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Author(s): Ronis Da Silveira, Emiliano E. Ramalho, John B. Thorbjarnarson, and

William E. Magnusson

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# Depredation by Jaguars on Caimans and Importance of Reptiles in the Diet of Jaguar

Ronis Da Silveira,<sup>1,5</sup> Emiliano E. Ramalho,<sup>2</sup> John B. Thorbjarnarson,<sup>3</sup>\* and William E. Magnusson<sup>4</sup>

ABSTRACT.—The jaguar (Panthera onca) is the largest Neotropical felid and in many parts of its range reptiles form a significant but relatively minor component of its diet. However, in the seasonally flooded varzea forests of the Amazon, terrestrial mammals, which form an important component of jaguar diet in other habitats, are largely absent and jaguars switch to alternative prey, including arboreal mammals and reptiles. In the Mamirauá Sustainable Development Reserve in the western Brazilian Amazon, we document predation by jaguars on two species of caiman (Caiman crocodilus and Melanosuchus niger), which are abundant in this varzea habitat. The smaller C. crocodilus seems to be particularly vulnerable because of its size and tendency to spend more time on land than the larger M. niger. Jaguars not only kill and eat caiman but are also a significant predator on eggs of both species. We place our findings into the context of jaguar predation on reptiles by reviewing studies of jaguar diet in a variety of biomes.

Caimans and jaguars are among the largest predators in the Amazon basin. The Black Caiman (*Melanosuchus niger*) can grow to more than 5 m in total length (TL) and weigh more than 400 kg. The smaller Spectacled Caiman (*Caiman crocodilus crocodilus*) attains a maximum size of approximately 2.2 m TL and 42 kg (Da Silveira, 2003). The jaguar (*Panthera onca*) is the largest Neotropical felid, reaching 185 cm TL (without tail) and 158 kg (Seymour, 1989).

Millions of skins of *M. niger* and *C. crocodilus* were exported from Amazonia until the 1960s, especially from Brazil (Plotkin et al., 1983). Commercial hunting of caiman in Brazil was outlawed in 1967 and caiman populations began a period of recovery (Thorbjarnarson, 1998). Since the 1980s, both species have been intensively hunted for their meat (Da Silveira and Thorbjarnarson, 1999) or to be used as bait to capture the Pilemodidae catfish *Calophysus macropterus* (Da Silveira and Viana, 2003). Since 2000, *M. niger* has been listed on the IUCN Red List as Lower Risk-conservation-dependent

(www.redlist.org). In 2007, the Brazilian population of *M. niger* was transferred from CITES Appendix I to Appendix II (Brazil, 2007), a move that will facilitate managed commercial use (Dacey, 2007). *Caiman crocodilus* is classified by the IUCN as a Lower Risk-least concern species and is included in the CITES Appendix II. Both species are abundant in Brazilian Amazonia, especially in seasonally flooded habitats (Da Silveira, 2002).

Jaguars and other mammals also were intensively hunted for their skins in most of the 20th century in Amazonia (Smith, 1980). The IUCN lists the jaguar as a near-threatened-species, and it is officially protected throughout their American range (www.redlist.org). A large population of jaguar is known to live in the seasonally flooded forest habitats in the Mamirauá Sustainable Development Reserve (MSDR) in western Brazilian Amazon (Ramalho, 2006), where our study took place. In this area, the Black Caiman population during the dry season can reach hundreds of individuals per kilometer of shoreline (Da Silveira, 2002).

Caimans and jaguars are generally opportunistic top predators with flexible diets (Emmons, 1987; Da Silveira and Magnusson, 1999). In most unflooded forest habitats, the bulk of the jaguar diet typically consists of mediumto large-sized terrestrial mammals (Rabinowitz

<sup>&</sup>lt;sup>1</sup>Departamento de Biologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Avenida General Rodrigo Otávio 3000, CEP 69077000, Manaus, Amazonas, Brazil; E-mail: ronis@ufam.edu.br

<sup>&</sup>lt;sup>2</sup>Instituto de Desenvolvimento Sustentável Mamirauá, Estrada do Bexiga 2584, Bairro Fonte Boa, CP 38, CEP 69470 000, Tefé, Amazonas, Brazil

<sup>&</sup>lt;sup>3</sup>Wildlife Conservation Society, PO Box 357520, Gainesville, Florida 32635 USA

<sup>&</sup>lt;sup>4</sup>Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia, CP 478, CEP 69011970, Manaus, Amazonas, Brazil

<sup>\*</sup>John B. Thorbjarnarson died of complications associated with malaria on 14 February 2010. Therefore, this will be one of his last contributions to the literature on crocodilians, which he advanced so far with his studies and mentoring throughout the world. We will miss him dearly.

<sup>&</sup>lt;sup>5</sup>Corresponding Author.

and Nottingham, 1986; Taber et al., 1997; Nunez et al., 2000). However, in varzea forests, particularly on seasonally flooded islands such as our Mamirauá study area, these mammals are absent (Mamirauá, 1996) and jaguars feed on alternative species (Ramalho, 2006). In this article, we describe jaguar predation on caiman and their eggs in an area of extensive varzea forest in the western Brazilian Amazon. We also survey available literature to evaluate the importance of caimans and other reptile species in the diet of jaguars in 11 biomes of eight countries.

# MATERIALS AND METHODS

The MSDR covers an area of 1,124,000 ha of seasonally flooded forest (varzea) located at the confluence of the Amazon and Japurá rivers, between 03°08′S, 64°45′W and 02°36′S, 67°13′W (Mamirauá, 1996). For detailed description of varzea habitats, see Junk (1997). As part of a population study of *C. crocodilus* and *M. niger* (Da Silveira et al., 2008), we carried out evaluations of caiman nesting ecology and movement patterns using radiotelemetry between 1994 and 1996 in the MSDR.

Nests were located by searching the margins of water bodies and adjacent areas of varzea forest during the annual dry season (September-December) when water levels are at their lowest and when caiman are nesting. When nests were found to be depredated, we used sign (e.g., footprints, the manner with which the nest and the eggs were opened, and the position of the egg remains) to determine the identity of the nest predator (Tupinambis teguixin, Cebus apella, P. onca, Homo sapiens, or unknown). We were not able to revisit all nests at the end of the nesting period to determine nest fate so rates of nest depredation represent minimum values. A Moultrie I-60 camera trap was used to take photographs of jaguars preying on caiman nests.

Caimans used for the radiotelemetry study were captured at night using a pole with a breakaway noose from a 4.7-m aluminum boat with a 15-hp motor. Caimans were equipped with Advanced Telemetry Systems (ATS) transmitters (164 MHz) fixed with Kevlar® line to the dorsal surface of the tail between the double rows of caudal scutes, immediately anterior to the single scale row of caudal scutes.

To examine the importance of reptile prey in the diet of *P. onca*, we reviewed 19 study sites in 11 biomes of eight countries. For each study, we determined the number of dietary samples reported, the total number of prey items found, and the number of species represented in the jaguar diets at that location. Percent occurrence (PO) of all reptiles, and three reptile categories

TABLE 1. Predation rates on nests of *Melanosuchus niger* and *Caiman crocodilus* between 1994 and 1996 in the Mamirauá Sustainable Development Reserve.

Predator or nest fate	M. niger	C. crocodilus	Subtotal
Tupinambis teguixin	10	5	15
Panthera onca	6	3	9
Homo sapiens	7	1	8
Cebus apella	_	2	2
Unknown predator	_	2	2
Flooded	3	1	4
Not depredated	20	2	22
Hatched	4	2	6
Subtotal	50	18	68

(squamates, chelonians, and caimans) was calculated by dividing the number of individuals identified for each reptile prey category (N) by the total number of prey identified (T), multiplied by 100,  $PO = N/T \times 100$  (Ackerman et al., 1984). Most of the studies used feces (scat) to estimate jaguar diet, except De Azevedo and Murray (2007), Ramalho (2006), Polisar et al. (2003), and Nunez et al. (2000) that also used data from animal carcasses killed by jaguar, and Hoogesteijn and Mondolfi (1992) and Almeida (1976) that used jaguar stomach contents.

#### RESULTS

We located 111 nests made by *M. niger* and 23 by *C. crocodilus*. Of these totals, we revisited 68 nests at the end of the nesting period to determine nest fate. Rate of depredation was 53% (36 nests), with 15 nests depredated by *Tupinambis teguixin*, nine by *Panthera onca*, eight by humans, two by *Cebus apella*, and two by unknown predators. Excluding four nests flooded by rising water levels and 28 not depredated or hatched, *P. onca* was responsible for 26.1% of depredated *M. niger* nests and 23.1% of the *C. crocodilus* nests (Table 1).

Radiotelemetry.—In total, 26 M. niger and two C. crocodilus was fitted with radiotransmitters. The sizes of M. niger ranged from 2.0 to 4.0 m TL and C. crocodilus from 1.3 to 1.5 m TL. Of this sample, one C. crocodilus, a gravid female (1.55 m TL; 15.5 kg), was killed by a jaguar. This C. crocodilus was sighted six times after its capture 26 September 1996 in a canal that connects Lago Mamirauá to the confluence of Japurá and Amazon rivers. During capture, and at four subsequent locations, it was in the water and on two other occasions it was found on land. Eleven days after release, the caiman was on land and permitted close observation, making it possible to check by hand (without capture) that the transmitter was well fixed on the tail. Between capture and 19 October 1996, the female moved 904 m.

The distance between subsequent locations decreased (152, 93, 76, 29, and 6 m, respectively) until the female moved 548 m into the forest. On 19 October at 0010 h, we found the female building a nest using leaf litter.

We returned to the nesting site 23 October and found only the remains of the female and numerous paw marks from an adult and a juvenile jaguar (*P. onca*). We found 24 eggshells scattered approximately 10 m from the nest in an area with recently broken herbaceous vegetation and disturbed leaf litter. We believe that these were signs of struggle, suggesting that this was where the female was killed before laying her eggs. Thirty meters from the nest, we found the partial remains of the caiman and the radiotransmitter.

Incidental Observations.—In September 1995, we found the remains of a female C. crocodilus (skull length = 18.5 cm, estimated total length = 1.3 m) adjacent to a depredated nest with the remains of 12 eggs scattered around the nest. In June 1999, we found a male M. niger 3.8 m TL that apparently had recently been killed by a jaguar. Based on the paw marks around the site, the caiman had been attacked by the jaguar while on a thick mat of floating vegetation in a canal located along the margin of Lago Mamirauá. In August 2007, a camera trap set along a trail in the Mamirauá Reserve captured a photograph of a jaguar with the remains of a C. crocodilus in its mouth. The photograph was taken in low restinga forest habitat, approximately 30 m from the nearest water body, and the estimated size of the caiman, between 1.2 and 1.5 m TL, is consistent with it being an adult female.

A camera trap recorded an adult female jaguar locating and consuming the eggs of a *M. niger* nest at Lago Tracajá (Mamiraua Reserve) on 17 December 2008. The jaguar found the nest at 1157 h and remained at the nest eating the eggs until 1313 h. It then left and returned at 1345 h for a brief visit (3 minutes), and again the following morning at 0842 h, but the jaguar had apparently consumed all the eggs on its initial visit.

Jaguar Predation on Reptiles.—We identified 1,231 prey items in a sample of 1,268 jaguar feces (scats), stomach contents, or carcasses of prey found at the 19 sites where jaguar diet were studied (Table 2). No reptiles were observed in the diet of jaguars at five of the sites. Excluding these, PO of reptilian prey varied between 2.2 and 54% (mean = 15.9, SD = 14.6). In eight sites, representing six biomes, the PO of reptile prey was greater than 9.9% (Table 2).

Chelonians were observed in jaguar diets at eight sites and were the most frequent reptilian prey in the Peruvian Amazonian flooded forest and in two sites in the Brazilian Atlantic forest biome (Table 2). Squamates were the most frequent reptilian prey in five of the nine sites (seven biomes).

Caimans were eaten by jaguars only in seasonally flooded habitats—two sites in Amazonian varzea flooded forest, two in the Brazilian Pantanal, and two in Venezuela. One of these was localized in the Venezuelan Llanos and the other in the north central region, in a site where 73% of the cover was represented by seasonally flooded lowland savanna or seasonally flooded semideciduous forest (Table 2).

Caimans were the most frequent reptilian prey for jaguars in four of six seasonally flooded habitats. At one Venezuelan site, caimans were consumed as frequently as squamates. In the Mamirauá Reserve, 54% of the prey items consumed by jaguars were reptiles, and 48% of these were caimans. In one Pantanal site, caimans were the only reptiles preyed on by jaguars (Table 2).

The number of species taken by jaguar in the 19 study sites varied between four and 23 (mean = 11.5, SD = 6; Table 2), and the number of reptilian species varied between one and five (mean = 2.4, SD = 1; Table 3). Reptile prey items represented 12% (N = 145; Table 3) of the total prey items found in the 19 jaguar diet studies (N = 1,231; Table 2). Of the 145 reptile items identified 51% were crocodilians, 27% squamates, and 22% chelonians (Table 3).

Reptiles consumed by jaguars included at least seven chelonians, six lizards, and three caiman species (Table 3). Chelonoidis denticulata represented 17.4% of the 109 reptile items, and it was documented in the Peruvian flooded forest and in two Brazilian Atlantic forest sites. Chelonoidis chilensis, Podocnemis unifilis, Podocnemis vogli, Platemys platycephala, Platemys radiolata, and Lepidochelis olivacea also were reported being preyed on by jaguars, with instances varying from one to two individuals, and represented 8.1% of the total reptile prey items. However none of these species were recorded from more than one site (Table 3).

Iguana iguana was the lizard most frequently found in jaguar diets, and 10 individuals were recorded in three sites studied. Another iguanid, Ctenosaura pectinata, was the second most frequent lizard species reported (N=8), but it was present in jaguar diets only in the Mexican deciduous dry forest site (Table 3). Seven Tupinambis teguixin were preyed on at two different sites, and five Tupinambis merianae at two other sites. These two species represented 11% of the total reptile prey items. One individual of Mabuya sp. was reported in jaguar diet in the Peruvian flooded forest, and five snakes (all in the Colubridae) were preyed on at five different sites (Table 3).

Caimans represented 51% of the 145 reptile prey items. Of this total, 38 were Caiman

TABLE 2. Frequency occurrence of reptiles in the diet of *Phantera onca* reported in 19 sites, showing the number of *P. onca* samples (N), the total number of different species (Spp), and the number of prey items (Prey) found in each study. The overall frequency occurrence of reptiles (Tot) is divided into three main reptile prey groups: chelonians (Chel), squamates (Squ), and caimans (Cai). \* = 73% of this study site was represented by seasonally flooded lowland savanna or seasonally flooded semideciduous forest.

Site	N	Spp	Prey	Chel	Squ	Cai	Tot	Biome – Country – Data source
1	39	7	50	0	6.0	48.0	54.0	Mamirauá flooded forest – Brazilian Amazonia – Ramalho, 2006
2	25	11	40	25.0	0	8.0	33.0	Flooded forest – Peruvian Amazonia – Emmons, 1987
3	16	6	16	0	13.0	13.0	26.0	Venezuelan Llanos – Hoogesteijn and Mondolfi, 1992
4	22	11	26	7.0	19.0	0	26.0	Lowland Wet Forest - Costa Rica - Chinchilla, 1997
5	13	7	15	20.0	0	0	20.0	Brazilian Atlantic Forest – Espírito Santo State – Fagure and Giaretta, 1996
6	72	11	72	2.8	0	11.0	13.8	North-central Venezuela – Scognamillo et al., 2003*
7	263	21	323	0	0	11.1	11.1	Brazilian Pantanal – Mato Grosso do Sul State – Azevedo and Murray, 2007
8	101	23	142	8.5	1.4	0	9.9	Brazilian Atlantic Forest – Espírito Santo State – Garla et al., 2001
9	73	16	106	0	7.0	0	7.0	Brazilian Atlantic Forest – Paraná State – Crawshaw et al., 2004
10	29	9	29	0	0	6.9	6.9	Brazilian Pantanal – Mato Grosso do Sul State – Almeida, 1976
11	69	8	134	0	6.0	0	6.0	Deciduous Dry Forest – Mexico – Nunez et al., 2000
12	37	12	48	2.0	2.0	0	4.0	Semideciduous, deciduous and Rain Forests – Mexico – Aranda and Sánchez-Cordero, 1996
13	228	17	185	1.0	2.0	0	3.0	Subtropical Wet Forest – Belize – Rabinowitz and Nottingham, 1986
14	106	23	135	0.7	1.5	0	2.2	Paraguayan Dry Chaco – Taber et al., 1997
15	8	4	4	0	0	0	0	Brazilian Atlantic Forest – São Paulo State – Guix, 1997
16	7	4	7	0	0	0	0	Caatinga-Xeric – Brazil – Olmos, 1993
17	23	6	23	0	0	0	0	Cerrado and Tropical Dry Forest – Brazil – Silveira, 2004
18	76	13	104	0	0	0	0	Lowland Tropical Forest – Guatemala – Novak et al., 2005
19	61	9	59	0	0	0	0	Brazilian Pantanal – Mato Grosso do Sul State – Crawshaw and Quigley, 2002
Total	1,268	_	1,231	_	_	_	_	11 biomes and 8 countries

crocodilus yacare (two sites), 27 individuals were C. crocodilus crocodilus (three sites), and three were M. niger (one site). Three caiman individuals from Cocha Cachu Reserve (Peru) and three from the Mamirauá Reserve were not identified to species (Table 3) but probably were C. crocodilus or M. niger due to the high abundance of these species at both sites.

## DISCUSSION

Melanosuchus niger and C. c. crocodilus in Amazonia feed on a wide variety of small- to medium-sized aquatic prey (Magnusson et al., 1987; Da Silveira and Magnusson, 1999). Jaguars prey primarily on medium to large terrestrial mammals in most of its range (Emmons, 1987; Farrell et al., 2000; Polisar et al., 2003), depending on the local availability of prey species (Seymour, 1989). Our review of the literature indicates that authors generally give little prominence to reptiles as prey of jaguar, even

though at least 16 reptile species were preyed upon by jaguar, and reptiles represented at least 20% of the reported diet of jaguars in five of the 19 studies we surveyed.

Caimans and chelonians were the reptiles most frequently consumed by jaguars in seasonally flooded habitats, with the exception of the Venezuelan Llanos, where squamates were as frequent as caimans (Hoogesteijn and Mondolfi, 1992), and in one Brazilian Pantanal site where no reptiles were found in the scat sample (Crawshaw and Quigley, 2002).

The results of our study and that of Ramalho (2006) suggest that in the varzea forests of the MSDR, jaguars are significant predators of caimans and their nests. The MSDR has the largest known populations of *M. niger* and *C. crocodilus* in the Amazon Basin (Da Silveira, 2002), and together these species made up almost 50% of the prey items in the jaguar diet in the MSDR (Ramalho, 2006). However, that jaguars would prey extensively on caimans in the MSDR is not

Table 3.	Frequency occur	rence and percent	occurrence	(parenthesis)	of reptile taxa	in relation to	109 reptile
prey items	found in a 14-jag	uar diet study. See	e Table 1 for	site and dat	a source detai	ls.	

Taxon/site-source	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Subtotal
Caimans															
Caiman c. yacare Caiman c. crocodilus Melanosuchus niger Unidentified caiman Subtotal	18 3 3 24	_ _ 3 3				7 - 7	36 — — 36	_ _ _ 0	_ _ _ 0	2 	_ _ _ 0				38 (26.2) 27 (18.6) 3 (2.1) 6 (4.1) 74 (51.0)
Squamates															
Iguana iguana Ctenosaura pectinata Tupinambis merianae Tupinambis teguixin Mabuya sp. Colubridae snake Unidentified squamate Subtotal		_ _ _ 1 _ _ 1	2 — — — — — 2	5     5				1 1 2	$-\frac{6}{1}$		- 8 4 - - - - 12		3 - - 1 4		10 (6.9) 8 (5.5) 5 (3.4) 7 (4.8) 1 (0.7) 5 (3.4) 3 (2.1) 39 (26.8)
Chelonians															
Chelonoidis denticulata Chelonoidis chilensis Podocnemis unifilis Podocnemis vogli Platemys platycephala Platemys radiolata Lepidochelis olivacea Unidentified chelonian Subtotal		6 -2 - 1 - - - 9			2 - - 1 - 3			11    1 12							19 (13.1) 1 (0.7) 2 (1.4) 2 (1.4) 1 (0.7) 1 (0.7) 2 (1.4) 4 (2.8) 32 (22.2)
Total reptile prey no.	27	13	4	7	3	9	36	14	7	2	12	2	6	3	145 (100)

unexpected, given the abundance of caiman and the absence of mammalian jaguar prey such as tapir, deer, and agouti (Mamirauá, 1996). These mammals, which make up an important component of the diet of *P. onca* in other parts of the species' range, are not found in the MSDR as a result of the area being extensively flooded for much of the year. Livestock, which are frequently taken by jaguars (Polisar et al., 2003), are also uncommon in the MSDR. As a result, *P. onca* feeds primarily on arboreal mammals, including the three-toed sloth (*Bradypus variegatus*) and red howler monkey (*Allouata seniculus*), and caimans (Ramalho, 2006).

Of the two main species of caiman in the Mamirauá Reserve (a third species, *Paleosuchus palpebrosus*, is also found in some areas at very low densities), there are a variety of factors that make *C. crocodilus* more vulnerable to jaguar predation. The most obvious is size. Although large male *C. crocodilus* are known to exceed 2.5 m TL in some parts of its range (Thorbjarnarson, 1994), the largest individuals we have captured in the Brazilian Amazon do not exceed 2.2 m TL. Most adult males are in the 1.4–2.2 m TL range, and adult females are typically 1.1–1.5 m TL. *Melanosuchus niger*, in contrast, grow much larger, with adult females reaching

2.0–3.0 m TL and adult males occasionally exceeding 5 m TL (Medem, 1983). Although juvenile *M. niger* and *C. crocodilus* are likely to be equally vulnerable to depredation due to their small size, as adults *M. niger* grow much larger than *C. crocodilus*, resulting in their being less susceptible to jaguar predation.

The second factor that predisposes *C. crocodilus* to jaguar predation is that they spend much more time on land than *M. niger*. In our experience conducting thousands of kilometers of day and night surveys in the Mamirauá Reserve (Da Silveira et al., 2008), it is a relatively rare event to see *M. niger* on shore. Alternatively, *C. crocodilus* will periodically emerge from the water during the day but does so more often at night, when individuals may be seeking to lower their body temperature (Lang, 1987).

Differences in nesting ecology of the two species also result in adult female *C. crocodilus* spending extended periods on land. *Melanosuchus niger* nests are found, almost without exception, at the water's edge. Of a sample of 31 nests in 1995–96, average distance to water was 2.1 m (R. Da Silveira and J. B. Thorbjarnarson, unpubl. data). Female *C. crocodilus*, in contrast, are much more plastic in their nesting habits, with some nests being along the margins of lakes

and canals, but others being inside the forest up to one kilometer from permanent water body. Whereas female *M. niger* can remain in the water while attending their nests, female *C. crocodilus* whose nests are not located along the water's edge are usually found hiding on land near the nest, frequently under leaf litter, or in the debris of fallen trees. When approached, they remain in a semi-torpid state and are very easy to capture, suggesting they rely primarily on crypsis as a defense when on land (Marioni et al., 2007).

Jaguar predation upon a nesting female C. crocodilus, and its eggs also was registered in the varzea forests along the Purus River in central Amazonia of Brazil. However, this was the only jaguar depredated nest from a sample of 137 M. niger and C. crocodilus nests (Marioni et al., 2007). In this area, varzea forests are contiguous with the unflooded terra firme habitats and jaguars can move easily between them and there is a reduced dependency of jaguars on caimans and their eggs as a protein source. This landscape matrix is very different from that found in the inland varzea forests of the Mamirauá Reserve, where the jaguars need to swim across >2 km of the Amazon or Japurá rivers to access terra firme habitats.

Jaguar movements are commonly associated with water bodies, and this is especially true in Amazonian sites (Emmons, 1989; Ramalho, 2006). Camera-trap data from Mamirauá Reserve indicates a high density of jaguars in the low water season (EER, unpubl. data). M. niger and C. crocodilus eggs were frequently consumed by jaguar, suggesting that they are an important food item for jaguars. No evidence of eggshells was found in jaguar scats in Mamirauá (Ramalho, 2006). However, we believe this was because jaguars do not eat the whole egg; instead they break the eggshell with their teeth and lick its contents (RDS and JBT, unpubl. data). Evidence of the consumption of bird eggs was found in very low frequency in the Caatinga (Olmos, 1993) and in the Atlantic forest (Facure and Giaretta, 1996) biomes; but in both areas, the eggs were smaller than those of caimans, and the jaguars probably ate them whole.

Our findings and those from previous studies suggest that reptiles form a significant component of the diet of *P. onca* in many part of the species range. This is particularly true in the Amazonia varzea flooded forest, where crocodilians are seasonally important in jaguar diet and healthy populations of jaguars can be maintained by large caiman populations.

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