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FOOD HABITS OF THE HARPY EAGLE, A TOP PREDATOR FROM THE AMAZONIAN RAINFOREST CANOPY

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Abstract.—The Harpy Eagle (*Harpia harpyja*), the heaviest and the most powerful bird of prey in the canopy of the Neotropical rainforests, is critically endangered in some parts of its range, mainly due to hunting pressure and habitat loss by deforestation. In this study, we found that the diet of five breeding pairs of Harpy Eagles in the central Amazonian rainforest over three years was dominated by two species of sloths (*Bradypus variegatus* and *Choloepus didactylus*) in terms of number of individuals and biomass consumed. Twelve other species, including primates, rodents, carnivores, and birds, also contributed to the Harpy Eagle diet in central Amazonia; there was no evidence of Harpy Eagle predation on livestock or domestic animals. Throughout the Harpy Eagle's entire range, 69 prey species have been documented, indicating that it can use a wide range of food resources. However, in our study, there was an evident diet specialization, resulting in a niche breadth which was relatively low (*Bsta* = 0.171). Conservation of Harpy Eagles should include protection of nesting trees, territories, and prey species to maintain the variability and availability of resources and its ecological functions throughout its geographic range.

Key Words: *Harpy Eagle*; Harpia harpyja; *Amazon*; *canopy*; *conservation*; *diet*; *mammals*; *nest*; *rainforest.*

HÁBITOS DE FORRAJEO DE *HARPIA HARPYJA*, UN DEPREDADOR TOPE DEL DOSEL DE LA SELVA LLUVIOSA AMAZÓNICA

Resumen.—*Harpia harpyja*, el ave de presa más pesada y poderosa del dosel de los bosques lluviosos neotropicales, está en peligro crítico en algunas partes de su distribución, principalmente debido a la presión de caza y la pérdida de hábitat por deforestación. En este estudio encontramos que la dieta de cinco parejas reproductivas de *H. harpyja* en los bosques lluviosos amazónicos centrales estuvo dominada a lo largo de tres años por dos especies de perezosos (*Bradypus variegatus* y *Choloepus didactylus*) en términos de número de individuos y biomasa consumidos. Otras doce especies, incluyendo primates, roedores, carnívoros y aves también contribuyeron a la dieta de *H. harpyja* en la Amazonía central; no hubo evidencia de depredación de ganado o animales domésticos por parte de *H. harpyja*. A lo largo de la distribución completa de *H. harpyja* se documentaron 69 especies de presa, indicando que la misma puede utilizar un amplio rango de fuentes de alimento. Sin embargo, en nuestro estudio hubo una evidente especialización de la dieta, resultando en un ancho de nicho relativamente estrecho (*Bsta* = 0.171). La conservación de *H. harpyja* debería incluir la protección de árboles nido, de territorios y de especies de presas para mantener la variabilidad y disponibilidad de recursos y sus funciones ecológicas a través de su distribución geográfica.
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The Harpy Eagle (*Harpia harpyja*; Aves: Accipitridae), the heaviest and most powerful raptor (Brown and Amadon 1968, Voous 1969), inhabits the canopy of Neotropical rainforests (Sick 1997), historically from southern Mexico to northeastern Argentina (Ferguson-Lees and Christie 2001). The diet of the Harpy Eagle has been described for almost all areas of its range, including the Brazilian Atlantic Forest (Aguiar-Silva et al. 2012), the Pantanal floodplain (Ubaid et al. 2011) and the forest enclaves in the *cerrado* (central Brazilian woody savanna; Pereira and Salzo 2006) where nesting records are scarce (Silveira et al. 2005, Srbek-Araujo and Chiarello 2006, Pereira and Salzo 2006, Aguiar-Silva et al. 2012). It feeds mainly on arboreal mammals such as sloths, monkeys, and porcupines (Fowler and Cope 1964, Rettig 1978, Eason 1989, Sanaiotti et al. 2001, Touchton et al. 2002, Ferrari and Port-Carvalho 2003, Aguiar-Silva 2007, Piana 2007, Benchimol and Venticinque 2010, Lenz and Reis 2011), and less frequently on reptiles and birds (Álvarez-Cordero 1996, Martínez et al. 1996, Touchton et al. 2002, Piana 2007, Rotenberg et al. 2012).

As a top predator, the Harpy Eagle is rare and has a low reproductive rate (Hilty and Brown 1986, Vargas and Vargas 2011), generally breeding every 2–3 yr and producing only one offspring per nesting effort (Rettig 1978, Álvarez-Cordero 1996, Sick 1997, Muñiz-López et al. 2007). These characteristics make it difficult for Harpy Eagle populations to recover from disturbances (Trinca et al. 2008, GRIN 2013), such as the deforestation that was responsible for decimating the Harpy Eagle population in the last century in the Brazilian Atlantic Forest (Albuquerque 1995, Brooks 1998, Pereira and Salzo 2006). Currently, it is assigned by the International Union for Conservation of Nature and Natural Resources (IUCN) to the category of Near Threatened species (IUCN 2013). Even with deforestation pressure, the Harpy Eagle probably has a widespread population in the extensive intact portion of the Amazonian forest. However, within the limits of its range, in southern Mexico, Central America, and the major part of the Brazilian Atlantic Forest, populations have been drastically reduced by overhunting and forest fragmentation (Álvarez-Cordero 1996, Matola 2006, Vargas et al. 2006, IUCN 2013). The reduction of its prey by human activities such as deforestation and hunting may also negatively affect the stability of its populations (Vargas et al. 2006).

Of all the countries in Central America, Panama is the only one that still has a viable, relatively stable population of Harpy Eagles, though they are considered rare in the country (Vargas et al. 2006, Vargas and Vargas 2011). It is now critically endangered in Belize (Meerman and Clabaugh 2012) and Panama (Vargas and Vargas 2011), and extinct in El Salvador (Vargas and Vargas 2011) and very uncommon (Slud 1964) in Costa Rica (it still exists in parts of the Oso Peninsula; Barrantes et al. 2002, Vargas et al. 2006, Sandoval 2009, Rotenberg et al. 2012). In South America, though the status of Harpy Eagles is somewhat better than in Central America (Vargas et al. 2006), this species is classified as endangered in Bolivia (Ergueta and de Morales 1996, Olivo 2001), Argentina (Chebez et al. 2011), and Paraguay (Brooks 1998); and vulnerable in Ecuador (Granizo et al. 2002) and Venezuela (Rodríguez and Rojas-Suárez 2008). In non-Amazonian Brazil, the Harpy Eagle is considered endangered, critically endangered, or probably extirpated in the wild in different regions of the Brazilian Atlantic Forest (Alves et al. 2000, Bencke et al. 2003, Mikich and Bérnils 2004, Simon et al. 2007, Machado et al. 2008, IGNIS 2008, Silveira et al. 2009).

Another threat to the Harpy Eagle, as for many raptors, has been the removal of individuals by hunting (Lees 2006, Trinca et al. 2008). It has been reported that raptors pursue livestock (Sick 1997, Lees 2006, Trinca et al. 2008, Lambertucci et al. 2009, Sarasola et al. 2010, DeLuca 2012), causing considerable conflicts between these birds and humans who believe that eagles prey on livestock and domestic animals (Álvarez-Cordero 1996, Valdez 2002, Vargas et al. 2006, Lees 2006, Trinca et al. 2008, Curti and Valdez 2009, DeLuca 2012). In this study, our goal was to (1) describe the diversity of prey species consumed by Harpy Eagles in the central Brazilian Amazon and compare this information to earlier reports from Central and South America, and (2) determine whether this species preyed upon livestock or domestic animals.

Study Area and Methods

Study Area. The present study was conducted in an area of ca. 78 270 ha in the central Amazonian rainforest (2°36.78′S, 56°40.85′W), in a settlement project of the Brazilian Federal Government (Instituto Nacional de Colonização e Reforma Agrária—INCRA) in Parintins, Amazonas state, Brazil (Fig. 1), with 54 communities containing 3115 people (Silva and Oliveira 2010). The region is covered by primary lowland tropical rainforest and seasonally flooded forests. The vegetation is a mosaic resulting from different land uses,

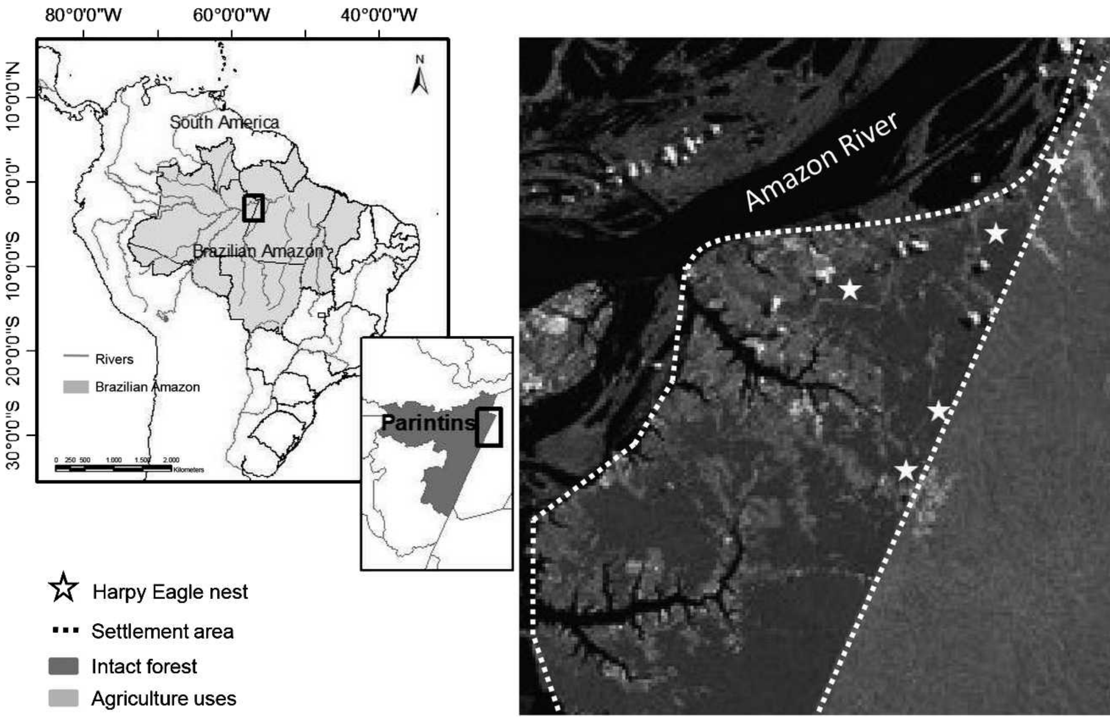

Figure 1. Location of study area in the central Amazonian forest, Parintins, Amazonas state, Brazil. Harpy Eagle diet was described from five active nests (stars) between September 2003 to November 2005.

dominated by secondary forests and areas of slash-and-burn agriculture and livestock pasture (Silva and Oliveira 2010). In spite of human activities, the region still has intact primary forest, due to Brazil's Forest Code, which stipulates that 80% of the forest should be preserved (Brasil 1965).

The topography of the region is typical of the central Amazonian forest with clay and drained soils on the plateaus and sandy soils in valleys. The area is drained by a dense system of small streams and creeks. Altitude ranges from 40–150 m above sea level. The climate is tropical humid, average annual rainfall is 2223 mm, and mean annual temperature is about 26°C (INMET 2005).

In 2013, there were 15 known Harpy Eagle nests in the study area, averaging 1.5 km (0.6 km–2.5 km) away from local communities. With this proximity, as in many forest regions, there are human-wildlife conflicts in the study area because there is a predominant belief that large forest animals, such as jaguar (*Panthera onca*) and Harpy Eagle, prey heavily on livestock or domestic animals and represent a threat to their community or family (Valdez 2002, Lees 2006, Trinca et al. 2008, Curti and Valdez 2009, DeLuca 2012).

Diet Assessment. We collected all prey remains and pellets in the nests and on the ground around five of the seven known nesting trees (through 2005) of Harpy Eagles. We collected from the ground monthly from September 2003 to November 2005 at the five nests, and at four of these, a climber collected prey remains from in the nest one time, when the juvenile was 2 yr old, by which age the young spend much of their time away from the nest.

Prey Identification and Analysis. We separated bone remains into cranial and postcranial elements. We used cranial bones, mandibles, teeth, claws, hair, feathers, and beaks to identify prey to the most specific taxonomic level possible. We compared bone remains with reference material deposited in the mammal and bird collections of National Institute for Amazonian Research (INPA/Amazonas state) and in the Museu Paraense Emilio Goeldi (MPEG/Para state), both in Brazil.

The number of prey from each nest was estimated from the remains. When skulls and mandibles were fragmented, we attempted to find and fit the complementary bone parts of all samples to quantify the minimum number of individuals consumed. We used the number of pelvises to identify and quantify primates.

We measured skulls and mandibles of specimens from reference collections and used regression analyses to estimate body mass for each prey species. Body masses by family of unidentified birds and primates were estimated from available literature (Sick 1997, Emmons and Feer 1997, Paglia et al. 2012) and were represented by the average weight of an adult of that family. The occurrence (number of times a prey species was found as a percentage of all species sampled) represents the importance of a prey in the diet and was utilized to estimate niche breadth. Prey items were classified by locomotor habits (arboreal and terrestrial), and by guild: carnivore, frugivore, folivore, insectivore, omnivore, and seed-eater. The geographical distribution and taxonomy of the prey species were based on Wilson and Reeder (1993), Voss and Emmons (1996), Emmons and Feer (1997), Rylands et al. (2000), Alfaro et al. (2012) and Paglia et al. (2012). We examined the conservation status of each Harpy Eagle prey species in the IUCN Red List of Threatened Species (IUCN 2013). We used a Kruskal-Wallis test to compare the number of individuals and estimated body mass for each species consumed (Zar 1999).

Diet Niche Breadth. We analyzed niche breadth using the standardized Levins index (Colwell and Futuyma 1971):

$$Bsta = (B-1)/(n-1)$$

where B is the Levins index ($B = 1/\Sigma p_j^2$), p_j is the percentage of occurrence of each prey species, and n the number of prey species. Standardized Levins index (*Bsta)* values range between 0 (minimum niche breadth and, consequently, maximum selectivity) and 1 (maximum niche breadth, minimum selectivity; Krebs 1999).

Dietary Patterns Across the Harpy Eagle's Range. Differences in diet composition were evaluated using the diet niche breadth and through a nonmetric scaling ordination (NMDS) using the Bray-Curtis dissimilarity matrix of genus-level composition (presence-absence). We compiled literature reports of the diet of 17 Harpy Eagles from nine countries in the neotropics: Argentina (Chebez et al. 1990, Anfuso et al. 2008), Belize (Matola 2006, Rotenberg et al. 2012), Brazil (Galetti and Carvalho, Jr. 2000, Sanaiotti et al. 2001, this study), Ecuador (Muñiz-López et al. 2007), Guiana (Fowler and Cope 1964, Rettig 1978, Izor 1985), Panama (Álvarez-Cordero 1996, Touchton et al. 2002), Peru (Piana 2007), Suriname (Ford and Boinski 2007) and Venezuela (Álvarez-Cordero 1996). The NMDS is a procedure for fitting a set of points (sites) in a space such that the distance between points corresponds as closely as possible to a given set of dissimilarities between a set of objects (prey genus-level). Comparisons among sites were made by multivariate analysis of variance for repeated measures for sites with replicated data (Argentina, Belize, Panama, Venezuela, Guiana, and Brazil). Multivariate analyses were carried out using the packages ''Vegan,'' ''Permute,'' and ''Mass'' in the R 2.15.2 statistical program (R Development Core Team 2013).

Results

Prey Species. Two species of sloths, the three-toed sloth (*Bradypus variegatus*) and two-toed sloth (*Choloepus didactylus*; Xenarthra), were the most frequent prey and represented the majority of the body mass consumed at five Harpy Eagle nests in Parintins, Amazonas state, Brazil (Table 1). Twelve other species, including primates, rodents, carnivores, and birds, also contributed to the Harpy Eagle diet; most of these (98%) were species with arboreal locomotor habits (Table 1).

Sloths represented 78% of the diet in terms of number of individuals (Kruskal-Wallis $H = 33.08$, df $= 11$, $P = 0.001$), whereas primates made up 11% of individuals consumed. The most common species of primate were red-handed howler monkey (*Alouatta belzebul*) at 4% and Hoffmann's titi monkey (*Callicebus hoffmannsi*) at 4%, followed by brown capuchin monkey (*Sapajus apella*) at 2%, white-nosed bearded saki monkey (*Chiropotes albinasus*) at 1%, and gray saki monkey (*Pithecia irrorata*) at 1%. All other nonprimate species added together equaled 5% (Table 1). Folivores were the dominant dietary items at 82%, followed by frugivores (9%), seed predators (3%), and omnivores (1%; Table 1). Sloths also accounted for 85% (436 kg; Kruskal-Wallis $H = 68.78$, df $= 11$, $P = 0.001$) of body mass of prey in the Harpy Eagle diet at the five nests during three years (Table 1). All prey weighed estimated between 0.3–6.5 kg (mean 2.6 ± 0.82 kg, $n = 252$; Fig. 2).

Diet Niche Breadth. There was an evident diet specialization of the Harpy Eagle, based on the niche breadth. $Bsta = 0.171$, which was relatively low (Table 2).

Dietary Patterns Across the Harpy Eagle's Range. The richness of prey species consumed by Harpy Ea-

Table 1. The relative abundance and estimated body mass of prey species at five nesting sites of Harpy Eagle from September 2003 to November 2005 in the central Amazonian forest, Brazil. Locomotor: A = Arboreal; T = Terrestrial.

PREY	NUMBER OF INDIVIDUALS	ESTIMATED BODY MASS (kg)	LOCOMOTOR[a,b]	GUILD[b]	IUCN[c]
Xenarthra					
Choloepus didactylus	99	235	A	Fo	LC
Bradypus variegatus	98	201	A	Fo	LC
Primates					
Alouatta belzebul	10	19	A	Fo, Fr	VU
Sapajus apella	4	9	A	Fr, Om	LC
Callicebus hoffmannsi	11	12	A	Fr, Fo	LC
Chiropotes albinasus	2	6.4	A	Fr, Sp	EN
Pithecia irrorata	2	4	A	Fr, Sp	LC
Cebidae and Pitheciidae	2	3.5	A	-	-
Rodentia					
Coendou prehensilis	1	3	A	Sp, Fo, Fr	LC
Coendou koopmani	6	6	A	Sp, Fo, Fr	DD
Dasyprocta leporina	1	1.5	T	Sp, Fr	LC
Carnivora					
Potos flavus	2	3.7	A	Fr, Om	LC
Didelphimorphia					
Didelphis marsupialis	2	2.4	A,T	Om	LC
Aves					
Ara chloropterus	1	1.5	A	Fr, Sp	LC
Ramphastos tucanus	1	1	A	Fr, Sp	LC
Unidentified birds[d]	11	13	A		-
TOTAL	252	521			

[a] Emmons and Feer (1997).
[b] Paglia et al. (2012).
[c] DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Threatened (IUCN 2013).
[d] None were domestic fowl as determined by testing mitochondrial DNA.

gles differed significantly, ranging from 3 to 20 species ($R^2 = 0.78$, $P = 0.04$); therefore, Levins diversity indices were low and similar between regions (Table 2). Prey species with arboreal habits dominated the Harpy Eagle diet (Table 1), and all seventeen studies revealed the same trend (Table 2).

The community structure of Harpy Eagle prey (genus-level) throughout its geographic range, based on presence/absence (NMDS $r^2 = 0.86$; stress = 0.1) was different among sites ($P = 0.04$; MANOVA - Pillai-Trace = 1432; Fig. 3). The high r^2 and low stress mean that the ordination was able to summarize and represent the pattern of data.

DISCUSSION

Prey Species. Sixty-nine species of mammals, birds, and reptiles (twenty-eight mammal genera) have been described as part of the Harpy Eagle diet from Central to South America (Fowler and Cope 1964, Rettig 1978, Izor 1985, Chebez et al. 1990, Álvarez-Cordero 1996, Galetti and Carvalho, Jr. 2000, Sanaiotti et al. 2001, Matola 2006, Touchton et al. 2002, Muñiz-López et al. 2007, Piana 2007, Anfuso et al. 2008, Rotenberg et al. 2012, including this study). Several other records of Harpy Eagle predation on mammal species have been reported (Eason 1989, Peres 1990, Sherman 1991, Ferrari and Port-Carvalho 2003, Martins et al. 2005, Benchimol and Venticinque 2010, Lenz and Reis 2011, Barnett et al. 2011), including black-headed uacari monkey (*Cacajao ouakary*; Barnett et al. 2011) that have not yet been documented in Harpy Eagle diet based on prey remains.

The prey brought to the nests in Parintins weighed an average of 2.6 kg (±0.82 kg, $n = 252$).

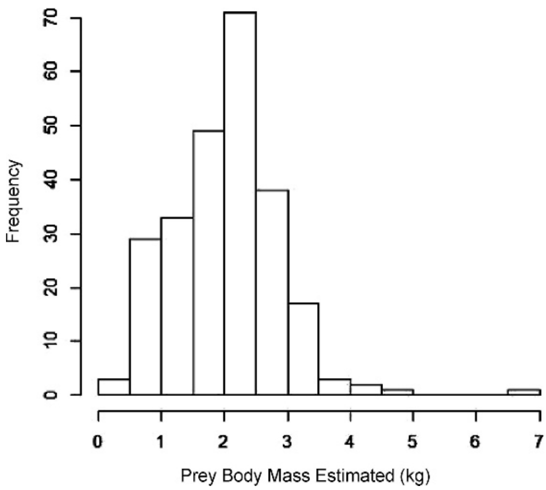

Figure 2. Frequency distribution of the estimated body mass of prey consumed (n = 252) by Harpy Eagles in five nests over 3 yr in Parintins, central Amazonian forest, Brazil.

Analyzing the range of estimated body mass of sloths recorded from this study and comparing with the adult weights, (5.5 kg for three-toed sloth and 8.5 kg for two-toed sloth; Emmons and Feer 1997), we assume that the major predation frequency was on juveniles and subadults. This assumption was supported based on analysis of cranial sutures, which were not completely fused in subadults and juveniles (Hoson et al. 2012).

A Harpy Eagle preyed on an infant monkey (*Sapajus apella*) at Balbina Hydroelectric Reservoir within the Uatumã Biological Reserve in the central Amazonian forest, by capturing the infant from the back of an adult female (Benchimol and Venticinque 2010). Similarly, we observed a baby sloth (*Bradypus variegatus)* of approximately 260 g being carried to a nest in the Carajas National Forest (T. Sanaiotti unpubl. data). Large prey can be more difficult to catch and handle, which reduces the probability of a successful attack. In some areas, a Harpy Eagle successfully attacked prey that could not be carried in flight and lost the prey between the ground and the canopy (Martins et al. 2005). In 2005, W. Magnusson (pers. comm.) observed a dead howler monkey (6 kg) dropped by a Harpy Eagle at the Adolpho Ducke Forest Reserve, Manaus, Amazonas state, Brazil.

We also found a bias among the type of prey remains collected in the nests, in that we more frequently found the upper body parts of sloths (skulls and forelimbs) but the lower body parts (thoracic, sacral and caudal vertebrae, pelvis and leg bones) of primates. Primate skulls were rarely recorded in the remains. We believe that the adults fed on the prey before bringing the remainder to the nest. The

Table 2. Richness, standardized Levins diversity index (*Bsta*), and percentage of arboreal and folivore species from seventeen Harpy Eagle diet studies from Central and South America. n = number of individuals.

SITES	NEST	n	RICHNESS	*BSTA*	ARBOREAL (%)	FOLIVORE (%)	SOURCE
Bel1	*	NA	7	-	71	29	Matola 2006
Bel2	1	17	9	0.715	89	33	Rotenberg et al. 2012
Pan1	**	71	12	0.309	67	50	Touchton et al. 2002
Pan2	3	11	8	0.683	80	63	Álvarez-Cordero 1996
Gui1	2	27	6	0.334	67	33	Fowler and Cope 1964
Gui2	1	57	16	0.395	73	27	Rettig 1978
Gui3	1	83	13	0.561	85	31	Izor 1985
Sur	1	NA	9	-	100	33	Ford and Boinski 2007
Ven1	3	91	19	0.342	74	21	Álvarez-Cordero 1996
Ven2	12	122	20	0.299	80	35	Álvarez-Cordero 1996
Peru	5	80	15	0.472	80	33	Piana 2007
Ecu	11	102	13	0.388	92	46	Muñiz-López et al. 2007
Bra1	1	21	3	0.586	100	67	Galetti and Carvalho, Jr. 2000
Bra2	1	26	6	0.359	100	50	Sanaiotti et al. 2001
Bra3	5	252	14	0.171	86	43	This study
Arg1	3	6	5	0.875	40	20	Chebez et al. 1990
Arg2	1	5	5	1	80	20	Anfuso et al. 2008

* Individual reintroduced.
** Pair reintroduced.
NA = Data not available.

same pattern was reported in other Harpy Eagle diet studies (Fowler and Cope 1964, Rettig 1978, Izor 1985, Muñiz-López et al. 2007).

In contrast to local beliefs, there was no evidence in the prey remains that Harpy Eagles fed on livestock or on domestic animals such as chickens or ducks, even where Harpy Eagle nesting territories overlapped human settlements. This was verified by testing mitochondrial DNA in birds not identified by bone samples (F.H. Aguiar-Silva unpubl. data). The biomass of wild animals in the study area is probably sufficient to support the population of Harpy Eagles, suggesting that there is enough forest cover to allow Harpy Eagles and arboreal mammals to coexist. In Acre (southwestern Amazonia) and Mato Grosso (central South America) states, humans killed adult Harpy Eagles due to perceived risk to livestock and domestic animals or to satisfy their curiosity (Lees 2006, Trinca et al. 2008, DeLuca 2012). Thus, effective conservation to maintain large areas of habitat for the Harpy Eagle are needed to prevent what has happened in Asia, where the Philippine Eagle (*Pithecophaga jefferyi*)—the most endangered eagle in the world (Salvador and Ibañez 2006) due to habitat loss—consumes chickens (*Gallus gallus domesticus*), cats (*Felis catus*), and dogs (*Canis lupus familiaris*; Concepción et al. 2006).

Diet Niche Breadth. Although the Harpy Eagles in our study preyed on a large variety of species such as primates, rodents, kinkajous, marsupials, and birds, the sloths *B. variegatus* and *C. didactylus* were the most frequent prey in their diet; this may be due to the habits of sloths, including slow movement (Montgomery and Sunquist 1978). Sloths accounted for two-thirds of the Harpy Eagle diet in the five nests of Parintins, central Amazonian forest, Brazil. Together the two species of sloths contributed a maximum of 436 kg in biomass of prey consumed by the five Harpy Eagle pairs and delivered to the nestlings in the nests. The behavioral habits of sloths in the canopy (Montgomery and Sunquist 1978, Queiroz 1995) probably increased their probability of detection by the Harpy Eagle. The low number of primates in the Harpy Eagle diet may be due to antipredation behaviors of primates (Gil-da-Costa 2007), which reduce the risk of attacks, at least for the dependent young (Neal and Norconk 2009). Researchers reported unsuccessful attempts of predation on howler monkey (*Alouatta seniculus*; Eason 1989; Peres 1990; Sherman 1991) and on bearded saki (*Chiropotes utahicki*; Martins et al. 2005) all of which live in groups. These researchers asserted that the presence of a group, which made it impossible for the Harpy Eagle to carry away the prey, resulted in an unsuccessful predation attempt.

The Harpy Eagle primarily consumed arboreal mammals (86% of species consumed; Table 1, 2) like other large eagles, including the Philippine Eagle in Asia (Ibañez et al. 2003) and the Crowned Hawk-Eagle (*Stephanoaetus coronatus*) in Africa (Mitani et al. 2001). The same pattern was recorded for almost the entire Harpy Eagle range, with the exception of Argentina (Arg1 = 40% arboreal; Table 2). Success rates of observed capture attempts by Harpy Eagles in Panama seem to be higher on solitary arboreal rather than for social arboreal animals (Touchton et al. 2002).

The percentage of folivores in the Harpy Eagle diet recorded for all Harpy Eagle diets (Table 2) supports the hypothesis that a predator can ''keep the world green'' (Terborgh et al. 2006). By consuming the most abundant herbivores in the forest, the Harpy Eagle helps limit herbivore impact on primary production; herbivores and granivores can have an important effect on forest regeneration (Dirzo and Miranda 1991). For example, in Panama the absence of large predators was associated with decreased tree diversity (Terborgh et al. 2006).

Dietary Patterns Across the Harpy Eagle's Range. The dissimilarity in richness and in Levins diversity index recorded in the Harpy Eagle diet (Table 2, Fig. 3) may be partly explained by the sources of data, which, although temporally and spatially independent, rely on diverse methodological approaches and sample sizes (Table 2). The richness of prey consumed by Harpy Eagle in our study area (n = 14 prey species) was low compared with the Harpy Eagle diet from Venezuela (n = 20 prey species; Álvarez-Cordero 1996), which was surprising because the central Amazonian forest, where the five Harpy Eagle nests we studied were located, has high species diversity (Voss and Emmons 1996, Myers et al. 2000, Paglia et al. 2012, Jenkins et al. 2013). It is possible that the small sample size (five nests) in our study area was responsible for the lower diet diversity.

Although most of the studies indicated a highly specialized diet, some of them, such as those in Argentina (Arg1, Arg2), Belize (Bel2), Panama (Pan2), and Brazil (Bra1), revealed minimal selectivity (Table 2). According to optimal foraging theory, as the abundance of a preferred food type in the diet increases in the foraging habitats used, the number of less-preferred food types included in the optimal diet will decrease (Pyke et al. 1977). Harpy Eagle diets in Belize and Argentina, where the sloths were absent (Moraes-Barros et al. 2010, Rotenberg et al. 2012) included increased consumption of other species, resulting in a less specialized diet (Table 2).

The composition of Harpy Eagle prey (by genera) was reduced to two axes by NMDS, with 78% of the total variation in diet composition explained. The configuration points (sites) pattern (Fig. 3) in the Harpy Eagle diet for each country reflects the presence/absence of some important species, such as the sloths. The Xenarthra, particularly the sloths, dominant in Neotropical forests (Eisenberg and Thorington 1973, Mascarenhas and Puerto 1988, Janson and Emmons 1990), decrease in diversity and abundance (Acevedo-Quintero et al. 2011, Catzeflis and Thoisy 2012) at the extreme limits of the Harpy Eagle distribution range (Belize and Argentina). Belize is at the northern edge of the range for sloths, and supports only two primate species (Rotenberg et al. 2012), which may explain the dissimilarity among diets reported in this study and those recorded in Argentina and Belize.

The first Harpy Eagle diet reported in Brazil (Bra1; Galetti and Carvalho, Jr. 2000) was separated from the other two Brazilian sites (Bra2, Bra3; Fig. 3) because the Harpy Eagle diet in that region exhibited low richness compared to this study and others (Table 2), which is likely explained by the sample size difference among these studies. Variations in the abundance and availability of prey species due to differences in demographic factors, weather and seasonal patterns (Montgomery and Sunquist 1978, Touchton et al. 2002), reproductive period (Dias et al. 2008), vegetation structure (Acevedo-Quintero et al. 2011), antipredator behavior of potential prey (Gil-da-Costa 2007), and exploitation of resources by human communities (Alvarez and Ellis 1994, Wright et al. 2000) may also explain variations in the diet of Harpy Eagles among locations.

Harpy Eagles tend to catch similar genera of prey species in different parts of their geographic range. The wide variety of prey species consumed by Harpy Eagles across their range may indicate opportunistic foraging behavior, as in other raptors (Skorupa 1989, Concepción et al. 2006) leading to a maximization of fitness (Pyke et al. 1977). This foraging behavior would allow the Harpy Eagle to use a wide range of prey species and to remain in areas surrounded by different kinds of land use.

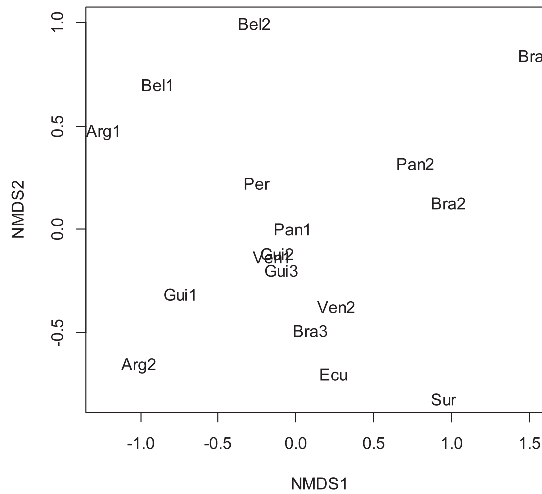

Figure 3. Axis 1 and 2 from the NMDS (nonmetric multidimensional scaling) ordination scores derived from a Bray-Curtis dissimilarity matrix of presence/absence of prey genus-level in the Harpy Eagle diet in its distribution range. Distances between points reflect a dissimilarity matrix created using the Bray-Curtis coefficient. Argentina – Arg1 (Chebez et al. 1990), Argentina - Arg2 (Anfuso et al. 2008), Belize – Bel1 (Matola 2006), Bel2 (Rotenberg et al. 2012), Brazil - Bra1 (Galetti and Carvalho, Jr. 2000), Brazil - Bra2 (Sanaiotti et al. 2001), Brazil - Bra3 (this study), Ecuador – Ecu (Muñiz-López et al. 2007), Guyana – Gui1 (Fowler and Cope 1964), Gui2 (Rettig 1978), Gui3 (Izor 1985), Panama – Pan1 (Touchton et al. 2002), Pan2 (Álvarez-Cordero 1996), Peru – Per (Piana 2007), Venezuela – Ven1, Ven2 (Álvarez-Cordero 1996).

The diversity of species taken by the Harpy Eagle throughout its geographic range suggests that this large predator might not be food-limited, but instead shows great feeding adaptability. This foraging behavior is a primary factor in the functional responses to maximize fitness (Pyke et al. 1977). There are breeding records from Venezuela (Alvarez and Ellis 1994, Álvarez-Cordero 1996) and Peru (Piana 2007), where Harpy Eagles have been breeding for years in areas dominated by human activities such as logging and manipulated forest, livestock grazing, and subsistence hunting. Optimal foraging theory (MacArthur and Pianka 1966, Pyke et al. 1977) suggests that dietary specialization can occur when a reliable and abundant food source is available. It seems likely that the abundance and accessibility of sloths, within their distribution range, has facilitated this level of dietary specialization. Even with the bias of different sample sizes in the studies throughout the Harpy Eagle's range, the patterns of resource use shown are valuable for understanding the dietary flexibility of the species.

Our analyses cannot show the extent to which a particular prey species was affected by Harpy Eagle predation because we do not have data on the relative population sizes of available prey. It seems reasonable that Harpy Eagle eat more sloths where sloths were common and eat more of other prey species where sloths are less common. Having a broader range of prey species reduces vulnerability from population fluctuations in any one prey species (Touchton et al. 2002).

Implications for Conservation. The patterns of prey species recorded in the Harpy Eagle diet are the result of various important factors acting on the foraging behavior and consequent predation success. Dietary studies of a top predator can show the interrelations between species, which can help researchers evaluate the carrying capacity in the remaining forests and in the protected areas in the near future. We found that in the central Amazonian forest, Harpy Eagle nesting territories that are near human development areas with different land uses (e.g., logging and small-scale agriculture) can support the reproduction of this large predator. Close proximity between Harpy Eagle nesting territories and human settlements has also been reported in Venezuela and Panama (Alvarez and Ellis 1994).

Conservation of the Harpy Eagle should include measures to protect nesting territories and prey to maintain the variety and availability of resources through its entire geographic range. We recommend outreach and environmental education within local communities to help reduce the belief that the Harpy Eagle is a threat to domestic animals (Curti and Valdez 2009). With traditional management focused on the species (Simberloff 1998), the Harpy Eagle can also be used as a charismatic keystone species (Simberloff 1998, Touchton et al. 2002, Curti and Valdez 2009), so that broader regions of these ecosystems may be protected.

The results from our study (1) extend our knowledge of food resources used by the Harpy Eagle, (2) suggest that the Harpy Eagle in this region does not include domestic animals in their diet, and (3) offer a comparison of the diet of the species throughout their range.

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