



Conservation implications of harpy eagle *Harpia harpyja* predation patterns

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ABSTRACT: Knowledge of the food habits of threatened taxa is key for their effective conservation, especially in top predators where prey species are frequently also hunted by humans. The harpy eagle *Harpia harpyja* is the largest living eagle, and is considered Near Threatened by the IUCN. Its main threats are persecution by humans and habitat loss. Predation patterns of this species have been the subject of several descriptive studies, each reflecting the idiosyncrasies of the study area. Systematizing these data permits a transition from descriptive treatments of harpy food habits to a predictive focus, based on defensive prey strategies and foraging theory. This generates information that can enhance management and conservation decisions. Literature data were summarized and standardized, allowing comparison between studies. Results indicate that harpy eagles feed mainly on sloths and other prey with passive antipredator strategies, with sloths accounting for 50 % of prey items and biomass consumed. Large monkeys such as howlers (*Alouatta* spp.) and capuchins (*Sapajus* and *Cebus* spp.) are the next most important prey, but combined, primates form only ~20 % of the consumed prey biomass. Predation seldom occurs on animals weighing more than 5 kg. This is positive from a conservation point of view, since sloths are not game species, precluding competition between harpy eagles and subsistence hunting.

KEY WORDS: Raptor · *Bradypus* · *Choloepus* · *Alouatta* · Prey defenses · Top predator · Diet

INTRODUCTION

Knowledge of the food habits of threatened taxa is essential for their effective conservation (Harper et al. 2006, Real et al. 2009). This is especially true for apex predators, since they are commonly dependent on large-bodied prey, which, in turn, are frequently hunted by humans (Hayward et al. 2012, Lyngdoh et al. 2014). Effective conservation planning (e.g. reintroductions, thematic conservation units, prevention of livestock losses) for such species must therefore include precise assessment of prey base composition. Predation patterns can be affected by a wide range of ecological constraints that vary across the geographic range of the predator species. Thus, local food habit descriptions may well have little practical utility in a range-wide conservation framework (Hayward & Kerley 2005, Schweiger et al. 2015). Other than local descriptions of prey-base composition,

such studies may offer little to improve the effective management of this type of species.

As predators with a large body size, raptors have low densities and high resource needs, both of which are strong predictors of high extinction risk (Krüger & Radford 2008, Lees & Peres 2008). The largest-ever raptor, the Haast eagle *Harpagornis moorei*, weighed up to 17 kg, preyed on giant moa and disappeared shortly after Maori colonization of New Zealand around 1400, probably due to prey loss, direct persecution, or both (Holdaway 1991, Scofield & Ashwell 2009). This kind of extinction event has occurred repeatedly on islands, and has affected both terrestrial and flying giant raptors, such as *Ornimegalonyx oteroi* in Cuba (Arredondo 1976) and *Stephanoaetus mahery* in Madagascar (Goodman 1994). The Philippine eagle *Pithecophaga jefferyi* (4.4–6 kg; Gamauf et al. 1998), the second largest raptor on earth, is categorized as Critically Endangered by the IUCN; no

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more than 250 pairs remain in the wild, and this species is faced with prey depletion, habitat loss, and poaching (Birdlife International 2013a).

The harpy eagle *Harpia harpyja* is the world's largest living eagle, weighing between 4.8 and 7.6 kg (Sick 1984, Ferguson-Lees & Christie 2001). In Central and South America, harpy eagles are threatened by retaliation for predation (imagined and real) on domestic animals, habitat loss, use as food, and by curious settlers and colonists who want to see the birds closer at hand (Trinca et al. 2008, Godoi et al. 2012, Freitas et al. 2014). The species is distributed over forest ecosystems in Central and South America, but has nearly vanished from Cerrado and Atlantic Forest environments (De Oliveira & Silva 2006, Aguiar-Silva et al. 2012, Silva et al. 2013). Harpy eagles are categorized as Near Threatened by the IUCN, with declining population trends (Birdlife International 2013b).

Foraging theory predicts that predators with low search costs act to maximize energy gain by preying on animals of low detectability, but with high catchability once detected (Stephens et al. 2007). In contrast to most large raptors, harpy eagles rarely soar, and prey searching is dependent on visual and hearing skills, with relatively low energy expenditure while hunting (Touchton et al. 2002). This suggests (sensu foraging theory) that prey such as sloths (Megalonychidae and Bradypodidae), which rely mainly on crypsis to avoid predation, are likely to be important prey for harpy eagles. Prey that practice flight as well as crypsis can increase manipulation and/or searching time (Eason 1989, Touchton et al. 2002, Ferrari & Port-Carvalho 2003). In the context of top-down theory, and since raptors strongly shape primate behavior (Gil-da-Costa et al. 2003, Willems & Hill 2009), the absence of harpy eagles can indirectly increase herbivore pressure on vegetation (Terborgh et al. 2001, Orihuela et al. 2014) via population growth and increased vegetation consumption.

Although several excellent studies have investigated prey composition by harpy eagles, all of them were restricted by local idiosyncrasies, such as regional prey abundances and habitat types. Hence, an overview of predation patterns over the entire distribution of harpy eagles is timely. Aguiar-Silva et al. (2014) conducted a review in order to compare their results with published literature, but they used political rather than habitat boundaries and did not distinguish between multiple nests in a single sample (e.g. Fowler & Cope 1964, Muniz-Lopez et al. 2007) or multiple studies of a single nest (e.g. Rettig 1978, Izor 1985).

In the present study, I synthesized the available information from a variety of previous studies on

harpy eagle diet, in order to answer the following questions: (1) What are the main prey items of harpy eagles, and what is their proportional biomass contribution to the diet? (2) Data on how many prey must be collected in order to adequately represent feeding habits? Additionally, 2 hypotheses, based on predictions from foraging theory, were tested: (1) the proportion of sloths in the diet will negatively affect niche width, and (2) the antipredator strategy of the main prey species will be passive, with morphological and behavioral specializations for crypsis. Such information can be used to help predict predation patterns and carrying capacity of unstudied populations, and have implications for viable and effective management and conservation strategies.

METHODS

Data acquisition and compilation

A data search was made with Google Scholar using *Harpia harpyja* and the following keywords: harpy eagle, *arpia*, *gavião-real*, *harpia* combined with diet, food habits, *hábitos alimentarios*, and *dieta*. This allowed me to access published and unpublished studies in English, Portuguese, and Spanish. Studies which were known to exist but which could not be downloaded were obtained in direct contact with authors or by contacting the Brazilian Harpy Eagle Conservation Program (gaviaoreal.inpa.gov.br).

I tabulated relevant data collected by direct observation or from analyses of bone material and pellets collected from beneath nest trees or from inside nests accessed by climbing. I considered only studies whose estimation of the minimum number of prey individuals included standardized collection procedures or studies that counted skulls, pelvises, and other unpaired bones or perfectly paired limb bones. This procedure permits the use of unpublished studies when data were derived from robust and standardized methods. Two studies (Chebez et al. 1990, Anfuso et al. 2008) were excluded because the sample sizes of prey items were small (<5) and uncertainties in prey item identification. A further 2 studies (Rettig 1978, Izor 1985) were collapsed into a single sample since they came from a single nesting event investigated at different times. When possible, I considered each individual bird as a replicate, but most studies used each nest as an independent unit, and others collapsed several nests into 1 data set. In those cases, nest data were computed as a single replicate.

Standardizing data

Raw data were compiled and tabulated as frequency of occurrence (FO). The FO for each prey species is the number of prey occurrences \times 100 divided by total sample size. Where prey species were similar in size and antipredator defense strategy, they were grouped in units that retained taxonomic and/or ecological significance. Species that were rarely preyed upon were grouped together irrespective of their size and strategy, as done elsewhere (Brodie et al. 1991). To estimate consumed biomass, the mean weight of each prey species were taken from canonical sources: Abe & Johansen (1987), Bodmer & Lozano (2001), Carvajal-Villarreal et al. (2012), Ceballos & Oliva (2005), de Barros & de Carvalho (2010), Ford & Davis (1992), Fournier-Chambrillon (1997), Handley & Pine (1992), Helgen et al. (2013), Hennemann (1985), Koster (2008), Mayor et al. (2011), McDonough (2000), Parry et al. (2009), Peres (1997), Richard-Hansen et al. (1999), Robinson & Redford (1986), Thiollay (1989), and Montgomery (1985). When species in the same category differed in weight, I used a calculated mean species weight to estimate biomass. Unidentified birds were assigned a mean body mass derived from all identified birds. Those mass data were then multiplied by the number of occurrences of each given prey, and then divided by the total prey mass, revealing the contribution of each prey species. Because in sloths, 30 % of raw body weight comes from ingested plant material (Goffart 1971), and this is not used as food by harpy eagles, I removed this effect by multiplying the biomass of sloths by a factor of 0.7. Both sloths and howler monkeys are known to be preyed on primarily when young (Touchton et al. 2002, Aguiar-Silva et al. 2014). Hence, to avoid overestimating their contribution to diet biomass by using adult body mass, a 0.7 correction factor was again deployed. This was applied to ungulates for the same reason, using 0.5 instead, since they are exclusively preyed upon when young (Touchton et al. 2002, Ferrari & Port-Carvalho 2003). These corrections do not apply to other prey species because there is no evidence that they are killed as young and no evidence that harpy eagles discard their viscera. To describe the size distribution of prey species, a histogram of prey mass was constructed based on the same literature (see Fig. 1). Touchton et al. (2002) offered a novel classification for harpy eagle prey, dividing the species into terrestrial, social arboreal, and solitary arboreal, but did not take into account the extensive work done on the subject of prey defense (Greene 1988, Brodie et al. 1991, Caro 2005). In the present study, I

followed Brodie et al. (1991) in prey categorization. Prey species were grouped into 3 categories based on their known antipredator strategies: (1) species that rely on low detectability or possess morphological mechanisms to avoid predation (hereafter called 'passive': includes sloths, armadillos, and porcupines); (2) species that use avoidance behavior linked with high vigilance to elude predators (hereafter called 'vigilant': includes primates, birds, agouties, and most carnivores); and (3) species that could not be clearly included in 1 of the 2 preceding categories (hereafter called 'others': includes kinkajous, opossums, ant-eaters, and reptiles).

Statistical analyses

To answer Question (1) regarding the main prey items of harpy eagles, and their proportional biomass contribution to the diet, I summarized general predation patterns for harpy eagles in 2 tables, which include general research effort and importance of each prey. For Question (2) regarding the number of prey samples which have to be collected in order to adequately represent feeding habits, I tested how many samples are enough to adequately detect the 4 main prey types, using expected species richness in random subsamples of 5 prey from the total sample until asymptotic stabilization was achieved as a sign of high detection probability. To address Hypothesis (1) (the proportion of sloth in the diet will negatively affect niche width), for each replicate, I tested the effect of sloth proportion in the diet on niche width with a Pearson correlation and compared the proportion of sloths in the diet with Levins diversity index. This is given by $B = B - 1 / (n - 1)$, where B is Levins index ($B = 1 / \sum p_i^2$), p_i is the FO of each group of prey species, and n is the total number of prey species (Krebs 1999). The obtained Pearson correlation result was compared with the correlation of 10 000 Monte Carlo simulations of the same dataset to guarantee independence. To test Hypothesis (2) (the antipredator strategy of main prey species will be passive, with morphological and behavioral specializations for crypsis), I tested the differences between categories of antipredator defenses using a Kruskal-Wallis test, having first transformed the data and found no fit to exponential curves (Shapiro-Wilks, $p < 0.05$). In this analysis, each category of antipredator strategy was a factor, and the FO was the explanatory variable. All statistical analyses were conducted using the *vegan* package in R (Oksanen et al. 2007). Significance levels were established at $\alpha = 0.05$.

Table 1. Descriptive data from harpy eagle (*Harpia harpyja*) food habit studies. Studies are ordered by the number of nests monitored. Touchton et al. (2002) worked on 2 reintroduced individuals. Rettig (1978) and Izor (1985) were considered as a single replicate as they include data from the same nest in different years. The number of species identified in the remains ('richness') and the number of prey remains collected (n) and identified are also shown

Source	Nests	Site	Richness	n	Identified
Touchton et al. (2002)	–	Barro Colorado, Panama	9	25	25
Touchton et al. (2002)	–	Barro Colorado, Panama	8	46	46
Fowler & Cope (1964)	1	Kanaku Montains, Guyana	3	11	11
Fowler & Cope (1964)	1	Kanaku Montains, Guyana	6	16	16
Rotenberg et al. (2012)	1	Bladen Nature Reserve, Belize	9	17	17
Galetti & de Carvalho (2000)	1	Cauaxi Farm, Brazil	3	21	21
Muñiz-López et al. (2007)	1	Esmeraldas, Ecuador	3	21	20
Seymour et al. (2010)	1	Sierra Imataca, Venezuela	2	23	14
Alvarez-Cordero (1996)	1	Guayana, Venezuela	8	45	37
Rettig (1978), Izor (1985)	1	Kanaku Montains, Guyana	16	85	69
Muñiz-López (2008)	1	Reserva Cuyabeno, Ecuador	16	109	102
Sanaïotti et al. (2001)	1	Manaus, Brazil	6	26	25
Alvarez-Cordero (1996)	3	Darien, Panama	19	97	91
Piana (2007)	4	Comunidad de Infierno, Peru	14	80	79
Aguiar-Silva et al. (2014)	5	Parintins, Brazil	14	253	240
Muñiz-López et al. (2007)	10	Esmeraldas, Ecuador	14	53	47
Alvarez-Cordero (1996)	11	Guayana, Venezuela	19	94	88
Total	43			1022	948

RESULTS

I reviewed 13 harpy eagle food habit studies spanning 8 countries. These reports analyzed between 11 and 253 prey remains from 1 to 11 nests, for a total of 43 nests plus 2 non-nesting reintroduced animals sampled. From these 94 individual birds, 1022 prey remains were collected, of which 948 were identified. The number of species represented in the remains varied from 2 to 19 (Table 1).

Sloths were by far the most common prey (Table 2). Combined, two- and three-toed sloths constituted some 53% of prey items and 50% of biomass consumed by harpy eagles, and were energetically the most important prey category. Howler monkeys (*Alouatta* spp.) were the second most important prey category, representing some 7% of prey, but because of their size (mean = 6.59 kg, 4.61 kg after correction), they represented over 12% of diet biomass. Numerically, capuchin monkeys (*Cebus* and *Sapajus* spp.) were the third most important category, but because of their smaller size, their biomass contribution was only 7%. Fourth were porcupines (genera *Sphiggurus* spp. and *Coendou* spp.), representing around 5% in both biomass and frequency. Other primates, plus several terrestrial and semi-arboreal prey, including agouties, carnivores, marsupials and birds, were all of lesser importance in both frequency and biomass. Most prey weighed less than 5 kg, although some predation on larger animals was

recorded (Fig. 1). The Pearson correlation value for proportion of sloths in the diet and niche width was strong, -0.8 (Fig. 2), and Monte Carlo randomization indicated that this was not the product of chance ($p < 0.05$). A Kruskal-Wallis test on different harpy eagle prey showed that most have passive antipredator strategies (mean occurrence of slightly over 30%), followed by vigilant prey (9%) and finally by other strategies with less than 5% ($df = 2$, $p < 0.05$, Fig. 3). Asymptotic stabilization of the rarefaction prey richness curve was reached at 25 collected prey to adequately represent the 4 main prey groups (Fig. 4), with prey in the fourth group contributing less than 5% of diet. Fig. 5 shows a series of photos of harpy eagles manipulating different prey items.

DISCUSSION

Sloths are the main prey of harpy eagles wherever both species co-occur. Contrary to common misconceptions, sloths are not defenseless animals. Researchers who have directly observed multiple events of predation on these animals described their defenses as 'formidable' (Touchton et al. 2002): both genera are capable of swinging their fore-claws at predators, and two-toed sloths also have a strong bite. Nevertheless, as in any predator-prey system, and based on known high sloth densities (Montgomery & Sunquist 1975), most sloths avoid most

Table 2. Harpy eagle *Harpia harpyja* prey ordered by importance in terms of frequency and biomass with data taken from food habit studies (data for individual studies show frequency, %, Rettig (1978) and Izor (1985) were considered as a single replicate as they include data from the same nest in different years

Prey	Aguilar-Silva et al. (2014)	Muniz-López, (2008)	Alvarez-Cordero (1996)	Alvarez-Cordero (1996)	Piana (2007)	Rettig (1978); Izor (1985)	Muniz-López et al. (2007)	Touchton et al. (2002)	Alvarez-Cordero (1996)	Sanabotti et al. (2001)	Touchton et al. (2002)	Galetti & de Carvalho (2000)	Muniz-López, (2008)	Rotenberg et al. (2012)	Fowler & Cope (1964)	Seymour et al. (2010)	Fowler & Cope (1964)	Overall frequency (%)	Overall biomass (%)
Sloths (<i>Bradypus</i> and <i>Choloepus</i>)	82.1	42.2	31.9	43.2	31.6	37.7	38.3	54.3	51.4	76.9	52.0	95.2	90.0	0.0	18.8	57.1	27.3	53.2	50.2
Howlers (<i>Alouatta</i>)	4.2	13.7	1.1	10.2	2.5	1.4	14.9	28.3	13.5	3.8	12.0	0.0	0.0	17.6	0.0	0.0	0.0	7.3	12.4
Capuchins (<i>Cebus</i> and <i>Sapajus</i>)	1.7	4.9	23.1	4.5	1.3	18.8	6.4	6.5	2.7	0.0	0.0	0.0	0.0	0.0	50.0	42.9	63.6	8.0	7.8
Porcupines (mostly <i>Coendou</i>)	2.9	2.0	7.7	8.0	19.0	7.2	6.4	0.0	2.7	0.0	4.0	0.0	0.0	0.0	6.3	0.0	9.1	5.3	5.2
Other primates	5.4	22.5	3.3	0.0	1.3	2.9	17.0	0.0	0.0	7.7	0.0	0.0	0.0	5.9	0.0	0.0	0.0	5.8	4.9
Agouties (<i>Dasyprocta</i>)	0.4	3.9	7.7	0.0	0.0	7.2	4.3	0.0	0.0	0.0	4.0	0.0	0.0	0.0	12.5	0.0	0.0	2.3	3.8
Carnivora (mainly <i>Nasua</i>)	0.0	1.0	5.5	4.5	8.9	4.3	0.0	2.2	0.0	0.0	12.0	0.0	0.0	17.6	6.3	0.0	0.0	3.0	3.2
Kinkajou (<i>Potos flavus</i>)	0.8	2.9	8.8	3.4	15.2	11.6	4.3	0.0	2.7	7.7	4.0	0.0	0.0	5.9	0.0	0.0	0.0	4.5	2.9
Ungulates	0.0	0.0	1.1	0.0	0.0	1.4	0.0	2.2	0.0	0.0	12.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.5
Anteaters (<i>Tamandua</i>)	0.0	0.0	1.1	0.0	11.4	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	1.3	2.2
Sakis (<i>Pithecia</i>)	0.8	2.0	1.1	3.4	0.0	1.4	2.1	0.0	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.6
Birds (mainly <i>Ara</i>)	0.8	3.9	3.3	11.4	5.1	0.0	6.4	0.0	2.7	3.8	0.0	0.0	10.0	17.6	0.0	0.0	0.0	3.5	1.2
Opossums (mainly <i>Didelphis</i>)	0.8	1.0	4.4	3.4	2.5	4.3	0.0	2.2	0.0	0.0	0.0	4.8	0.0	23.5	6.3	0.0	0.0	2.3	0.9
Armadillos	0.0	0.0	0.0	3.4	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7
Reptiles (mainly <i>Iguana iguana</i>)	0.0	0.0	0.0	4.5	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	0.7	0.5

harpies most of the time (Endler 1991), probably thanks to their very low detection probability. This is supported by the fact that sloths have seldom been observed during studies estimating population sizes of arboreal animals, regardless of the sampling effort (Galetti & de Carvalho 2000), although sloths are probably the most abundant mammal in the rainforest canopy, reaching a density of 800 animals km⁻² (Montgomery & Sunquist 1975; but see Carvajal-Nieto et al. 2013 for a recent review). Rescues from flooding hydroelectric dam reservoirs also indicate their overwhelming abundance in Neotropical forests: 28 925 three-toed sloths *Bradypus tridactylus* and 11 935 two-toed sloths *Choloepus didactylus* were rescued in the 2230 km² Tucuruí Power Dam filling (Alho 2011), yielding estimates of 18 sloths km⁻² for the entire area of the reservoir, i.e. including open environments where sloths do not occur.

If this value is similar, at least in its order of magnitude, in other rainforests where sloths and harpies interact, the abundance of the most common primate in the area covered by Alho (2011), viz. the red-handed howler monkey *Alouatta belzebul*, is only ca. half that of sloths (i.e. 19 652 individuals). This would have interesting consequences, since it would mean that sloths are in reality preyed upon more than expected by chance, and that primates are, proportionately, less strongly selected for.

If predation on primates is preferential, it could be due to their superior energetic content per unit mass. Sloth metabolism is slow, and around a third of their body mass comes from leaves that are still in the process of being digested (Goffart 1971). They also have very thick skin and little muscle tissue. Although primates have more energy per body mass unit and are easily detected when compared to sloths, they are harder to capture. On Barro Colorado Island,

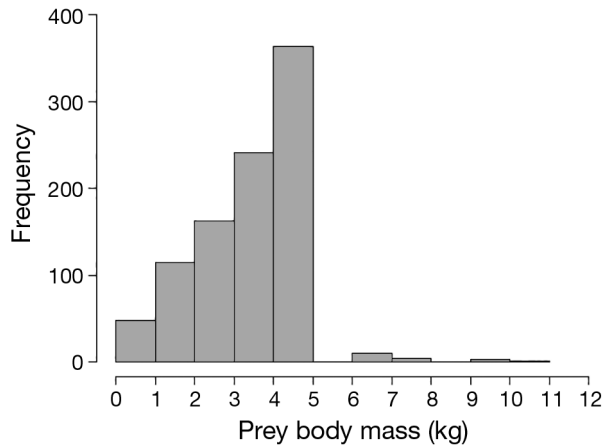


Fig. 1. Prey mass frequency distribution. Predation was most common on animals <5 kg, although larger animals were also killed. The left side of the distribution is likely to be longer, since small prey have a smaller detection probability; therefore, these data should be interpreted with caution

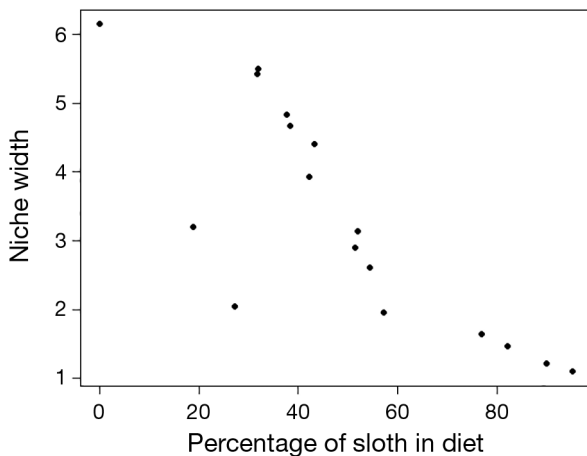


Fig. 2. Effect of sloths (as a proportion of diet) on harpy eagle *Harpia harpyja* diet niche width, which describes how an organism or population responds to the variation in distribution of resources changing the form of realized and fundamental niche hypervolume. In areas where harpy eagles eat fewer sloths, a broader niche width is observed. Monte Carlo randomization indicates that this is not the product of chance ($p < 0.05$)

Touchton et al. (2002) recorded a 30% success rate for harpy predation attempts on monkeys, compared with 55% success when preying on sloths. Monkeys are also capable of showing aggressive behavior toward predators (Gautier-Hion & Tutin 1988, Jones et al. 2006), and could potentially harm harpy eagles. It is noteworthy that both capuchins and howlers (particularly males) direct intense mobbing behavior at predators, unlike other primates, whose main defensive behavior is evasion (Barnett et al. 2011,

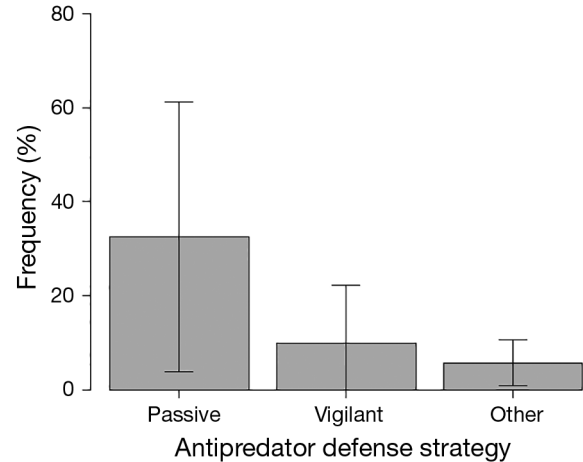


Fig. 3. Effects of antipredator strategy on the frequency of predation. Values are means \pm SD (Kruskal-Wallis test). See 'Methods' for category definitions

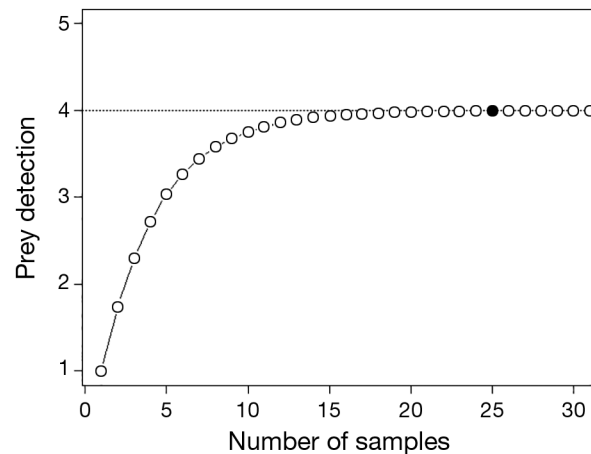


Fig. 4. Sample size plotted against detection probability of the 4 main prey species, indicated by the dotted line. Above 25 samples (indicated by the black dot), there is high detection probability for main prey species

Lenz & dos Reis 2011). This defensive behavior may be the reason why capuchins and howlers are the most common primate prey, underscoring the difficulties for harpy eagles to successfully capture agile prey. Strategies involving flight appear to be more effective against predation by harpy eagles than fighting or camouflage. Addressing the issue of prey selection by harpy eagles within the framework of foraging theory could help improve our understanding of the costs of predation on prey that are low risk but of low detectability (sloths), compared with those that are easy to detect but have low catchability and/or are more dangerous (monkeys).



Fig. 5. Although they primarily prey on sloths, harpy eagles *Harpia harpyja* feed upon a diversity of prey types. (A) Two-toed sloth *Choloepus didactylus* and (B) howler monkeys *Alouatta* sp. are among the most frequently killed mammals. (C) Porcupines (*Coendou* sp., already plucked) are important prey in some areas. (D) Terrestrial prey such as agouties *Dasyprocta* spp. are rarely killed in forest areas. (E) Arboreal nocturnal carnivores such as kinkajou *Potos flavus* are commonly killed in some areas, but because of their small size have a low contribution to harpy diet biomass. Harpy eagles are capable of acting opportunistically: (F) and (G) show eagles preying on *Iguana iguana* and on olive oropendula *Psarocolius bifasciatus* nestlings. Photos by Danilo Mota (A), César Alexandre (B), Alex Costa (C), Marcos Cruz (D), Christopher Borges (E), João Gomes (F), and Francielly Reis (G); all photographs used with permission

The Pearson correlation shows that the lower the proportion of sloths in the diet, the more diverse the harpy eagle feeding niche, indicating that eagles have some degree of specialization on this prey type and become less stenophagic when sloths are rare or absent. Rotenberg et al. (2012) showed the highest niche width (6.15) in a slothless area (Bladen Nature Reserve, Belize). Harpy eagles in northern Argentina, which were not included here because of their small sample size, were the only other individuals investigated in slothless tropical forests and showed the highest niche width in a review performed by Aguiar-Silva et al. (2014).

Rarefaction curve results show that at least 25 samples are needed to adequately represent the 4 main prey species of harpy eagles. I restricted the analysis to the 4 main prey because after the 4 main prey, the importance in biomass of other species decreases to less than 5%. Therefore, I recommend that researchers in tropical forests like the Amazon, Central America, and the Atlantic Forest should aim at collecting at least 25 prey remains. Studies in slothless areas, where the diet is likely to be broader, will probably need a greater sample size to guarantee representativeness. Future studies should also aim to quantify the diet of non-breeding birds. Previous research suggests that eagles feed on larger prey items when they do not need to carry them to the nest (Watson 2010). My small sample size of non-breeding animals ($n = 2$) precludes any statistical analysis on this subject.

The overwhelming number of sloths in the general harpy eagle diet begs the question as to what harpy eagles kill in slothless regions. Areas like the Pantanal, the Cerrado, and semideciduous Atlantic Forest are outside the distribution of *Bradypus* and *Choloepus*, and these regions currently have small, if any, populations of harpy eagles (Godoi et al. 2012, Silva et al. 2013), and present studies are incapable of attributing a cause to this pattern. If the hypothesis presented here is correct and harpy eagles are truly specialized in preying on species with passive anti-predator defenses, I predict that animals with similar strategies, such as armadillos and porcupines, will probably be substitutes for sloths in such areas. If, on the other hand, harpies prey on sloths only because they are abundant, prey substitution will place monkeys as the main prey in those areas, assuming they are abundant. These hypotheses are not mutually exclusive, but the first could indicate that such eagle populations are hunting terrestrial prey, which would challenge the existing literature (Touchton et al. 2002, Aguiar-Silva et al. 2014). This could be the

case in areas that are more open when compared to the Amazon, such as the Cerrado and the Pantanal, where assessing terrestrial prey is easier.

I recommend that future studies of harpy eagle predation patterns attempt to address prey population densities in order to understand the relationships between diet preferences and the relative abundance of species comprising the prey base. Most prey species could be censused using techniques described by Buckland et al. (1993). However, one of the main premises of linear transects is that all study objects have an equal probability of being detected. This is strongly violated by sloths, the main harpy prey. Some success has been achieved in estimating populations of cryptic mammals by mtDNA (which can be accessed by means of studies of feces to genotype individuals), and such methods could help greatly in future sloth population estimates (Miotto et al. 2014, Roques et al. 2014). Drones are also changing wildlife monitoring practices and can be combined with infrared cameras to make sloths detectable in line transects (Tang & Shao 2015). Another aim for future research should be monitoring prey consumption in nests at sites outside Amazonia and Central America, where harpy eagles are likely to be dependent on other, non-sloth, prey species. This would lead to a better understanding of why they disappeared from these areas first, since other non-sloth species are popular game, and prey competition could be involved. Such information is critically important for the effective conservation of the species.

Clearly, any effort to increase nest monitoring in other areas is handicapped by the costs and logistics of doing so in such vast and remote areas. Techniques such as camera traps have greatly enhanced our capacity to monitor a larger number of nests without substantial investments in people and money (Cox et al. 2012). Furthermore, such monitoring can provide data on parental care and nestling survivorship, which is key for conservation. Combining this technology with solar panels will give great autonomy to cameras, thereby greatly reducing the costs for harpy eagle nest monitoring and thus allowing simultaneous monitoring of several nests in an area. This could be a solution for studying nests that are in inaccessible areas and cannot be visited regularly.

The high proportions of sloths in the diet of harpy eagles in the Amazon Forest and Central America, the main strongholds of the species, is good news for the long-term survivorship of this raptor. Sloths are not game species and are hunted only by a few indigenous communities (Ross et al. 1978). Thus,

competition with humans is probably rare, and prey depletion would likely not be a problem. Sloths are incapable of surviving in clear-cut areas, but they can maintain populations in mosaic landscapes (Cassano et al. 2011, Mendoza et al. 2015), where harpy eagles are also able to survive (Alvarez-Cordero 1996, Aguiar-Silva et al. 2014). Additionally, areas that still retain a strong population of sloths, but which have lost their former harpy eagle populations, might be able to sustain reintroduction programs such as the ongoing one in Central America (Campbell-Thompson et al. 2012), if the causes of harpy eagle extirpation are eliminated. This applies to several Atlantic Forest conservation units (Chiarello 1999, 2000), where populations of this raptor could be established. This ecosystem has been the subject of extensive deforestation over the last 5 centuries (Dean 1996), and apex predator loss is pervasive (Jorge et al. 2013).

Formerly considered somewhat theoretical, the fields of antipredator defense strategies and foraging theory instead provide a comprehensive basis for conservation biology (Caro 2005, Stephens et al. 2007). Combining these theories can lead to optimality-based research which can efficiently monitor populations of threatened species. Foraging theory can explain underlying needs and preferences, as well as fundamental community organization (Agüera et al. 2015, Schweiger et al. 2015). Over much of its range, the harpy eagle forages principally on prey species that have exceptional morphological and behavioral traits to avoid detection. Although sloths have thickened skin and large claws, their chances of survival after being attacked by harpy eagles are small (Touchton et al. 2002). The predator-prey relationships of harpy eagles and sloths provide a framework in which new aspects of ecological theory could be applied, involving low-detection prey species that cannot switch habitats to avoid danger from flying predators which hunt from perches, carefully listening and looking for their prey.

The data summarized here make it possible to move from a description-based study of harpy eagle predation patterns to a predictive focus, founded on prey defensive behavior and foraging theory. Using this approach, wildlife management and conservation institutions should be able to predict what harpy eagles will kill in an area in the absence of any previous data, and to plan accordingly. From a conservation viewpoint, when planning reintroductions and translocations, confirming the presence of an adequate prey base with suitable species will increase the chances of success.

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