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Research Article

Prey Composition of Harpy Eagles (*Harpia harpyja*) in Raleighvallen, Suriname

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Abstract

Apex predators are in widespread decline, in many occasions as a consequence of the demise of their prey. Harpy Eagles (*Harpia harpyja*) are the largest extant eagles on Earth and keystone predators in the tropical forests they inhabit. Although Harpy Eagle prey composition has been described by a number of studies, diet data from primary forests are rare on the literature. Here, I describe the diet of Harpy Eagles living in the Central Suriname Reserve primary forests and review literature data to provide an accessible reference to all known reports of Harpy Eagle prey species. In Central Suriname Nature Reserve, Harpy Eagles made frequent use of game prey such as large primates, large birds, and terrestrial animals, besides what is considered their staple prey, sloths. Nine new prey species were recorded, most of them game animals. This totals 102 prey species when summed with literature data. This information provides new insights into the autecology of Harpy Eagles in Neotropical forests, enabling a better understanding of the ecological effects of apex predator.

Keywords

apex predator, primate predation, primary forest, nonhunted forest, aerial predator, canopy

Introduction

Predators have widespread regulatory potential over the biological landscapes they inhabit (Newsome et al., 2017) and are thus prioritized in the conservation biology agenda (Sérgio, Newton, Marchiesi, & Pedrini, 2006). An adequate prey basis is one of the most important determinants of predator persistence (Barber-Meyer et al., 2013; Lamichhane et al., 2018). To better understand the importance of predator–prey interactions, we need to understand composition of the prey base in detail (Uulu, Wegge, Mishra, & Sharma, 2014). Indeed, prey composition is a trademark of apex predator's scientific literature (Hayward & Kerley, 2005; Schweiger, Fünfstück, & Beierkuhnlein, 2015).

The Harpy Eagle (*Harpia harpyja*; Figure 1) is the largest extant eagle on Earth, weighting from 4.9 to 6.9 kg in males and from 5.9 to 9.1 kg in females. They hunt by sight and hearing, carefully scanning the canopy for prey species (Touchton, Hsu, & Palleroni, 2002). Harpy Eagles have been recognized as keystone predators, and in their absence, overgrown prey populations can cause trophic cascades (Orihuela, Terborgh, Ceballos, & Glander, 2014; Terborgh et al., 2001). Harpy Eagles are threatened by habitat loss and shooting (Muñiz-López, 2017). While they have disappeared from much of their former distribution (Vargas-González et al., 2006), Amazonia remains their last stronghold. Harpy Eagles have been described as sloth (Pilosa order) specialists in Amazonia (Aguiar-Silva, Sanaiotti, & Luz, 2014; Miranda, 2015), preying extensively on them wherever they occur together. Sloths are the most abundant vertebrates in Neotropical forests (Taube, Vie, Fournier, Genty, & Duplantier, 1999). Nonetheless, Harpy Eagles also rely upon other prey, such as large-sized monkeys (Barnett, Schiel, & Deveny, 2011), large birds, and some terrestrial animals (Alvarez-Cordero, 1996). There is currently no catalog of Harpy Eagles' prey species diversity in the scientific literature.

The most common method used to characterize Harpy Eagle prey composition is to search their nests for prey remains. However, finding Harpy Eagle nests

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Figure 1. Harpy Eagle eating a Howler monkey in Suriname (Photo credit: Rienus Van Der Wal, Kabalebo Nature Resort).

is a challenging task. Densities as low as 3 to 6 nests per 100 km^2 (Vargas-González & Vargas, 2011) make the ornithological community celebrate every nest discovery (Pereira & Salzo, 2006; Rotenberg, Marlin, Pop, & Garcia, 2012; Ubaid, Ferreira, de Oliveira, & Antas, 2011). Half a century of research on the species has identified over 50 nests that allowed the collection of more than one thousand individual prey remains (Miranda, Campbell-Thompson, Muela, & Vargas, 2017). Nevertheless, these discoveries were made by indigenous people, poachers, loggers, and other people involved in a diverse range of land uses. Those nests are therefore mostly located in modified landscapes. Hence, prey composition of Harpy Eagles in primary forests is still poorly known.

Here, I report the prey composition of a pair of Harpy Eagles in a primary forest site, the Central Suriname Reserve, and collate a complete prey species list for this key raptor. With this, I plan to advance the knowledge of Harpy Eagle prey composition in primary forests and to provide contemporary researchers with a single, accessible reference to all known reports of species used as prey by Harpy Eagles.

Methods

Study Site

Raleighvallen (4°39′30.6″N 56°10′43.4″W) is part of the larger Central Suriname Nature Reserve, which consists of 1.6 million ha of primary and tropical forest that has not been hunted for several decades. The site is limited on the northwestern part by the eastern bank of the Coppename River and has a mean altitude of 30 m. Rainfall averaged 1967 mm between 2000 and 2005. Rainfall shows multimodal seasonality, with a brief rainy season in December to January, a brief dry season in February to March, a long wet season in April to July, and a long dry season in August to November. Minimum and maximum temperatures, noted daily, averaged 23.7°C and 28.9°C, respectively, during the study period (Vath, 2008).

Data Collection and Identification

Workers of the Monkey-Forest Project discovered a Harpy Eagle nest in 2002. A field crew visited the site once a week to monitor activity and to retrieve bones and other prey body parts beneath the nest. This continued up to a second nesting cycle in 2004. Bones and other materials were identified by comparison with reference collections: Southern Illinois University for primates and other mammals, and Florida Museum of Natural History for birds and reptiles.

Literature Review

I conducted an extensive literature search concerning interactions between Harpy Eagles and their prey using Google Scholar, Web of Science, Scopus, and Scielo search engines. I also consulted other researchers for unpublished studies and literature unrevealed by online searches. In my search, I used the following keywords: *Harpy Eagle*, *Harpia harpyja*, *harpia*, *águila arpía*, and *águila harpía* combined with *diet*, *feeding habits*, *food habits*, *habitos alimentarios*, and *dieta*. This allowed me to find published and unpublished data in English, Portuguese, and Spanish.

Biomass Calculation

As differently sized prey offer different energetic contributions to predators, I added a biomass calculation to prey composition. All prey individuals were considered average sized adults, and whereas it is known that Harpy Eagles prey over juveniles of many species (Aguiar-Silva et al., 2014), the proportions of adults and juveniles were not known in data presented here. An exception was made for ungulates, which are known to be preyed exclusively when young and were therefore considered to weight one fifth of total adult body mass. As undigested leaves inside sloths average one third of their body mass (Goffart, 1971), this reduction was applied on their biomass score. Biomass proportion of tortoises was reduced to two thirds, given that this is the proportion of edible tissue (Emmons, 1989). A complete list of bibliographical records used to obtain prey average body mass and their respective sample sizes is given in Table 1.

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Table 1. Body Mass, Sample Sizes, and Sources Used in the Consumed Biomass Calculation.

Species	Mass (kg)	Sample size (N)	Source
Tayassu tajacu	18.40	9	Richard-Hansen, Vié, Vidal, and Kéravec, 1999
Ateles paniscus	9.02	8	Parry, Barlow, and Peres, 2009
Choloepus didactylus	6.07	21	Wetzel and Montgomery, 1985
Chelonoidis denticulatus	5.90	50	Moskovits, 1985
Alouatta macconnelli	5.35	7	Ford and Davis, 1992
Boa constrictor	5.08	106	Bertona and Chiaraviglio, 2003
Tamandua tetradactyla	4.80	43	Richard-Hansen et al., 1999
Dasypus novemcinctus	4.60	19	McDonough, 2000
Dasyprocta leporina	4.37	62	Richard-Hansen et al., 1999
Bradypus tridactylus	4.01	7	Wetzel and Montgomery, 1985
Coendou prehensilis	3.60	70	Richard-Hansen et al., 1999
Cabassous unicinctus	3.44	2	Richard-Hansen et al., 1999
Crax alector	2.87	10	Dunning, 1992
Chiropotes chiropotes	2.85	33	Ford and Davis, 1992
Sapajus apella	2.71	203	Peres, 1997
Cebus olivaceus	2.60	3	Koster, 2008
Leopardus wiedii	2.40	9	Carvajal-Villarreal et al., 2012
Iguana iguana	2.29	54	Koster, 2008
Pithecia pithecia	2.10	9	Ford and Davis, 1992
Potos flavus	1.76	12	Richard-Hansen et al., 1999
Penelope sp.[a]	1.32	–	Dunning., 1992
Tupinambis teguixin	1.09	110	Herrera and Robinson, 2000
Didelphis marsupialis	1.08	131	Richard-Hansen et al., 1999
Psophia crepitans	1.03	14	Dunning, 1992
Saimiri sciureus	0.87	20	Ford and Davis, 1992
Didelphis imperfecta	0.76	18	Catzeflis, Richard-Hansen, and Fournier-Chambrillon 1997
Saguinus midas	0.54	40	Ross, 1991
Aratinga sp.[a]	0.10	–	Dunning, 1992

Note. [a]Averaged body masses of the species in the genus occurring at the study site.

Results

Remains collected under the Harpy Eagle nest at the Raleighvallen primary forest revealed 220 individual prey records, of a minimum of 26 species. Prey remains were mainly composed of sloths, which represented 39.1% of prey frequency and 43.6% of biomass consumed. From these, 19.5% were two-toed sloths, 10.45% unknown sloths, and 9.1% tree-toed sloths. Primates were the following most important prey, representing 34.5% of prey frequency and 40.4% of biomass consumed. The remaining prey were primarily medium-sized mammals, followed by large-sized birds and finally large reptiles (Table 2). The literature review revealed a total of 93 prey species, totalizing a prey list of 102 species given the 9 new prey records presented here (Table 3).

Discussion

The feeding habits of Harpy Eagles in the Raleighvallen primary forest are characterized by a high diversity of prey species—chiefly sloths and primates. Sloths are the most abundant folivore in the canopy of Neotropical forests. Primates, on the other hand, have an important role as prey in the primary forest of the study site because of their high energetic contribution to Harpy Eagle diet. The extensive trophic links between this apex predator and its highly diverse prey have tempting implications for the functioning of tropical ecosystems.

Sloths may appear ideal prey for a giant raptor, given their body size and slow-moving habits associated with heterothermy and low metabolism. A close examination of sloth biology suggests otherwise: (a) Sloths feed mainly on leaves, which average one third of their body mass (Goffart, 1971), reducing edible tissue availability for carnivores; (b) sloths have half the muscular mass (i.e., meat) of a mammal of comparable size (Britton & Atkinson, 1938), further constraining energetic availability to predators. (c) Contrary to popular perception, sloths are formidable prey (Touchton, 2010), ready to swing claws against predators, and two-toed sloths are vicious biters. Consequently, sloths are less cost effective when compared with primates but otherwise easier to catch (55% vs. 17% success rate by Harpy Eagles; Touchton et al., 2002). Higher predation rates over sloths is a possible result of more sophisticated methods of predation avoidance by primates (Barnett

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Table 2. Prey Composition of Harpy Eagles in Raleighvallen, Suriname.

Prey species	Body mass (kg)	Frequency % (*N*)	Biomass %
Two-toed sloth *Choloepus didactylus*	6.07	19.54 (43)	24.90
Red howler monkey *Alouatta macconnelli*	5.35	12.27 (27)	20.88
Unidentified sloths[a]	5.04	10.45 (23)	11.06
Pale-throated sloth *Bradypus tridactylus*	4.01	9.09 (20)	7.65
White-faced saki *Pithecia pithecia*	2.10	9.09 (20)	6.07
Red-backed saki *Chiropotes chiropotes*	2.85	4.54 (10)	4.12
Red-faced spider monkey *Ateles paniscus*	9.02	1.36 (3)	3.91
Green iguana *Iguana iguana*	2.29	5 (11)	3.64
Tufted capuchin *Sapajus apella*	2.71	2.72 (6)	2.35
Kinkajou *Potos flavus*	1.76	4.09 (9)	2.29
Wedge-capped capuchin *Cebus olivaceus*	2.60	2.72 (6)	2.25
Nine-banded armadillo *Dasypus novemcinctus*	4.6	0.90 (2)	1.33
Red-humped agouti *Dasyprocta leporina*	4.37	0.90 (2)	1.26
Yellow-footed tortoise *Chelonoidis denticulatus*	5.90	0.90 (2)	1.13
Lowland paca *Cuniculus paca*	6.25	0.45 (1)	0.90
Black curassow *Crax alector*	2.87	0.90 (2)	0.83
Red-tailed boa *Boa constrictor*	5.075	0.45 (1)	0.73
Lesser anteater *Tamandua tetradactyla*	4.80	0.45 (1)	0.69
Grey-winged trumpeter *Psophia crepitans*	1.49	1.36 (3)	0.65
Collared peccary *Tayassu tajacu*	3.68	0.45 (1)	0.53
Brazilian porcupine *Coendou prehensilis*	3.60	0.45 (1)	0.52
Naked-tailed armadillo *Cabassous unicinctus*	3.44	0.45 (1)	0.50
Squirrel monkey *Saimiri sciureus*	0.87	1.36 (3)	0.38
Unidentified small cat *Leopardus* sp.[b]	2.40	0.45 (1)	0.35
Guianan opossum *Didelphis imperfecta*	0.76	1.36 (3)	0.33
Gold tegu *Tupinambis teguixin*	1.09	0.90 (2)	0.32
Unidentified guan *Penelope* sp.[c]	1.317	0.45 (1)	0.19
Common opossum *Didelphis marsupialis*	1.08	0.45 (1)	0.15
Red-handed tamarin *Saguinus midas*	0.54	0.45 (1)	0.08
Unidentified conure *Aratinga* sp.[c]	0.10	0.45 (1)	0.01
Unidentified primates	–	2.72 (6)	-
Unidentified birds	–	1.81 (4)	-
Unidentified fish	–	0.45 (1)	-
Unidentified crab	–	0.45 (1)	-
Total		(220)	

Note. [a]Mean mass of the two other sloth species.
[b]Body mass of *Leopardus wiedii*, smallest cat in the study site.
[c]Averaged body masses of all species in the genus occurring in the study site.

et al., 2017; Mourthé & Barnett, 2014). In addition, sloths are more abundant, they outnumber even the most abundant primate species (the folivore-frugivore howler monkey, *Aloutatta* spp.) from a two-to-one (Alho, 2011) up to a seven-to-one ratio (Sergio et al., 2014). Sloths are therefore abundant but of low energetic cost effectiveness.

Harpy Eagle prey diversity encompasses 102 known prey species, a number that will rise steadily in the forthcoming years given the poorly explored species' autecology in tropical forests. Data reviewed here show that they prey over many of the largest species on Neotropical canopies, as Hyacinth macaws, Great curassows, Spider monkeys, and Green iguanas, as well as over smaller passerines and parakeets. Comparatively, the widespread and best studied predator of the Neotropics, the jaguar (*Panthera onca*), preys on 84 vertebrate species (Nowell & Jackson, 1996). The publication of detailed prey inventories and diet composition are important initial steps in conservation and management.

I emphasize that primary forest nests of Harpy Eagles—as the one described here—are mostly absent from the literature, given the idiosyncrasies that constrain nest finding. In summary, I have shown that Harpy Eagle prey composition in the Raleighvallen primary forest is mainly formed by sloths and primates. At Raleighvallen, Harpy Eagle diet includes a comparatively high amount of game species such as terrestrial mammals, large primates, and game birds, some recorded here for the first time. While the connection

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Table 3. Harpy Eagle Prey Species Recorded in the Literature and the Number of Predation Records (*n*).

Order	Species	n
Mammals		
Pilosa	*Bradypus trydactylus*	74
Pilosa	*Bradypus variegatus*	256
Pilosa	*Choloepus didactylus*	366
Pilosa	*Choloepus hoffmanni*	80
Pilosa	*Tamandua mexicana*	12
Pilosa	*Tamandua tetradactyla*	18
Primates	*Alouatta arctoidea*	1
Primates	*Alouatta belzebul*	10
Primates	*Alouatta macconnelli*	16
Primates	*Alouatta palliata*	25
Primates	*Alouatta pigra*	3
Primates	*Alouatta seniculus*	62
Primates	*Aotus azarae*	1
Primates	*Ateles geoffroyi*	1
Primates	*Ateles paniscus*	4
Primates	*Cacajao ouakary*	1
Primates	*Callicebus brunneus*	1
Primates	*Callicebus discolor*	7
Primates	*Callicebus hoffmannsi*	10
Primates	*Callicebus lucifer*	3
Primates	*Callicebus moloch*	1
Primates	*Cebus albifrons*	9
Primates	*Cebus capucinus*	7
Primates	*Cebus olivaceus*	66
Primates	*Cebus yuracus*	7
Primates	*Chiropotes albinasus*	3
Primates	*Chiropotes chiropotes*	1
Primates	*Chiropotes satanas*	16
Primates	*Chiropotes utahicki*	1
Primates	*Lagotrix lagotricha*	13
Primates	*Pithecia aequatorialis*	1
Primates	*Pithecia irrorata*	1
Primates	*Pithecia milleri*	1
Primates	*Pithecia monachus*	3
Primates	*Pithecia pithecia*	34
Primates	*Saguinus graellsi*	5
Primates	*Saguinus midas*	1
Primates	*Saguinus nigricollis*	4
Primates	*Saimiri macrodon*	17
Primates	*Saimiri sciureus*	14
Primates	*Sapajus apella*	32
Primates	*Sapajus cay*	1
Primates	*Sapajus robustus*	2
Primates	*Sapajus xanthosternos*	1
Primates	*Sapajus nigritus*	1
Carnivora	*Bassaracyon alleni*	6
Carnivora	*Cerdocyon thous*	1
Carnivora	*Eira barbara*	4
Carnivora	*Leopardus pardalis*	1
Carnivora	*Leopardus wiedii*	1
Carnivora	*Nasua narica*	20
Carnivora	*Nasua nasua*	17
Carnivora	*Potos flavus*	56
Carnivora	*Procyon cancrivorus*	1
Cingulata	*Cabassous centralis*	1
Cingulata	*Cabassous unicinctus*	2
Cingulata	*Dasypus novemcinctus*	9
Rodentia	*Agouti paca*	1
Rodentia	*Coendou bicolor*	20
Rodentia	*Coendou koopmani*	5
Rodentia	*Coendou mexicanus*	1
Rodentia	*Coendou prehensilis*	45
Rodentia	*Coendou spinosus*	1
Rodentia	*Dasyprocta fuliginosa*	6
Rodentia	*Dasyprocta leporina*	14
Rodentia	*Dasyprocta punctata*	2
Rodentia	*Sphiggurus melanurus*	1
Rodentia	*Sphiggurus insidiosus*	1
Didelphimorphia	*Didelphis albiventris*	4
Didelphimorphia	*Didelphis marsupialis*	27
Didelphimorphia	*Didelphis imperfecta*	1
Didelphimorphia	*Philander opossum*	1
Artiodactyla	*Mazama americana*	2
Artiodactyla	*Mazama guazoubira*	1
Artiodactyla	*Mazama temama*	2
Artiodactyla	*Tayassu tajacu*	6
Birds		
Psittaciformes	*Amazona farinosa*	1
Psittaciformes	*Amazona* spp.	3
Psittaciformes	*Anodorhyncus hyacinticus*	1
Psittaciformes	*Ara ararauna*	2
Psittaciformes	*Ara chloropterus*	1
Psittaciformes	*Aratinga* sp.	1
Galliformes	*Aburria cumanensis*	1
Galliformes	*Crax alector*	3
Galliformes	*Crax fasciolata*	1
Galliformes	*Crax rubra*	3
Galliformes	*Penelope* sp.	1
Galliformes	*Pipile pipile*	3
Passeriformes	*Cacicus haemorrhous*	4
Gruiformes	*Psophia crepitans*	1
Gruiformes	*Psophia leucoptera*	3
Piciformes	*Ramphastos culminatus*	1
Piciformes	*Ramphastos tucanus*	1
Suliformes	*Anhinga anhinga*	1
Opisthocomiformes	*Opisthocomus hoazin*	2
Cariamiformes	*Cariama cristata*	1
Reptiles		
Squamata	*Amphisbaena alba*	1
Squamata	*Boa constrictor*	1
Testudines	*Chelonoidis denticulatus*	2
Squamata	*Iguana iguana*	29
Squamata	*Tupinambis merianae*	1
Squamata	*Tupinambis teguixin*	2

Note. Given the very large number of references, a complete version of the table with all literature can be found in Supplementary Material Table 1.

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of human overhunting to the dietary traits described here cannot be straightly established, the multiple research groups that are working with dozens of Harpy Eagle nests may have an opportunity to advance on this question.

Implications for Conservation

Large primates, game birds, and terrestrial mammals such as armadillos and pacas are among the most persecuted prey by poachers in Amazonia, having disappeared from vast forest tracts (Jerozolimski & Peres, 2003; Peres & Palacios, 2007) but are abundant in Central Suriname Reserve (Vath, 2008). Five of the nine new prey records presented here are from widespread vertebrates that are game species, such as the lowland paca, the grey-winged trumpeter, and the yellow-footed tortoise. Despite limited direct evidence, poaching seems a remarkable phenomenon which led to the greater role of game prey species on the diet of Harpy Eagles in Raleighvallen when compared with other study sites. The same applies for the higher amounts of large primates on eagle diet. If my hypothesis survives further research, future efforts may address if trophic restructuring in secondary landscapes is in fact related with forest vertebrate elimination through hunting.

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Supplemental Material

Supplemental material for this article is available online.

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