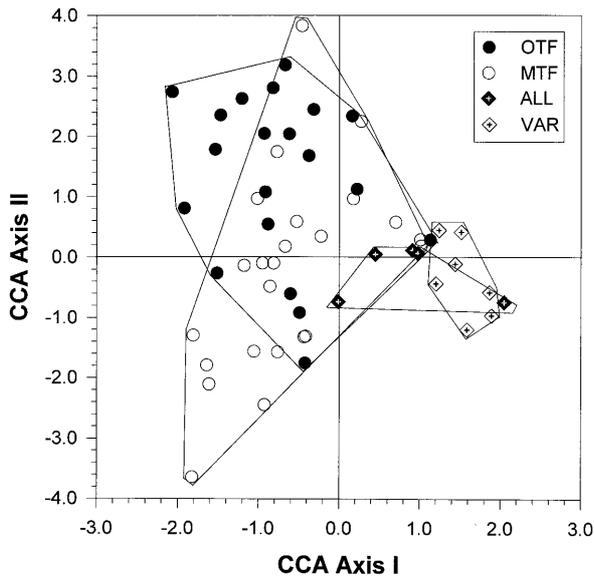
26.7% of the variance of the species data, while the intra-set correlations of soil variables with the first two axes changed only negligibly. Consequently we present CCA results for the full data set.

Table 3 shows the inter-set correlations of forest type and hunting pressure with the first two environmental axes of the CCA. These are the correlation coefficients between the environmental variables and the species axes consisting of sample scores (ter Braak 1987–1992). In addition, for each of these environmental variables the canonical coefficients for each of the first two CCA axes are shown with their associated *t*-values. These are the coefficients of a weighted multiple regression of sample scores on the standardized environmental variables. As these are canonical coefficients and not regression coefficients, *t*-values are included for exploratory use and cannot be used to test the significance of the coefficients (ter Braak 1987–1992). The first axis was largely determined by forest type variables, while hunting pressure was the variable with the strongest loading on the second CCA axis.

Primate ecospecies responses to habitat gradients and hunting pressure are represented by their location on the first two CCA axes (Fig. 1). Environmental effects are indicated by the centroids of each of the forest type variables and by a vector for the quantitative variable “hunting pressure” (HP). The centres of distributions of the 16 ecospecies ordered strongly along the first axis in response to forest type, with considerable scatter along the second axis, which was more influenced by hunting pressure. A cluster of ecospecies typical of várzea forests – squirrel monkeys (*Saimiri* spp.), white-fronted capuchins (*Cebus albifrons*), uakaries (*Cacajao* spp.) and howler monkeys (*Alouatta* spp.) – could be distinguished along the second axis, associated with the centroids of alluvial (ALL) and várzea (VAR) forests. A group of terra firme forest specialists, including marmosets (*Callithrix* spp.), collared titi monkeys (*Callicebus torquatus*) and bearded sakis (*Chiropotes* spp.), were clearly associated with nutrient-poor terra firme forests (OTF). Effects of hunting pressure may be examined by considering the orthogonal projections of ecospecies onto the HP vector. The ecospecies most susceptible to hunting in Amazonian and Guianan forests (Peres 1990) – woolly monkeys (*Lagothrix* spp.), spider monkeys (*Ateles* spp.) and to a lesser extent howler monkeys (*Alouatta* spp.) – tended to be negatively associated with the HP vector. In contrast, all small-bodied ecospecies were positively associated with the HP vector, with the exception of squirrel monkeys (*Saimiri* spp.). Goeldi’s monkey (*Callimico goeldii*) was the greatest outlier of all ecospecies, probably because it is extremely rare, largely restricted to western Amazonian bamboo forests (here classified as MTF), and consistently ignored by subsistence hunters.

The location of all sites in relation to the first two axes of the CCA shows a large overlap between the biplot scores corresponding to the two classes of terra firme forests (OTF and MTF), and a disjunct cluster corresponding to várzea forests (VAR) (Fig. 2). As expected, alluvial floodplain sites (ALL) fell intermediately between terra firme and várzea forests, as they do geochemically and in a number of habitat characteristics.

However, clearly distinguishing the effects of hunting pressure on community structure by CCA alone is problematic, as hunting pressure and forest type are not fully independent due to imbalances in the structure of the data set (Table 2). Further analyses were thus undertaken to test for compensatory effects of reduction in large-bodied primate biomass while controlling for forest type.



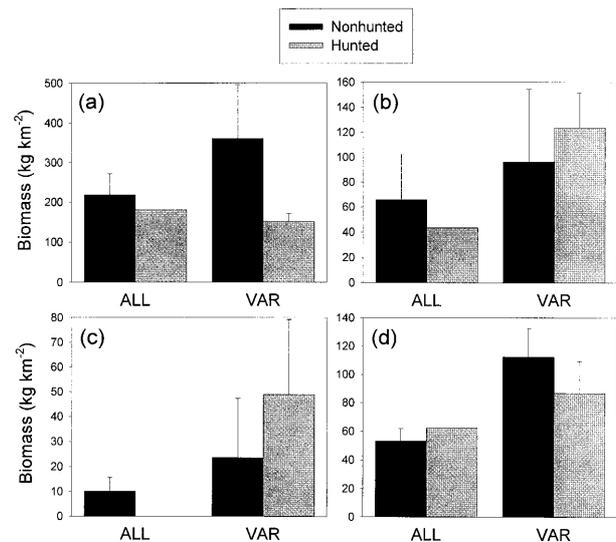
**Fig. 2** CCA site ordination. The location of each forest category in relation to CCA axes I and II is shown by the *minimum convex polygons* formed by the outlying samples. Centroids of forest types and vector of hunting pressure are shown in Fig. 1

#### Compensatory responses of primate biomass in inundated forests: effects of hunting pressure and forest type

As no floodplain sites received heavy hunting pressure, effects of hunting pressure were reduced to a simple contrast between two groups: nonhunted (merging sites subjected to no or light hunting) versus moderately hunted. Due to small sample sizes for floodplain forests (Table 2) statistical tests of effects of hunting and forest type have low statistical power, with high chance of type II error. Although most contrasts were non-significant, it is useful to compare trends against the expected direction of effects of selective hunting and potential compensatory release.

The mean total biomass of primates appeared to be higher in várzea ( $501 \pm 83.3 \text{ kg km}^{-2}$ ) than in alluvial forest ( $317.4 \pm 122.0 \text{ kg km}^{-2}$ , two-way analysis of variance controlling for hunting,  $R^2=0.237$ ) but this difference was not significant (effect of forest type,  $F_{1,8}=1.59$ ,  $P=0.242$ ). Likewise, although hunting appeared to reduce total primate biomass, this effect was also not significant (ALL: nonhunted  $n=4$ , mean  $=347.6 \pm 94.5 \text{ kg km}^{-2}$ , hunted  $n=1$ ,  $287.1 \text{ kg km}^{-2}$ ; VAR: nonhunted  $n=3$ , mean  $=592.7 \pm 181.4 \text{ kg km}^{-2}$ , hunted  $n=4$ , mean  $=410.9 \pm 79.9 \text{ kg km}^{-2}$ ; effect of hunting,  $F_{1,8}=0.67$ ,  $P=0.589$ ).

Figure 3 shows the biomass of different groups of primate ecospecies, in relation to inundated forest type and hunting pressure. Results of analyses of variance that consider the effects of hunting for each forest type and primate size class are shown in Table 4. For each of the four primate groups, mean biomass predicted for várzea by two-way analysis of variance (controlling for hunt-



**Fig. 3** Primate biomass density for **a** large-bodied, **b** hunted medium, **c** nonhunted medium and **d** small-bodied species in alluvial (ALL) and várzea (VAR) floodplain forests in relation to two levels of hunting pressure. For nonhunted sites only, results of *t*-tests (pooled variance) contrasting biomass density in ALL ( $n=4$ ) versus VAR ( $n=3$ ) sites are as follows: large-bodied  $t=1.10$ ,  $P=0.321$ ; hunted medium-bodied  $t=0.47$ ,  $P=0.661$ ; nonhunted medium-bodied  $t=0.65$ ,  $P=0.545$ ; small-bodied  $t=2.98$ ,  $P=0.031$ . For VAR sites only, results of *t*-tests (pooled variance) contrasting biomass density in moderately hunted ( $n=3$ ) versus nonhunted ( $n=4$ ) sites, are as follows: large-bodied  $t=2.29$ ,  $P=0.070$ ; hunted medium-bodied  $t=0.79$ ,  $P=0.468$ ; nonhunted medium-bodied  $t=1.52$ ,  $P=0.190$ ; small-bodied  $t=0.97$ ,  $P=0.376$

ing) was greater than that for alluvial sites. Likewise, for seven of the eight contrasts within levels of hunting pressure, mean biomass in várzea sites was greater than that in alluvial sites. However, within two-factor analyses of variance controlling for hunting, forest type was not significant for any of the primate groups. Because only one hunted alluvial site was available, biomass was also compared between nonhunted alluvial and várzea sites. Biomass did not differ significantly between these two forest types for large and medium-bodied primates, whether or not they were hunted (*t*-tests,  $P>0.3$  in each case; Fig. 3). However, for small-bodied primates, biomass in várzea sites was significantly greater than that in alluvial sites ( $P=0.031$ ). Finally, a two-factor analysis of variance of all nonhunted sites ( $n=28$ ) that controlled for primate group (small, hunted medium, nonhunted medium, large) was not significant for forest type ( $R^2=0.603$ ,  $F_{1,20}=0.80$ ,  $P=0.381$ ).

Moderate hunting was expected to selectively reduce the biomass density of large-bodied primates. Hunted medium-bodied species will be hunted less intensively in these sites and also have a higher rate of intrinsic population increase compared to large-bodied species. We thus expect the biomass density of hunted medium-bodied species to be reduced less by moderate hunting than that of large-bodied species. In addition, the reduction of medium-bodied species by hunting may be offset by any compensatory response. No significant effects of

**Table 4** ANOVAs relating biomass density of each primate size class to forest type and hunting pressure for floodplain (*ALL*, *VAR*) and terra firme (*OTF*, *MTF*) forests. Means ( $\pm$ SE) for each level of hunting pressure and forest type are shown in Figs. 3,4 respectively

Primate size class	$R^2$	Forest type (FT)		Hunting pressure (HP)		FT×HP		Biogeographic Covariate	
		$F_{1,8}$	$P$	$F_{1,8}$	$P$	$F_{1,8}$	$P$		
Floodplain forests									
Large	0.343	0.172	0.690	1.592	0.243	1.051	0.335	–	–
Hunted medium	0.204	0.861	0.381	0.288	0.606	0.002	0.963	–	–
Nonhunted medium	0.380	1.925	0.203	0.014	0.908	2.829	0.131	–	–
Small	0.455	3.466	0.100	0.050	0.830	0.945	0.360	–	–
Primate size class	$R^2$	$F_{1,37}$	$P$	$F_{2,37}$	$P$	$F_{2,37}$	$P$	$F_{1,37}$	$P$
Terra firme forests									
Large	0.779	4.805	0.035	63.675	<0.001	5.953	0.006	6.142	0.018
Hunted medium	0.264	0.907	0.347	5.759	0.007	0.192	0.827	0.444	0.509
Nonhunted medium	0.594	<0.001	0.992	3.088	0.058	0.526	0.596	40.193	<0.001
Small	0.359	1.499	0.229	0.658	0.524	0.510	0.605	8.958	0.005

hunting were found for any species group within two-way analyses of variance controlling for forest type (Table 4). As only one hunted alluvial site was available, the effect of hunting was also considered for várzea sites alone. Figure 3a shows an apparent reduction in the biomass of large-bodied species, which was significant in hunted várzea sites ( $t$ -test,  $P=0.070$ ; or  $P<0.05$  in a one-tailed test of the hypothesis that hunting reduces the biomass of large primates). However, the biomass of hunted medium-bodied species appears to be greater in várzea sites, although this effect was not significant ( $t$ -test,  $P>0.4$ ).

It was hypothesized that a reduction in large-bodied primates may lead to density compensation in the biomass of nonhunted medium-bodied primates. In contrast, density compensation in small-bodied primates may be less likely, due to greater differences in diet and ecology compared to large-bodied ecospecies. Biomass of nonhunted medium-bodied species appeared to be greater in hunted várzea forests (Fig. 3c), although this was not significant within analyses of variance controlling for forest type. When this contrast was restricted to várzea sites, the greater biomass of nonhunted medium-bodied primates in moderately hunted sites was near significant ( $t$ -test, one-tailed  $P<0.1$ ). For small-bodied primates, mean biomass was again lower in hunted than in nonhunted várzea sites, but this difference was not significant ( $t$ -test,  $P>0.3$ ).

All floodplain forests for which biomass data were available are located in western Amazonia, with the single exception of Marajó Island, an alluvial gallery forest of the Amazon estuary. Excluding this site from analyses did not change the qualitative nature or significance of any contrasts when controlling for forest type, and this site had already been excluded from contrasts that considered várzea sites only.

#### Compensatory responses of primate biomass in terra firme forests: effects of hunting pressure and forest type

Data for primate biomass density were available from 44 terra firme sites, compared to just 12 sites from floodplain forests, allowing more detailed and robust analyses. Sites were available from both western (OTF:  $n=11$ , MTF:  $n=19$ ) and eastern Amazonia (OTF:  $n=9$ , MTF:  $n=5$ ). In a matrix of forest type versus hunting pressure (aggregated into two levels: “nonhunted”, combining no and light hunting; and “hunted” combining moderate and heavy hunting), sites from each of the two biogeographic regions occurred in each cell. This allows inclusion of biogeography as an additional categorical factor in analyses of variance (see Table 5). However, effects of moderate and heavy hunting showed important qualitative differences, such that it was preferable to retain these as separate categories in analyses of hunting effects (giving three levels of hunting pressure: “nonhunted”, combining no or light hunting; “moderately hunted”; and “heavily hunted”). Where hunting pressure was modelled as a factor with three levels against two levels of forest type, one of the six cells does not contain sites from both biogeographic regions. Therefore, biogeography was included as a covariate rather than as a categorical variable in such models. Biogeography was a significant covariate in three of the four models for different primate groups and is retained in all models presented here. The exclusion of biogeography×hunting pressure and biogeography×forest type interaction terms, when considering biogeography as a covariate rather than as a categorical variable, is justified; as in full categorical models with just two levels of hunting pressure these interaction terms were non-significant (for each of the four primate groups, all biogeography×forest and biogeography×hunting interaction terms have  $P>0.2$ , see Table 5).

Significant biogeographical effects result from higher biomass densities in western compared to eastern Amazonia (Table 5). The large-bodied, hunted medium-bodied and small-bodied primate ecospecies are represented

**Table 5** Effects of biogeography within ANOVAs of primate biomass density in 44 Amazonian terra firme forests, contrasting two categories of forest type (OTF and MTF) and hunting pressure (no

or light hunting vs. moderate or heavy hunting). Mean ( $\pm$ SE) biomass in each biogeographic region was predicted from an ANOVA model controlling for forest type and hunting pressure

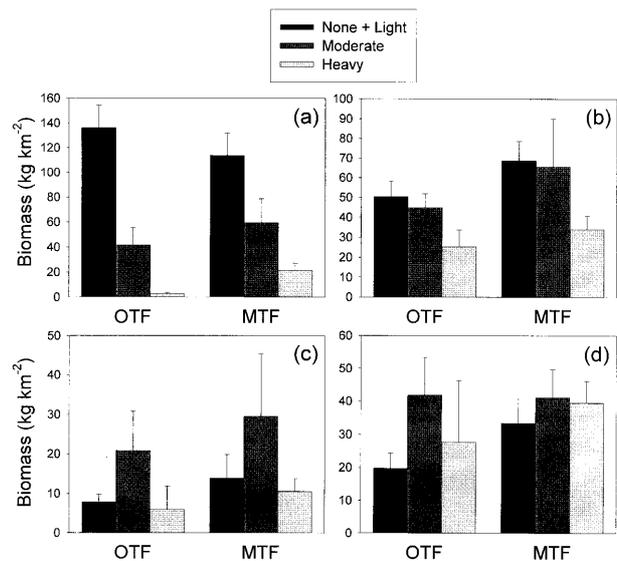
Size class	Biomass density (kg km <sup>-2</sup> )		<i>R</i> <sup>2</sup>	Effects	<i>F</i> <sub>1,36</sub>	<i>P</i>
	West <sup>a</sup> ( <i>n</i> =30)	East <sup>b</sup> ( <i>n</i> =14)				
Large-bodied	96.5 $\pm$ 8.1	47.9 $\pm$ 13.7	0.610	Forest type (FT)	1.21	0.278
				Biogeography (BG)	4.11	0.050
				Hunting pressure (HP)	33.87	<0.001
				FT $\times$ BG	0.59	0.448
				FT $\times$ HP	2.66	0.112
				HP $\times$ BG	0.00	0.955
				FT $\times$ HP $\times$ BG	0.39	0.538
Hunted medium-bodied	54.4 $\pm$ 6.1	47.2 $\pm$ 10.3	0.225	Forest type (FT)	2.45	0.126
				Biogeography (BG)	0.13	0.718
				Hunting pressure (HP)	2.33	0.136
				FT $\times$ BG	1.21	0.279
				FT $\times$ HP	0.04	0.841
				HP $\times$ BG	0.45	0.507
				FT $\times$ HP $\times$ BG	1.38	0.249
Nonhunted medium-bodied	18.9 $\pm$ 3.3	0.8 $\pm$ 5.5	0.587	Forest type (FT)	0.45	0.508
				Biogeography (BG)	39.90	<0.001
				Hunting pressure (HP)	1.02	0.319
				FT $\times$ BG	0.99	0.327
				FT $\times$ HP	0.28	0.601
				HP $\times$ BG	0.42	0.519
				FT $\times$ HP $\times$ BG	1.29	0.264
Small-bodied	38.7 $\pm$ 3.7	19.4 $\pm$ 6.3	0.430	Forest type (FT)	4.18	0.048
				Biogeography (BG)	8.54	0.006
				Hunting pressure (HP)	1.06	0.311
				FT $\times$ BG	1.38	0.247
				FT $\times$ HP	0.11	0.747
				HP $\times$ BG	0.49	0.488
				FT $\times$ HP $\times$ BG	3.85	0.058

<sup>a</sup> West includes all western Amazonian sites

<sup>b</sup> East includes all sites east of the Rio Madeira and Rio Negro

in both regions. Although biomass densities tend to be lower in eastern Amazonia, in each case the effects of hunting and forest type are consistent between regions. In contrast, biomass of nonhunted medium-bodied primates was negligible in this region. For this primate group, analyses were repeated restricting the contrasts to western Amazonia.

The aggregate biomass of each primate size class in relation to hunting pressure and forest type (Fig. 4) was contrasted using analyses of variance, while controlling for biogeography in the case of the more numerous terra firme sites (Table 4). Although hunting had a significant effect on the biomass of both large-bodied ( $P<0.001$ ) and hunted medium-bodied primates ( $P=0.007$ ) these two groups differed in their response to increasing intensities of subsistence hunting (Fig. 4a,b). The biomass of large-bodied primates declined significantly with moderate hunting (Tukey,  $P<0.001$ ) and a further significant reduction occurred with heavy hunting (contrast with moderately hunted:  $P<0.001$ ; with nonhunted:  $P<0.001$ ). For hunted medium-bodied species, the biomass in moderately hunted sites did not differ significantly from that in nonhunted sites (Tukey means contrast,  $P=0.689$ ), but a significant reduction did occur in heavily hunted sites (contrast with nonhunted:  $P=0.005$ ; with moderately



**Fig. 4** Primate biomass density for **a** large-bodied, **b** hunted medium, **c** nonhunted medium and **d** small-bodied species in oligotrophic (OTF) and mesotrophic (MTF) terra firme forests in relation to three levels of hunting pressure

hunted:  $P=0.123$ ). Biomass of hunted medium-bodied species appeared to be higher in nonhunted and moderately hunted forests in mesotrophic terra firme forests compared to non-flooded oligotrophic forests, but the effects of forest type were not significant ( $P=0.347$ , Fig. 4b). For large-bodied primates, forest type had a significant effect (two-way analysis of variance with biogeography as a covariate; adjusted means  $\pm$  SE, OTF:  $60.2\pm 12.1$  kg km<sup>-2</sup>; MTF:  $64.8\pm 10.2$  kg km<sup>-2</sup>,  $P=0.035$ ). Furthermore, the effect of subsistence hunting on the biomass of large-bodied primates differed between the two forest types (forest $\times$ hunting interaction,  $P=0.006$ ). A Tukey multiple contrast of all 6 cell means shows that biomass did not differ significantly between the two forest types where there is no hunting (OTF:  $136.4\pm 18.3$  kg km<sup>-2</sup>, MTF:  $113.8\pm 18.2$  kg km<sup>-2</sup>, means contrast  $P=0.990$ ), or moderate hunting (OTF:  $41.6\pm 13.9$  kg km<sup>-2</sup>, MTF:  $59.4\pm 19.1$  kg km<sup>-2</sup>,  $P=0.999$ ). However, heavily hunted mesotrophic terra firme forests retained a greater residual biomass of large-bodied species ( $21.3\pm 5.9$  kg km<sup>-2</sup>) than did oligotrophic terra firme forests ( $2.5\pm 1.3$  kg km<sup>-2</sup>,  $P=0.008$ ).

The substantial and significant reduction of the biomass of large-bodied and hunted medium-bodied species that occurred with increasing levels of hunting pressure (Fig. 4a,b) provides an experiment within which to test for density compensation. Again, as with inundated forests, compensatory responses are primarily expected amongst "nonhunted" medium-bodied primates, but possibly also amongst small-bodied primates. For both of these groups, there was a consistent pattern for biomass to increase from nonhunted to moderately hunted sites, but to then decrease in heavily hunted sites (Fig. 4c,d). The effect of hunting was not significant for small-bodied primates ( $P=0.524$ ). For nonhunted medium-bodied species, the effect of hunting was near significant ( $P=0.057$ ). As no significant effects of forest type ( $P=0.992$ ) or forest $\times$ hunting interaction ( $P=0.596$ ) were detected, analysis of variance was repeated without including forest type ( $R^2$  model fit decreased from 0.594 to 0.582, but this was not significant according to the ratio of change in residual SS to the residual MS of the initial model,  $F_{1,37}=1.18$ ,  $P>0.5$ ). Again, hunting effect was near significant in the reduced model ( $F_{2,40}=3.15$ ,  $P=0.054$ ). Finally, as most sites in eastern Amazonia lacked nonhunted medium-bodied ecospecies, hunting effect was tested for sites in western Amazonia alone ( $n=30$ ), but this was also not significant (full model retaining forest type,  $R^2=0.191$ , hunting pressure  $F_{2,24}=2.59$ ,  $P=0.096$ ; forest type  $F_{1,24}=0.28$ ,  $P=0.603$  and hunting $\times$ forest interaction  $F_{2,24}=0.36$ ,  $P=0.670$ ; reduced model excluding forest type and forest interaction terms,  $R^2=0.156$ , decrease in model fit  $F_{1,24}=1.04$ ,  $P>0.5$ , hunting pressure effect  $F_{2,27}=2.50$ ,  $P=0.101$ ).

## Discussion

We have examined the evidence for density compensation in overhunted primate communities using the largest available data set for structurally undisturbed neotropical forests (Peres 1999a). Few non-experimental studies of density compensation have accounted for environmental differences between sites (Faeth 1984). We attempted to examine changes in the biomass density of nonhunted species following potential competitive release resulting from the overkill of large-bodied sympatric species, while controlling for environmental differences between forest types. Despite the strongly unbalanced data set and small number of floodplain sites, these results provide reasonably good evidence for the release of nonhunted medium-bodied ecospecies following the huge collapse in the biomass of large-bodied and hunted medium-bodied species. However, we have found only weak or no evidence for compensatory release of small-bodied species in hunted sites with increasing levels of hunting pressure. In the larger set of terra firme forests, a consistent trend was observed for increased biomass in small-bodied and nonhunted medium-bodied species in moderately hunted sites followed by a decrease in heavily hunted sites. This trend was strongest for nonhunted mid-sized species, but also appears to occur in small-bodied primates in low productivity sites. We interpret the initial increase in mid-sized primate biomass in moderately hunted sites as a compensatory response. Subsequent declines in heavily hunted areas may reflect a shift in the prey spectrum selected by Amazonian subsistence hunters who increasingly target medium- and perhaps even some small-bodied primates as larger, more profitable species are depleted or driven to local extinction (A. Jerzolimski and C.A. Peres, unpublished work).

Differences in primate biomass at sites with differing levels of hunting pressure were unlikely to be confounded by any release from natural predation at hunted sites (see Case 1975; Emlen 1978) because all sites had a full complement of predator species including the most important Amazonian raptors known to frequently prey on either small or large primates (*Spizaetus ornatus* and *Harpia harpyja*, respectively: Terborgh 1983; Peres 1993b). Abundance responses to different forest types and hunting pressure were also unlikely to have been obscured by temporal variation in population abundance (Faeth 1984) because platyrrhine primates have low reproductive rates and long average adult life spans (Ross 1992). Moreover, the species considered here are year-round residents that are not known to undergo pronounced population fluctuations through time, which may exert strong effects on competition coefficients (Fox and Luo 1996). Because target primate species at all hunted sites have been harvested for subsistence at least since the 1890s (and for as long as 10,000 years: Roosevelt 1989), it is unlikely that further density compensation would eventually result given a sufficiently long time-lag. Numerical responses to competitive release in the callitrichids and the nonhunted cebid pri-

mates, which clearly have a greater reproductive rate than the large-bodied atelines, should also have been relatively fast, and require perhaps no more than a few decades to take effect.

The apparently weak compensatory response of small-bodied species to hunting of co-occurring atelines and capuchin monkeys need not be interpreted as competitive release. As reflected in the canonical ordination, the abundance of small-bodied taxa appeared to depend primarily on environmental gradients that were largely independent of hunting pressure, such as canopy structure and understorey density. Although overlap in resource use occurs between different size-classes, small-bodied neotropical primates generally make greater use of the forest understorey and subcanopy, and rely more heavily on (1) small-crowned fruiting trees producing small fruit crops, (2) plant species producing smaller and less protected fruits, (3) arthropods rather than leaves to supplement their dietary protein, and in many cases (4) sources of nectar and exudates as alternative plant resources during periods of acute fruit scarcity (Terborgh 1983; Peres 1994a, 1996). Although some feeding overlap is observed across primate size classes, much of the fruit resources made available by the removal of large-bodied species may not be garnered by smaller-bodied species. Most fruit crops shared by large and small primate species in Amazonian forests become available during periods of super-abundant resources (Terborgh 1983; Peres 1994b), when exploitation and interference competition are less likely to affect the demography of subordinate species. Moreover, during periods of overall fruit scarcity, dietary switches by different sympatric species of Amazonian primates tend to target different sets of alternative resources, which are mostly of lower nutritional value or require longer handling time. Examples of such dietary switches characteristic of “lean times” of the year include: squirrel monkeys devoting most of their time to large patches of figs and arthropod foraging (Terborgh 1983), tamarins shifting to nectar and plant exudates (Terborgh 1983; Peres 1996), pitheciines to immature seeds (Ayres 1986; Peres 1993a), capuchins to palm pith, palm nuts and other keystone fruit resources (Spironelo 1986; Janson 1988; Peres 1994a), and howlers, spider monkeys and woolly monkeys to immature foliage (Milton 1980; Symington 1988; Peres 1994c). There is therefore little evidence from the feeding ecology of these species to suggest that resource competition will be an important regulator of population interactions between small and large-bodied ecospecies (Terborgh 1983; Peres 1994a, 1994b). For instance, Schoener’s index of feeding overlap for plant resources between tamarins and woolly monkeys is on average only 0.260–0.266 over the annual cycle, compared with 0.845 between two similar-sized tamarin species in the same study area (Peres 1994b, 1996).

In contrast, sympatric populations of mid-sized and large-bodied platyrrhine primates may share many of the ripe and unripe fruit crops produced by medium and large-crowned food trees (Stevenson in press; C. Peres, unpublished work). Moreover, there have been several

suggestions that competitive exclusion may occur between ecologically similar genera (e.g. large-bodied *Ateles* and *Lagothrix*: Rylands 1987; medium-bodied pitheciines *Chiropotes* and *Cacajao*: Ayres 1986). The clear evidence of density compensation of nonhunted mid-sized species to hunted medium and large-bodied species may therefore reflect some competitive release between ecologically convergent genera, particularly in relation to their dry-season feeding ecology.

Studies of tropical forest vertebrate communities harvested by game hunters have found little implicit or explicit evidence for density compensation. However, many of these earlier tests are weakened by lack of replication, small sample size or potentially confounding environmental effects. Based on a comparison of 11 hunted and 3 protected forest sites in Peru and Bolivia, Freese et al. (1982) found that the densities of both mid-sized (0.5–3.5 kg) and large-bodied (>4 kg) primates were positively correlated and higher in the protected areas. While this may be interpreted as lack of density compensation, it is more likely that hunting had depressed all but the small-bodied primate taxa in the hunted areas surveyed in this study. No evidence for density compensation can be discerned from the encounter rates of both game and non-game mammal species censused by Emmons (1984) at 5 hunted and 2 nonhunted Amazonian lowland forests. While the importance of competitive interactions between large- and small-bodied species is acknowledged in her study, variation in mammal abundance was largely attributed to key environmental variables such as soil fertility and undergrowth density. In a study comparing Guianan primate censuses conducted in 1994 with those at the same undisturbed forest sites 20 years earlier (Muckenhirn et al. 1975), Sussman and Philips-Conroy (1995) reported no obvious changes in the encounter rates of small-bodied species (tamarins and squirrel monkeys), although those of howler monkeys and spider monkeys were 3 times lower in 1994, presumably because of increased hunting pressure in the intervening period. Our study thus appears to be the first showing convincing evidence of density compensation in platyrrhine communities.

Tentative evidence for density compensation in paleotropical primate communities can be seen in southeast Asia where different species of macaques (*Macaca* spp.) on relatively small islands – where other primate species including gibbons (*Hylobates* spp.) may be absent – reach the highest recorded population densities known for any non-supplemented wild population of this genus. For example, densities of *M. fascicularis fusca* on Simeulue (Sugardjito et al. 1989) and *M. nigra* on Sulawesi (J.R. MacKinnon, K.S. MacKinnon and D.J. Chivers, unpublished work) are substantially higher than those of congeners on much larger islands (e.g. Borneo and Sumatra) where a greater richness of primate species, squirrels and large frugivorous birds co-occur sympatrically (C. van Schaik, personal communication). Although these authors do not describe this phenomenon in the same terms, this could be interpreted as density compensation similar to that of other impoverished island faunas.

In African primates, competitive release has been suggested for insular populations in the absence of potential competitors such as the Zanzibar red colobus monkey (*Procolobus kirkii*), which occurs at far greater densities than its mainland ecological counterparts (T. Struhsaker, personal communication). This island population also shows evidence of expansion of niche breadth in that it occupies a greater range of forest habitats than any of the mainland red colobus populations (Struhsaker and Siex 1996). The large variation in blue monkey (*Cercopithecus mitis*) densities at six mid-elevation forest fragments in Uganda has also been attributed to competitive release; this generalist species is thought to be adversely affected by high-forest specialists in species-rich primate communities, particularly red colobus (*Colobus badius*) and mangabeys (*Cercocebus albigena*) (Struhsaker 1978). However, primate densities in these forest isolates may be confounded by habitat fragmentation.

Evidence of compensatory release has also been sought in marine ecosystems following human exploitation of one or more species. Dramatic shifts in the structure of marine fish communities are common and it has often been suggested that depletion of one species by fishing has allowed another to proliferate, as a result of reduced competition or predation. However, Jennings and Kaiser (1998) reviewed putative examples of population release following exploitation of competitors and found little convincing evidence that such replacements are compensatory. Rather, they attributed the apparent proliferation of "replacement" species to the large-amplitude environmental variation characteristic of many marine systems. Similarly, Clapham and Brownell (1996) reviewed changes in the abundance and reproductive rates of baleen whales in the Southern Ocean but found no evidence to support the hypothesis that these changes were a response to large-scale commercial harvest. There is, therefore, little or no clear evidence for compensatory release of competitors in exploited marine systems.

This study lends further support to the overwhelming importance of forest type and soil fertility as determinants of primate abundance and resilience to game harvest (Oates 1996; Peres 1997, 1999a; Bodmer et al. 1999). There is also a tight correlation between forest productivity (as defined by annual litterfall) and primate species richness in South America, both increasing up to a maximum rainfall of 2500 mm year<sup>-1</sup> but then declining in wetter forests (Kay et al. 1997; but see Peres and Janson 1999). There was a consistent trend across all size classes for mean primate biomass to be higher in seasonally flooded várzeas than in supra-annually flooded alluvial forests. Although the biomass of large-bodied and hunted medium-bodied species did not differ significantly between the two inundated forest types, that of small-bodied species in nonhunted and lightly hunted várzea sites was significantly greater than in alluvial sites. The biomass of large-bodied species was also significantly greater in mesotrophic compared to oligotrophic unflooded forests. In particular, the magnitude of the reduction of large-bodied primate biomass occurring in heavily hunted terra firme

forests was significantly lower in mesotrophic than in structurally equivalent oligotrophic sites. This appears to be due to differences in forest productivity so that lower rates of population increase in nutrient-poor sites may result in a greater reduction in average population density when exposed to persistent hunting (Peres 1999b). In contrast to large-bodied primates, no significant habitat effects were detected for hunted medium-bodied primates. However, for both small-bodied and mid-sized species that are rarely or never hunted, the magnitude of the compensatory effect was greater in oligotrophic than in mesotrophic sites, as would be expected if resource competition and compensatory release are greater in low-productivity forest sites.

It is often assumed implicitly that taxonomically cohesive faunal assemblages form relatively tight ecological guilds or communities (Simberloff and Dayan 1991). However, taxonomically related species can form matrices of weak competitive interactions showing no evidence of density compensation (Findley and Findley 1985) just as entirely unrelated taxa, such as granivorous ants and rodents, can show strong evidence for density compensation (Davidson et al. 1984). In our study, it might have been informative to consider data on the density (and biomass) of other important frugivores, including bats and birds, but unfortunately such data were unavailable. Similar problems have plagued studies of density compensation in islands where avian communities are taxonomically rather than resource-defined (Wright 1980). It is unlikely, however, that a more inclusive analysis would have altered our main conclusions as all species of large-bodied arboreal frugivores are systematically harvested by hunters, so that their removal covaries with that of large primates.

Yet neotropical primate assemblages are better described as non-random sets of interacting species, rather than as haphazard samples of a regional species pool that collectively accommodate varying environmental conditions. Primate ecospecies were not randomly distributed across all sites, and there were clear community signatures in terms of species composition and relative abundance associated with different forest types, as shown by previous analyses (Peres and Janson 1999) and by the CCA presented here. A data set of over 270 neotropical primate assemblages (at which the full species composition is known) indicates that species forming mutually exclusive functional groups are highly predictable within size classes, but hardly at all across size classes (C.A. Peres, unpublished work). This further supports our conclusion that apparent density compensation in small-bodied species should not be seen as evidence for significant levels of interspecific competition across different size classes.

These results suggest that while game harvest significantly reduces the average body size in forest vertebrate assemblages (Peres 1999b, in press), depletion of large-bodied species is not necessarily followed by replacements by smaller community members in terms of either population density or biomass. Although the direction of some abundance responses was consistent with positive

density compensation, these were clearly under-compensatory compared to the magnitude of reduction of biomass density of large-bodied primates in hunted sites. This has important conservation implications for both the qualitative and quantitative effects of subsistence hunting in tropical forests on the residual faunal assemblage, because hunting is likely to reduce the existing

pool of game species but provide only weak density-dependent mechanisms for compensatory release in taxonomically related non-game species. These species are thus unlikely to make up for some of the reduced "wild-life value" of an overhunted forest, and contribute with quantitatively similar or alternative ecosystem services, such as dispersal of large-seeded plants.

**Appendix 1** Forest sites and profiles of primate communities considered in the analyses. Sources of data are provided in Peres (1999a)

Forest site	Region, Country	Forest type <sup>a</sup>	Hunting pressure <sup>b</sup>	Species richness <sup>c</sup>	Density (no. km <sup>-2</sup> )	Biomass (kg km <sup>-2</sup> )
Urucu	Amazonas, Brazil	OTF	N	11	137	324
Igarapé Açú	Amazonas, Brazil	OTF	N	10	106	313
SUC-1	Amazonas, Brazil	OTF	N	10	77	217
Oleoduto	Amazonas, Brazil	OTF	N	9	103	253
Curimatá	Amazonas, Brazil	OTF	N	12	79	222
São Domingos	Acre, Brazil	OTF	H	8	175	138
Kaxinawá Reserve	Acre, Brazil	MTF	H	8	145	173
Riozinho	Amazonas, Brazil	OTF	M	12	157	226
Porongaba	Amazonas, Brazil	MTF	H	11	210	163
Sobral	Amazonas, Brazil	MTF	H	9	175	122
Condor	Amazonas, Brazil	MTF	L	9	195	279
Penedo	Amazonas, Brazil	MTF	H	7	129	118
Altamira	Amazonas, Brazil	MTF	L	11	227	463
Barro Vermelho I	Amazonas, Brazil	MTF	M	12	165	261
Fortuna	Amazonas, Brazil	MTF	M	11	216	297
Igarapé Jaraquí	Amazonas, Brazil	OTF	M	9	137	131
Vira Volta	Amazonas, Brazil	MTF	L	12	182	282
Vai Quem Quer	Amazonas, Brazil	MTF	M	10	124	176
Sacado	Amazonas, Brazil	VAR	M	4	126	245
Nova Empresa	Amazonas, Brazil	VAR	M	5	185	410
Boa Esperança	Amazonas, Brazil	VAR	L	5	355	953
Barro Vermelho II	Amazonas, Brazil	VAR	M	7	213	361
Lago Fortuna	Amazonas, Brazil	VAR	M	6	358	627
Lago Teiú	Amazonas, Brazil	VAR	L	4	181	377
Lago Mamirauá	Amazonas, Brazil	VAR	L	3	266	448
Ponta da Castanha	Amazonas, Brazil	OTF	M	10	156	188
Açaituba	Amazonas, Brazil	OTF	L	11	68	244
MCSE Reserve	Amazonas, Brazil	OTF	N <sup>d</sup>	6	24	81
Rio Iaco	Acre, Brazil	MTF	H	8	56	53
Fazenda União	Acre, Brazil	MTF	M	9	61	50
Antimarí	Acre, Brazil	MTF	H	9	40	33
Samuel	Rondônia, Brazil	MTF	L	8	77	175
Aripuanã	Mato Grosso, Brazil	MTF	L	10	70	197
Maracá Island	Roraima, Brazil	MTF	N	5	42	105
Marajó Island	Pará, Brazil	ALL <sup>e</sup>	L	2	71	128
Pucuruí	Pará, Brazil	MTF	L	5	81	157
Remansinho	Pará, Brazil	MTF	L	5	72	147
Vila Braba	Pará, Brazil	MTF	H	5	75	112
Kayapó Reserve	Pará, Brazil	MTF	L	5	68	177
Tailândia	Pará, Brazil	OTF	H	4	22	30
Rio Capim	Pará, Brazil	OTF	H	4	30	27
Irituia	Pará, Brazil	OTF	M	4	36	52
Gurupí	Pará, Brazil	OTF	L	5	35	70
Cahuana Island	Eastern Peru	ALL <sup>f</sup>	L	6	120	328
Cocha Cashu	Southern Peru	ALL	N	11	249	590
Tahuayo-Blanco	Eastern Peru	MTF	H	12	90	125
Yavari-Miri	Eastern Peru	MTF	L	10	158	310
Yomiwato	Southern Peru	MTF	M	9	75	191
Diamante	Southern Peru	ALL	M	8	150	287
Samiria	Eastern Peru	ALL	L	7	161	345
Upper Nanay	Eastern Peru	OTF <sup>g</sup>	H	6	40	51
Tahuamanu	Northern Bolivia	MTF	H	9	73	51
Voltzberg Reserve	Central Surinam	OTF	N	7	103	244
Pakani Area	Central Guyana	OTF	N	6	135	242
Petit Saut	French Guiana	OTF	L	5	40	73
Saut Pararé	French Guiana	OTF	N	6	103	289

<sup>a</sup> Forest type: *OTF* oligotrophic terra firme forests of remote interfluvial areas; *MTF* mesotrophic terra firme forests, usually adjacent to fluvial sources of alluvial sediments; *ALL* mature floodplain forests; *VAR* seasonally flooded várzea forests

<sup>b</sup> Level of hunting pressure: *N* none; *L* light; *M* moderate; *H* heavy

<sup>c</sup> Number of sympatric diurnal primate species co-occurring at each site

<sup>d</sup> MCSE Reserve: although recorded as nonhunted, this site may have experienced some light hunting at time of surveys (L. Emmons, personal communication)

<sup>e</sup> Marajó Island: a brackish-water tidal gallery forest in the Amazon estuary (Peres 1989), recorded as *ALL*

<sup>f</sup> Cahuana Island: recorded as *ALL*, but may be considered intermediate towards *VAR* (Soini 1986, personal communication)

<sup>g</sup> Upper Nanay: primarily a floodplain forest supplied by black-water river; in terms of geochemistry and forest productivity similar to *OTF* (Freese et al. 1982)

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