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FORAGING ECOLOGY OF REINTRODUCED CAPTIVE-BRED SUBADULT HARPY EAGLES (*HARPIA HARPYJA*) ON BARRO COLORADO ISLAND, PANAMA

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Resumen. – Dieta de Águilas Arpía (*Arpia harpyja*) reintroducidas en la isla de Barro Colorado, Panamá. – Un macho y una hembra de Águila Arpía (*Harpia Harpyja*), ambos sub-adultos criados en cautividad y reintroducidos, fueron observados en la isla de Barro Colorado, Panamá, durante 89 y 205 días, respectivamente, desde Junio de 1999 a Agosto del 2000. El macho capturó 25 presas de nueve especies de mamíferos, y la hembra capturo 46 presas de 8 especies de mamíferos y una especie de reptil. El 52% de las capturas del macho fueron perezosos de dos dedos (*Choloepuus hoffmanni*) y de tres dedos (*Bradypus variegatus*). El 54% de las presas de la hembra fueron perezosos. Por término medio, el macho capturó una presa cada 3,6 días, con un consumo medio diario de 888 g. La hembra capturó, por término medio, una presa cada 4,4 días, con un consumo diario de 812 g. Las águilas atacaron especies arbóreas solitarias a una distancia de 1–50 m, algunas veces tras varios intentos precalculados a unos 5 m. Especies arbóreas sociales fueron atacadas la mayoría de las veces por sorpresa y a menos de 30 m, mientras que especies terrestres fueron atacadas por sorpresa y a menos de 10 m. El águila hembra fue observada capturando más especies arbóreas solitarias, de manera significante, durante tiempo soleado y durante la temporada seca. Del mismo modo, fue observada capturando más especies arbóreas sociales durante tiempo nubloso y en la temporada de lluvias. Los promedios de capturas con éxito para el águila macho y el águila hembra fueron de 38% y 49% respectivamente.

Abstract. – A male and female Harpy Eagle (*Harpia harpyja*), both reintroduced captive-bred subadults, were observed on Barro Colorado Island (BCI), Panama for 89 and 205 days, respectively, between June 1999 and August 2000. The male captured 25 individuals from nine different mammalian species and the female captured 46 individuals from 8 different mammalian and one reptilian species during the period of observation. Fifty-two percent of captures by the male were of two-toed (*Choloepus hoffmanni*) and three-toed (*Bradypus variegatus*) sloths. Fifty-four percent of captures by the female were of sloths. On average, the male made a capture every 3.6 days with a daily average consumption of 888 g. The female made a capture on average every 4.4 days with a daily average consumption of 812 g. The eagles attacked solitary arboreal prey species from 1–50 m distance, sometimes with several calculated attempts from within 5 m. Social arboreal prey species were most often attacked by surprise from less than 30 m, and terrestrial prey species were attacked by surprise from less than 10 m. The female eagle was observed to capture solitary arboreal prey significantly more during sunny weather and the dry season. She was also observed to capture social arboreal prey significantly more during cloudy weather and the wet season. Capture success rates of observed predations for the male and female eagle were 38% and 49%, respectively. *Accepted 14 March 2002.*

Key words: Harpy Eagle, *Harpia harpyja*, Barro Colorado Island, foraging ecology, predation.

INTRODUCTION

The Harpy Eagle (*Harpia harpyja*) is a large predator, member of a guild foraging primarily on mid-sized mammals in the forest canopy, and considered the world's most powerful raptor (Brown & Amadon 1968). Harpy Eagles formerly inhabited tropical lowland rain forests from southern Mexico to northern Argentina (Wetmore 1965). Due to the destruction and fragmentation of rainforests and heavy hunting pressure by humans, the Harpy Eagle is presently rare or extinct in much of Central America north of Panama. The Harpy Eagle is currently considered near-threatened throughout its current range (Collar *et al.* 1994).

Raptors have some of the lowest densities of all rainforest birds (Thiollay 1986). Presence of Harpy Eagles has been said to indicate an intact ecosystem (Albuquerque 1995) as top predators are often among the first species to disappear when pristine habitat undergoes human alteration or fragmentation (Leck 1979, Willis 1974, 1979a; Thiollay 1985b, 1985c; Noss & Cooperrider 1994, Terborgh *et al.* 1997). More recent findings show however, that Harpy Eagles sometimes occur in forest near recently disturbed areas (Alvarez-Cordero 1996). The generation of data on Neotropical raptor ecology and population densities is crucial to evaluate the impact of fragmentation on raptors in tropical communities (Thiollay 1980, 1985a, 1985b, 1985c; Whitacre & Thorstrom 1992). Terborgh (1988, 1990, 1991, 1992, 1997) has argued that top predators such as jaguars, pumas, and Harpy Eagles are keystone predators and that their removal from an ecosystem can cause profound changes in Neotropical forest communities (See also Wright *et al.* 1994). It is not yet clear how important raptors are as regulators of herbivore populations.

All previous field observations of Harpy Eagles have focused on nest behavior or brief observations of a single behavioral incident. Few natural history descriptions (mostly anecdotal or fragmentary) exist for the Harpy Eagle (Bond 1927, Friedmann 1950, Gochfeld 1978) and sightings are scarce (Chebez *et al.* 1990, Albuquerque 1995, Galetti *et al.* 1997). Predation records of the Harpy Eagle have included two observed attempts (Eason 1989, Peres 1990) and one post-predation encounter (Sherman 1991). Fowler & Cope (1964) initiated more detailed studies of the Harpy Eagle at two sites in British Guiana that described nests and provisioning behavior. Rettig (1977, 1978) continued studies at one of these nest sites and was able to provide a more detailed account of breeding behavior. More recently, Alvarez-Cordero (1996) conducted a study that documented initial investigations of the current status of Harpy Eagles and nesting home ranges for the Harpy Eagle in Venezuela and Panama. Despite these studies, Harpy Eagle foraging behavior had not been observed. Due to the potentially important role of this predator in tropical community dynamics, studies of the Harpy Eagle foraging behavior merit further attention.

The release of five radio-tagged captive-bred juvenile Harpy Eagles into Soberania National Park, Panama, commenced in January 1998 with a male and female. The third release was a male in May 1998, the fourth a female in August 1998, and the fifth a male in September 1998. The third and forth of these released eagles were transported to Barro Colorado Island in June 1999 and October 1999, and became the focus of this study. As a result of the ease and finesse with which these eagles captured their first prey in Soberania National Park without any human or parental guidance, we have made the assumption these subadult Harpy Eagles would exhibit the same behavioral ontogeny as wild Harpy Eagles.

With the reintroduction of these two eagles onto Barro Colorado Island we had the rare opportunity to collect extensive first-hand observations of foraging ecology and behavior in a natural setting where the last Harpy Eagle sighting was in 1950 (Willis & Eisenmann 1979b). Objectives of this study were to collect numbers and species of prey taken by these subadult eagles, hunting methodology used, prey response, and how these findings could impact the prey community dynamics on Barro Colorado Island.

STUDY AREA AND METHODS

This study was conducted on Barro Colorado Island (BCI), Panama (9º9'N, 79º51'W), a protected 1500-ha island which rises 137 m above Lake Gatun in the Panama Canal. BCI is covered by primary and secondary lowland tropical moist forest (Croat 1978, Windsor 1990). Annual rainfall averages 2638 mm and temperature averages 26°C. BCI experiences a pronounced wet season which begins in April or May and usually ends in December followed by a dry season ending in April. The dry season averages only 293 mm of rainfall per year (Paton per. com.). Fruitfall peaks between March and June, and between September and October (Foster 1982a), thereby producing seasonal changes in food availability for frugivorous mammal populations. Mammal descriptions for BCI may be found in Leigh *et al.* (1982). Extensive accounts of the ecology and history of BCI were provided by Croat (1978), Leigh *et al.* (1982), Gentry (1990), and Leigh (1999).

The subjects of this study were two captive-bred Harpy Eagles (a two-year old male and female) hatched and reared at the Zoological Society of San Diego, California and transferred to the World Center for Birds of Prey, Boise, Idaho at 118 and 87 days of age, respectively. At the World Center for Birds of Prey they were puppet-provisioned and placed in an enclosure with an adult female Harpy Eagle. Near fledging age (165 and 161 days), the eagles were transferred separately to an enclosure in Soberania National Park, Panama in 1998 where they were habituated to the area during four and five weeks prior to being released. Eagles were supplied with dead native mammalian prey until they ceased to visit the provisioning site (11 months). The male eagle did not stray far from the release site. Due to security concerns, he was shortly taken back into captivity until his release onto BCI on 16 June 1999 at 20 months of age. The female took long dispersals in intervals away from the release site starting at 13 months, traveling along a drainage system. She was captured 5.5 km from the release site when 20 months old and re-located to BCI with the male on 10 October 1999. Eagles were equipped with both Biotrack backpack harness mount and Merlin tail feather mount VHF radio transmitters operating in the 216 MHz range. Transmitter mass was 90 g.

The male was observed for 623 h on BCI during 89 days from 16 June to 11 October 1999. The female was observed for 1204 h on BCI during 205 days between 01 January and 24 August, 2000. Eagles were located on a daily basis by telemetry using a Telonics TR-2 or Wildlife Materials TRX-1000 receiver and 3-element hand-held yagi antennae. Once eagles were located, observations on eagle behavior, and the behavior of other animal species within sight, earshot, or vision was recorded. Additional data were collected on map position and weather. Tracking and observations made on the eagles occurred from dawn to dusk. Observations were taken when activity changed, or every 5 min. During predation events, data were also recorded on estimated weight and sex of prey species, and the method of attack the eagles used to capture their prey. Observations were made either unassisted or with 10x25 or 8x32 binoculars. Observers took care to avoid disturbing the eagles and remained as distant as possible consistent with accurate observa-

TABLE 1. Number of captures of each prey species, the percentage of total captures consumed of each prey group, and percent of total mass consumed for each species during the observation period of 89 days for the male eagle and 205 days for the female eagle.

			Male predations			Female predations		
	Age[1]	Ave. weight (kg)	N	%N	% total mass	N	%N	% total mass
Marsupiala								
Common opossum (*Didelphis marsupialis*)	A	1.8				1	2.2	1.1
Xenarthra								
Brown throated three-toed sloth (*Bradypus variegates*)	J	0.3-2.0	1	4	1.3	5	10.9	3
	A	3.2-4.0	2	8	9.5	19	41.3	40.8
Hoffman's two-toed sloth (*Choloepus hoffmanni*)	A	4.3	10	40	56.4	1	2.2	2.6
Primates								
Mantled howler monkey (*Alouatta palliate*)	J	2	3	12	7.9	2	4.4	2.4
	A	5.5				11	23.9	36.1
White-faced capuchin (*Cebus capucinus*)	A	2.5				3	6.5	4.5
Iguanidae								
Green iguana (*Iguana iguana*)	A	4.5				2	4.4	5.4
CarnÌvora								
White nosed coati mundi (*Nasua narica*)	J	1	3	12	3.9			
	A	3				1	2.2	1.8
Kinkajou (*Potos flavus*)		3	1	4	3.9			
Artiodactyla								
Red-brocket deer (*Mazama americana*)	J	4	1	4	5.3	1	2.2	2.4
	A	28						
Collared peccary (T*ayassu tajacu*)	J	1.5-4.0	2	8	3.9			
	A	12.0-20.0						
Rodentia								
Mexican porcupine (*Coendou mexicanus*)	A	2.0-4.0	1	4	3.9			
Central American agouti (*Dasyprocta punctata*)	A	2.0-4.0	1	4	3.9			
TOTAL 12			25			46		

[1]J = juvenile; A = adult.

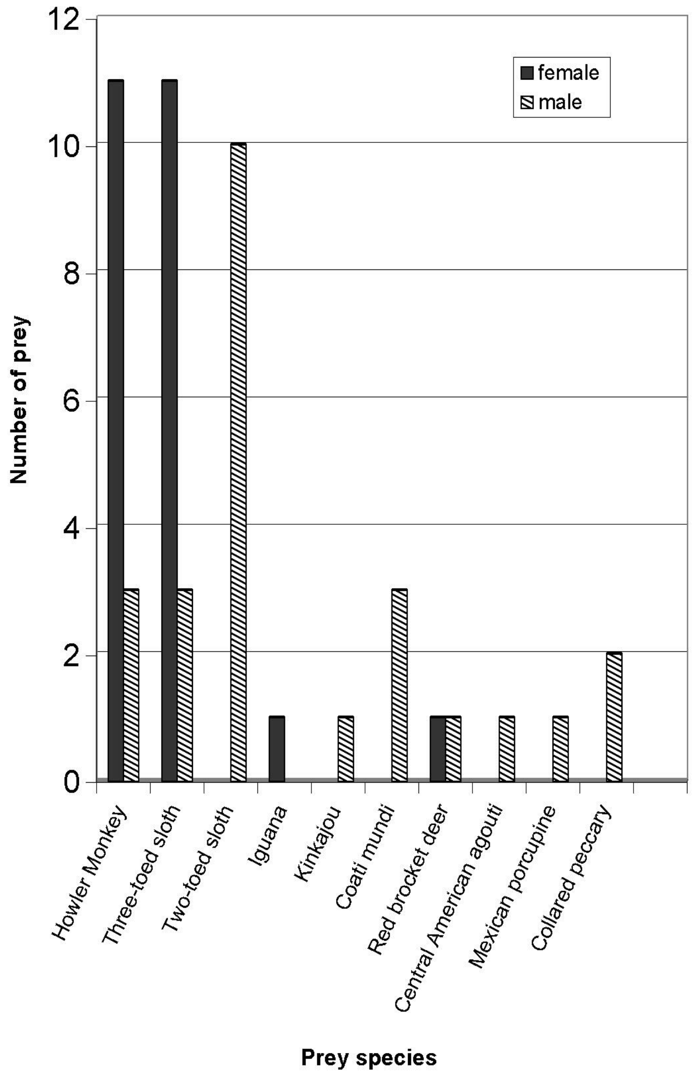

FIG. 1. Prey composition comparison for the eagles over 89 days observation time in the wet season.

tion. The male was observed throughout his entire foraging cycle (from prey capture through to next prey capture), including when he was eating. For the first three months of this study the female was observed in the same manner to document feeding behavior. Afterwards, she was left alone to eat when she had captured prey and was only checked on momentarily until she finished her carcass.

RESULTS

Prey species captured and foraging rates. During 89 days of observation the male captured 25 prey individuals, 52% of which were

TABLE 2. Prey preference determined by calculating expected prey numbers form prey abundance estimates (Giacalone & Willis pers. com). Actual prey data from 89 days of observation of the male eagle and 205 days of observation for the female eagle.

	Age[1]	Male				Female			
		Actual (N)	Expected (N)	c^2_1	*P*	Actual (N)	Expected (N)	c^2_1	*P*
Common opossum	A					1	3.1	1.1	0.30
Brown throated three-toed sloth	J	1	2.6	0.7	0.40	5	3.3	0.3	0.56
	A	2	10.4	5.7	0.02	19	13.3	6.3	0.01
Hoffman's two-toed sloth	A	10	3.5	3.1	0.08	1	4.4	2.1	0.14
Mantled howler monkey	J	3	0.4	2.0	0.16	2	0.5	0.9	0.34
	A					11	5.3	2.0	0.16
White-faced capuchin	A					3	1.3	2.3	0.13
Green iguana	A					2	13.3	8.3	0.004
White nosed coati mundi	J	3	0.1	2.7	0.10				
	A					1	1.3	0.4	0.84
Kinkajou	A	1	0.9	0.0	0.94				
Red-brocket deer	J	1	0.0	1.0	0.32	1	0.0	1.0	0.32
	A								
Collared peccary	J	2	0.1	1.7	0.19				
	A								
Mexican porcupine	A	1	1.7	0.2	0.67				
Central american agouti	A	1	5.2	2.8	0.09				

[1]J = juvenile; A = adult.

two-toed (*Choloepus hoffmanni*) or three-toed (*Bradypus variegatus*) sloths (Table 1). During 205 days of observation the female captured 46 prey individuals, 54% of which were two-toed or three-toed sloths (Table 1). Actual island abundance values of prey species (Giacalone & Willis pers. com.) were used to determine prey preference. Both eagles showed a strong preference for three-toed sloths. The male eagle also showed a preference towards two-toed sloths (Table 2).

An 89-day comparison between the male and female during the rainy season showed that the male preyed upon nine species, while the female preyed on four (c^2_1 = 1.92, P > 0.05) (Fig. 1). Forty percent of the individuals the male captured and 17% of the individuals the female captured during this period were juveniles. This difference, however, is not significant (c^2_1 = 2.57, P > 0.05). During this time, the male captured significantly more terrestrial prey than the female (c^2_1 = 4.5, P < 0.05).

The male captured one prey item per 3.7 days (SD = 1.9, n = 24). The two juvenile peccaries captured by the male were considered one item for this calculation as they were captured at the same time, one in each foot, after their mother ran off. The female captured one prey item per 4.4 days (SD = 2.2, n = 46). These foraging rate differences are not significant (U = 463, df = 1, P > 0.05). The maximum number of days between successful attacks was 8 for the male, and 9 for the female. A significant positive correlation was found for the female eagle between capture day intervals and the weight of the animal captured (r^2 = 0.14, P = 0.01). The male did not show the same positive correlation (r^2 = 0.07, P = 0.26).

Based on entire carcass mass estimates, the male consumed a daily average of 888 g, which amounted to roughly his entire body mass (6.0 kg) per week. The female consumed a daily average of 812 g, eating roughly 70% of her body mass (8.0 kg) per week. These consumption rates are significantly different (c^2_1 = 8.67, P < 0.003).

According to recent population estimates from island census work of Harpy Eagle prey species (Giacalone & Willis, pers. com.), combined data of the male and female suggest that a pair of Harpy Eagles would annually consume 1.4% of BCI's standing crop of available Harpy Eagle prey. Extrapolating from these data two-toed sloths lose a larger proportion of their population than three-toed sloths, due to the male Harpy Eagle's depredations. Adult primate prey would experience a projected annual loss less than 2% (Table 3).

Foraging classes and success rates. We separated Harpy Eagle prey species into three general classes: social arboreal, solitary arboreal, and terrestrial prey. Species within each class display similar patterns in daily activity, movement, and location within the forest. The following dry season data pertain only to observations of the female eagle as the male was only observed during the wet season.

Social arboreal prey included howler monkeys, white-faced capuchins (*Cebus capucinus*), and tamarins (*Saguinus geoffroyi*). Out of 30 observed predation attempts on social arboreal prey by the eagles (seven of which were successful), all but three were abandoned after the first attack if unsuccessful. The longest sequence of attacks on social arboreal prey was by the male eagle on a howler monkey, totaling four attempts lasting from 14:41 to 16:11 and all unsuccessful. Prior to this sequence of attempts, only one howler monkey had successfully been captured on BCI. Predation attacks by the eagles were made within 30 m, horizontally or at a downward angle, attempting to surprise the prey within the canopy. Successful captures were made by the eagle grabbing the prey individual out of the tree and either flying to

TABLE 3. Annual estimates for captures made by both eagles and estimated percentage of BCI prey species standing crops, based on BCI census data in 2000 (Giacalone & Willis pers. com.).

	Age[1]	BCI population estimate[2] (N)	Male (N)	Female (N)	Male + Female	Male + Female % of BCI population
Common opossom	A	700		1.8	1.8	0.3
Brown throated three-toed sloth	J	750	4.1	8.9	13.0	1.7
	A	3000	8.2	33.7	41.9	1.4
Hoffman's two-toed sloth	A	1000	40.9	1.8	42.7	4.3
Mantled howler monkey	J	120	12.3	3.6	15.8	13.2
	A	1200		19.5	19.5	1.6
White-faced capuchin	A	300		5.3	5.3	1.8
Green iguana	A	3000		3.6	3.6	0.1
White nosed coati mundi	J	30	12.3		12.3	40.9
	A	300		1.8	1.8	0.6
Kinkajou	A	250	4.1		4.1	1.6
Red-brocket deer	J	10	4.1	1.8	5.9	58.7
	A	75				
Collared peccary	J	20	8.2		8.2	40.9
	A	120				
Mexican porcupine	A	500	4.1		4.1	0.8
Central American agouti	A	1500	4.1		4.1	0.3
TOTAL 12		12875	102.3	81.7	183.9	1.43

the ground with it, or dropping it. In all cases, the eagles would pierce and squeeze their prey until movement ceased. None of the attempts on tamarins, all made by the male eagle, were successful.

Solitary arboreal prey species consisted primarily of three-toed and two-toed sloths. A total of 34 attacks were observed, 19 of which were successful. Ten out of 11 two-toed sloth predations were by the male eagle. Attacks were made from one to 50 m away. An eagle could attack the same sloth several times over a period of many hours. The longest observed sequence of attacks on solitary arboreal prey species was by the male eagle: it lasted nearly nine h (08:39 to 17:25). To attack a three-toed sloth, the eagle would fly in or walk in on a branch and grab the sloth on top of their branch, often in a tree crown. They would then squeeze the sloth in the same position captured until movement of the sloth ceased, or they would move to a nearby branch with the sloth if unstable. In the case of two-toed sloths, who generally hung underneath a branch, the eagles would fly in underneath the sloth, invert in the air, and attempt to pull the sloth off the branch. If successful, the eagle would fly down to the ground while still holding onto the sloth, or drop the sloth to the ground.

Five observations were made of attacks on terrestrial prey species, four of which were successful. All terrestrial prey were either captured successfully or abandoned after one attempt by the eagles aside from an attempt by the male on a Mexican porcupine (*Coendou mexicanus*). Four attempts were made from 12:54 to 14:51 before the porcupine was suc-

TABLE 4. Successful observed captures of each prey class by the female eagle in 65 days in the wet and dry seasons (n = 34).

	N - wet season[1]	N - dry season[1]	c^2_1	*P*
Social arboreal	11	1	8.3	0.004
Solitary arboreal	5	14	4.3	0.04
Terrestrial	1	2	0.3	0.56

[1]Over 65 days observation.

TABLE 5. Successful observed captures of each prey class by the female eagle in different types of weather (n = 17).

	Cloudy[1]	Sunny	c^2_1	*P*
Social arboreal	4	0	4.0	< 0.05
Solitary arboreal	1	11	8.3	< 0.004
Terrestrial		0	1.0	< 0.32

[1]Includes light rain.

cessfully captured.

Seasonal and weather patterns affected foraging success of the female eagle differently for each prey class. Foraging success is defined as the number of prey successfully captured. The female eagle was observed attempting predations for all three classes during both the wet and dry seasons. However, successful captures of social arboreal prey occurred significantly more often in the wet season and solitary arboreal prey significantly more in the dry season (Table 4). During observation weather was categorized as sunny, cloudy (including times of light rain), or heavily raining. No eagle activity was observed during heavy rain. Social arboreal prey were captured more during times of cloudy weather, whereas solitary arboreal prey were captured far more during times of sunny weather (Table 5).

Observed successful versus unsuccessful capture attempts made on social arboreal prey occurred more during the afternoon hours of the day for both eagles while capture attempts on solitary arboreal prey occurred more during the noon hours for the female (Table 6). For all observed capture attempts made by both eagles, the female exhibited a higher success rate than the male (Table 7) yet not significantly higher ($c^2_1 = 0.43$, $P < 0.51$). No significant change in success rates were observed for either eagle from the first third to the last third of study. Success rate is defined as the ratio of observed successful captures versus observed total number of attempts.

DISCUSSION

Prey captured and foraging rates. Differences in prey choice observed between the male and female Harpy Eagle could result from individual differences, different levels of development, or gender-specific differences related to morphology. Prey diversity collected for a male Harpy Eagle provisioning a nest (Rettig 1978) are similar to this study's observations on the subadult male except for the Guyana male's captures of *Cebus* sp. which could reflect an adult's greater hunting experience. Birds of prey often display gender specific foraging behavior and niche partitioning (Snyder & Wiley 1976). Male raptors, typically smaller than females, are thought to be of a size that allows them to catch the most available sizes and types of prey (Cade 1982). Male Harpy Eagles may capture quicker species like *Cebus* sp., and animals in less accessible places such as sloths hidden in lianas.

TABLE 6. Observed capture attempts of each prey class made by both eagles during different times of the day.

	06:00–10:00	10:00–14:00	14:00–18:00	c^2_2	*P*
Male eagle (n = 34)					
Social arboreal	1	6	11	8.3	0.02
Solitary arboreal	1	5	6	3.5	0.17
Terrestrial	1	1	2	0.5	0.77
Female eagle (n = 35)					
Social arboreal	0	5	7	6.5	0.04
Solitary arboreal	2	15	5	23.4	0.001
Terrestrial	0	0	1	2.0	0.37

TABLE 7. Success rates of both eagles for observed capture attempts made on each prey class.

	Social arboreal	Solitary arboreal	Terrestrial	Total
Male eagle				
Total individuals attacked	18	12	4	34
% Successful captures	16.7	58.3	75.0	38.2
Female eagle				
Total individuals attacked	12	22	1	35
% Successful captures	33.3	54.5	100.0	48.6

Female Harpy Eagles may capture bigger animals such as male howler monkeys. These gender differences indirectly may reduce pressure on preferred prey within a Harpy Eagle home range and provision a chick with a greater diversity of food items (White & Cade 1971). Moreover, having a broader range of prey species reduces vulnerability from population fluctuations in any one prey species (Foster 1982b, Glanz 1982, Milton 1982, Russell 1982, Giacalone pers. com.).

Both eagles displayed great variability in predation rates that was consistent with rates of adult breeding birds in Guyana (Rettig pers. com.), suggesting that success rates may be little affected by age and experience and that hunting behavior is innate. Alternately, this study may have not been long enough to observe changes in predation success rates of the eagles as they grew older. At this point we may not ascertain that any other factors aside from prey size affect predation rates.

Effects on prey populations. Yearly consumption estimates for the male and female eagle of this study are 364 kg^{-1} year and 296 kg^{-1} year, respectively. This is roughly consistent with Crowned Hawk Eagles (*Stephanoaetus coronatus*), primate hunters of the Kibale national Park, Uganda, that reside in a home range similar to some Harpy Eagles (3.8 km^2) (Mitani *et al.* 2001). Nutrition requirements estimate that Crowned Hawk Eagles would consume approximately 430 kg^{-1} year (Brown *et. al.* 1982). An adult Verreaux's Eagle (*Aguila verreauxi*), another large eagle of Africa known to take prey between 1.8 and 5.5 kg (Kingdon 1997) is estimated to consume approximately 120 kg^{-1} year (Gargett 1993). Emmons (1987) estimated food consumption for a wild ocelot (*Felis pardalis*), (approximately the same weight as a female Harpy Eagle), to be 175–263 kg^{-1}

year. Latest observations have characterized up to 30 potential resident ocelots on BCI (Giacalone & Willis pers. com.). Despite the slightly lower daily consumption rate of ocelots, given these estimations, they must have a far greater impact on overlapping prey populations than Harpy Eagles given their home range.

Because Harpy Eagles normally reside in pairs within home ranges comparable to the entire size of BCI (Rettig per. com., Alvarez-Cordero 1996), we believe it is reasonable to consider the male and female eagle of this study equivalent to a territorial pair when considering their impact on prey populations. Combining data collected on the male and female eagle from this study provides rough estimates of prey compositions. We do not know whether male eagles have seasonal shifts in hunting preferences, as our data for that individual only encompassed wet season captures. Therefore, possible errors are inflated in the numbers of Table 3. Although the prey population numbers given for BCI are based on latest census data, populations of several species such as red brocket deer, peccary (*Tayassu tajacu*), coati (*Nasua narica*), and agouti fluctuate greatly from year-to-year, and others, such as sloths, have never been adequately surveyed. Despite the room for error, we feel that this exercise is empirically useful for gauging the impact of a pair of Harpy Eagles on prey populations.

The estimated annual predation for two-toed sloths is the only adult population with a greater loss than 2% of their numbers. If male Harpy Eagles consume fewer two-toed sloths per month in the dry season than in the rainy season, this estimated loss would be lower.

The highest estimated losses were juvenile red brocket deer, juvenile coati, and juvenile collared peccary. Juveniles often experience high mortality rates and observe fluctuating population numbers. For example, the number of juvenile coatis born each year, and the proportion surviving varies according to the amount of fruit available the preceding October (Russell 1982). Juvenile howler monkeys experience a minimum of 39% annual mortality rate from starvation, falls, or parasites (Milton 1982). It is therefore difficult to determine to what degree the predation on juveniles made by Harpy Eagles may affect overall population dynamics.

The impact on the collared peccary, however, is likely grossly overestimated as this predation was due to observer influence. We included these data to demonstrate that the eagles may take advantage of a situation such as a mother peccary being scared away from her young due to a large cat, for example. Normally, observation influence was minimal as a majority of the mammals inhabiting BCI are habituated to human presence.

Factors affecting foraging methods and trends. Both changes in weather and seasonal patterns affect location and anti-predator behavior of potential prey. The location and anti-predator behavior of potential prey influence an eagles' ability to capture them, as was seen with the female eagle. We assume that the combination of these factors, in addition to prey abundance, influence overall foraging success and therefore foraging patterns of Harpy Eagles.

The location of prey animals (influenced by their behavior) greatly affects the ability of the eagles to find them. Social arboreal animals are located visually, acoustically, or by chance encounter. Eagles may see howler monkeys moving through the canopy in search of fruiting trees, or sleeping in a group in the sunshine. They may also be heard when chorusing at dusk and dawn. Eagles attacked monkeys resting, grooming, or foraging. Under attack the howler monkeys alarm called and ran toward the trunks of trees while large males ran towards the eagles swinging their forelimbs. Capuchins dropped out of the tree and fled the area on the ground. Tamarins would run to the ground, wait, and then return.

Because most solitary arboreal animals move and vocalize little, the eagles sight them from above the upper canopy. If a sloth is obscured by dense foliage and lianas the eagles may have a more difficult time finding them. Both species of sloth exhibited formidable anti-predator strategies. Aside from hiding in inaccessible areas, they growled and swung fore-claws at the eagles. No evidence was ever observed that the eagles experienced any harm by prey individuals.

Physiological condition of prey plays a role in their behavior and therefore vulnerability to predation by Harpy Eagles. Three-toed sloths drop their body temperature nightly to ambient temperature and raise it closer to normal mammalian temperature by basking in sunlight during the day (Montgomery & Sunquist 1978, McNab 1978). Because they usually thermoregulate by basking in the upper canopy, during times of bright sunshine three-toed sloths are more easily spotted by Harpy Eagles. Two-toed sloths are nocturnal and maintain a more constant body temperature in lowland forests than three-toed sloths (Montgomery & Sunquist 1978). Therefore, they are often found sleeping in masses of lianas or hanging from lower branches covered by vegetation during the day, making them harder to see during times of bright sunshine than three-toed sloths. In this study, more attempts were made by the female eagle at capturing sloths during the noon hours, when they would be more likely to be basking in the sunlight of the warmest part of the day.

Weather may further influence prey behavior and affect the likelihood of Harpy Eagle predation. In this study, the female eagle captured more howler monkeys during cloudy weather. Howler monkeys not only vocalize at dusk and dawn, but also when rain begins and sometimes after, increasing the opportunity for eagles to locate howler troops by sound.

Although certain weather patterns are more prominent in the wet or dry season, foraging differences observed for the female eagle in each season may be a result of an overall seasonal effect. The female eagle's greater success in capturing primates in the wet season might be attributed to a weakened state of the howler monkeys during this time. Mid-late rainy season (Aug.–Nov.) is the time when higher quality food for howler monkeys on BCI is most scarce (Milton 1982). During this time howler monkeys often experience dietary stress and may therefore be more vulnerable to Harpy Eagle predation. Similarly, puma (*Felis concolor*) were found to have a higher frequency and biomass of primates in their diet [howler monkey, spider monkey (*Ateles geoffroyi*), and white-faced capuchin] during the wet season in Corcovado National Park, Costa Rica (Chinchilla 1997).

The ease of encountering prey by these Harpy Eagles was influenced by weather and seasonal patterns that affected prey species behavior due to physiology. The change in prey behavior during different weather classes and seasons not only affected the eagles' ability to encounter prey, but also the success of the eagles' predation efforts. Prey encounter rates by the eagles also varied according to prey species abundance. Foraging patterns by these eagles were therefore indirectly or directly affected by weather and seasonal patterns, and prey species abundance.

Conclusions. Our observations of Harpy Eagles capturing prey have provided several new insights to the foraging ecology of this top predator. Gender-specific differences in prey selection were observed as the male took a more diverse set of prey species, including more juvenile and terrestrial prey animals, than the female. We were able to measure foraging rates and consumption rates to estimate the potential impact Harpy Eagles may have on prey populations in comparison to other predators in the same area, such as the ocelot.

Seasonal and weather patterns that may influence Harpy Eagle foraging behavior were also discovered. The female eagle was able to capture solitary arboreal prey significantly more successfully during sunny weather and the dry season, and social arboreal prey significantly more during cloudy weather and the wet season.

Future studies of Harpy Eagles should include the observation of an increased sample size of both sexes at the same time of year to eliminate individual differences when examining gender differences, weather influences, and seasonal differences. Additionally, the developmental foraging changes over a longer period of time into adulthood should be studied. This study, in addition to these proposed studies, will provide the knowledge necessary to determine how great a role the Harpy Eagle plays in tropical forest dynamics, as well as contribute to the conservation of this rare species.

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