



Nest attendance influences the diet of nesting female spectacled caiman (*Caiman crocodilus*) in Central Amazonia, Brazil

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Although nesting ecology is well studied in crocodilians, there is little information on the diet and feeding habits of nesting females. During the annual dry season (November–December) of 2012, we studied the diet of female spectacled caiman (*Caiman crocodilus*) attending nests ($n=33$) and far from nests ($n=16$) in Piagaçu-Purus Sustainable Development Reserve (PP-SDR), Central Amazonia, Brazil. The proportion of empty stomachs in nest-attending females was larger, and the occurrence of fresh food items was lower when compared to females not attending nests. Fish was the most frequent prey item for non-nesting females, while terrestrial invertebrates and snail operculae were the prey items most commonly recovered from stomachs of nesting females. Our study demonstrates that, despite enduring periods of food deprivation associated with nest attendance, nesting females of *C. crocodilus* still consume nearby available prey, possibly leaving their nest temporarily unattended.

Key words: Amazonia, diet, feeding, nest, parental care, spectacled caiman

INTRODUCTION

Understanding the diet of an organism is important to understand its ecology (Rosenberg & Cooper, 1990). Crocodilians prey on a wide variety of invertebrates and vertebrates (Magnusson et al., 1987; Ross, 1989; Alderton, 1991), and their opportunistic feeding strategies can affect their behaviour, body condition, growth and reproduction (Chabreck, 1971; Joanen & McNease, 1987; Delany et al., 1999; Rice, 2004). Although nesting ecology is well studied in several crocodilian species (Kushlan & Kushlan, 1980; Staton & Dixon, 1977; Platt & Thorbjarnarson, 2000; Webb et al. 1977), there is still little information on the diet and feeding habits of nesting females. It has been suggested that female *Alligator mississippiensis* nesting may have opportunities to consume terrestrial vertebrates near shoreline or in marshes (Delany & Abercrombie, 1986). Nesting female *Crocodylus niloticus*, however, appear to spend much of their time lying in a comatose state on or close to the nest, and preliminary examination of stomach

contents indicated that they fast during the three month incubation period (Mrosovsky & Sherry, 1980).

At least three of the four crocodilian species that occur in the Amazon basin construct their mound shaped nests in varzea (seasonal flooded forest) habitats during the annual dry season, when the water levels are at their lowest values (Thorbjarnarson & Da Silveira, 2000; Villamarín et al. 2011). The spectacled caiman (*C. crocodilus*) is a mid-size crocodilian which builds nests along the margins of lakes and canals but also at distances of hundreds of metres from a permanent water body (Staton & Dixon, 1977; Da Silveira et al., 2010; Villamarín et al. 2011). Nesting female *C. crocodilus* usually hide near the nest in an almost comatose state (Staton & Dixon, 1977; Marioni et al., 2007). Although the diet and feeding behaviour of *C. crocodilus* has generally been investigated (Staton & Dixon, 1975; Gorzula, 1978; Magnusson et al., 1987; Thorbjarnarson, 1993a, b; Marioni et al., 2008; Laverty & Dobson, 2013), there is still no information available on the diet of nesting females. In the flood-plains of the Anavilhanas Archipelago in

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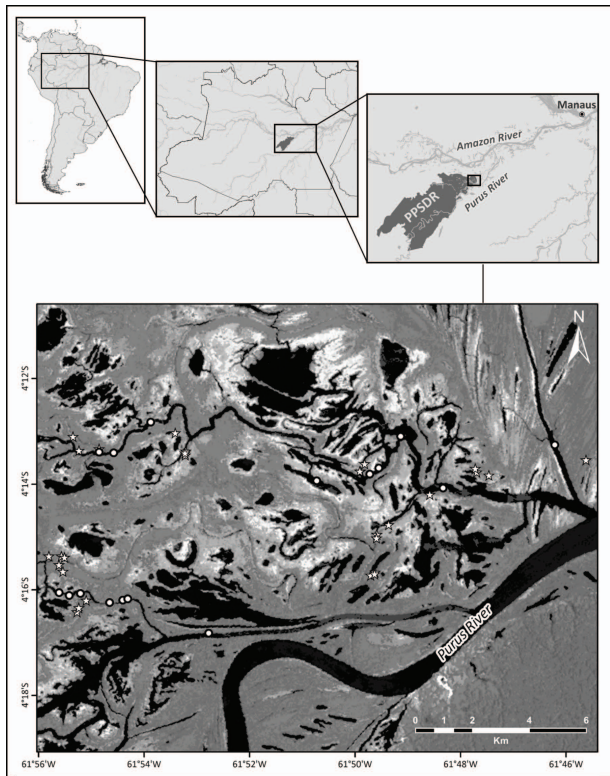


Fig. 1. Location of Piagaçu-Purus Sustainable Development Reserve and capture sites of nesting (stars) and non-nesting (circle) females of *Caiman crocodilus*. Each point represents a female.

Central Amazonia, adult male and non-nesting females eat mainly fish and crabs, though other prey items such as insects, spiders and snails are also commonly found in stomach contents (Da Silveira & Magnusson, 1999).

The main objectives of our study were to examine whether nesting females feed less frequently than non-nesting females, and to evaluate whether nest attendance influences the types of prey that females eat.

MATERIAL AND METHODS

The Piagaçu-Purus Sustainable Development Reserve (PP-SDR) is located between the Purus and Amazonas Rivers (04°05'S, 61°44'W and 5°20'S, 63°20'W; Fig. 1), approximately 350 km southwest of Manaus, Amazonas State, Brazil. PP-SDR encompasses about 834,245 ha of terra-firme forest and seasonally inundated forests (varzea), which are influenced by an annual inundation pulse of nutrient-rich, silt-laden waters (Junk, 1997; Junk et al., 2010). In PP-SDR, varzea covers about half of the reserve, and includes lakes and canals covered by floating vegetation, as well as forest (Haugaasen & Peres, 2006).

We carried out the study between November and December of 2012. This period coincides with the annual dry season, when caimans are nesting (Marioni et al., 2007). Nests of *C. crocodilus* are mound-shaped and were located by walking along the margins of 14 permanent water bodies and adjacent areas of varzea forest (up to 100 metres inside the forest; Villamarín et al., 2011). When a nest was located, its coordinates were registered with a GPS recorder (Fig. 1). Nesting females were

captured and physically restrained using a pole-snare (Ketch-All Animal Restraining Pole), ropes and tapes (Da Silveira et al., 1997). Captured females had their mass determined and snout-vent length (SVL) measured with a metric scale (± 0.5 mm), and were marked by removal of an individual combination of three vertical tail scutes (Da Silveira et al., 1997). All procedures were performed on site and all animals were released within 20 minutes of being captured.

In PP-SDR, all females with SVL > 60 cm are reproductively active (Souza et al., 2010). Non-nesting females were located by their eyeshine during nocturnal surveys using an aluminium boat with a 15 HP motor, captured using a pole with a break-away noose, and physically restrained using ropes and tapes (Da Silveira & Magnusson, 1999). Sex was confirmed by cloacal inspection (Ziegler & Olbort, 2007). Captured females were measured (SVL), weighed and marked as described for nesting females (Da Silveira & Magnusson, 1999). GPS coordinates were registered at each capture (Fig. 1).

Stomach contents of nesting and non-nesting females were obtained by stomach flushing (Taylor et al., 1978; Webb et al., 1982; Da Silveira & Magnusson, 1999), a safe technique demonstrated to recover >95% of ingested prey from crocodilian stomachs (Fitzgerald, 1989; Rice et al., 2005). After manually opening the jaws for the insertion of a piece of polyvinyl chloride (PVC) tube, both jaws were tightly secured with rubber bands and duct tape. A metallic spoon lubricated with mineral oil was carefully inserted to stir the stomach content and aid in its removal, before a rubber hose, also covered in mineral oil, was inserted to pump in filtered water. Stomach contents were collected in a bucket and preserved in 70% alcohol after excess water was drained off (Da Silveira & Magnusson, 1999). Stomach contents were analysed in the laboratory within 3 months of collection. Prey items were identified to the level of order, family or genus, classified as recently ingested or old fragments, and then grouped within five prey categories: terrestrial invertebrates, aquatic invertebrates, molluscs, fish and other vertebrates. Molluscs and insects were only considered recently ingested if intact or with evidence of active digestion (Thorbjarnarson, 1993a). Crabs and most fish remains were classified as recently ingested because these prey items are digested relatively rapidly (Delany & Abercrombie, 1986; Magnusson et al., 1987). Fish remains were considered as old fragments when only a few degraded scales were present (Rice, 2004).

Preliminary dietary analysis was conducted by comparing the proportion of empty stomachs (without any food items) between nesting and non-nesting females. As chitinous exoskeletons of some invertebrates may remain in crocodilian stomachs for periods of up to several months (Garnett, 1985), we also compared the proportion of stomachs containing at least one recently ingested prey. Percent occurrence was calculated (Rosenberg & Cooper, 1990; Platt et al., 2013) for each prey category by dividing the number of stomachs containing at least one item included in that prey category by the total of non-empty stomachs analysed. Proportions for nesting and non-nesting females were calculated separately.

All comparisons were tested for statistical significance using the Mann-Whitney rank-sum test (Zar, 1999). We also used non-metric multidimensional scaling ordination (NMDS) to evaluate if observed differences in diet composition were influenced by size-related trends in the percent occurrence of prey categories between nesting and non-nesting females. In this analysis, we used the Bray-Curtis index implemented in the program PC-ORD (McCune & Mefford, 1999) to construct a dissimilarity matrix between individual females. This index has been recommended for use in ecological (Minchin, 1987; Borg & Groenen, 1997) and dietary (Horna et al., 2001) studies. The NMDS was used to generate a single ordination of prey categories among females based on the Bray-Curtis

distance matrix. The resulting axis from the ordination was used as the dependent variable (Horna et al., 2001) in an Analysis of Covariance (ANCOVA), in which the categorical variable nest (i.e. nesting or non-nesting female) was used as the predictor variable and SVL was used as a covariate.

RESULTS

We obtained stomach contents of 33 nesting and 16 non-nesting females. SVL varied from 66.2 to 83.7 cm (mean=75.8±4.2) in nesting females, and from 61.0 to 79.8 cm (mean=72.4±9.3) in non-nesting females. Body mass of nesting and non-nesting females ranged

Table 1. Occurrence (O), percent occurrence (%O), frequency (N) and relative frequency (%N) of prey items found in stomach contents of nesting and non-nesting females of *Caiman crocodilus* in PP-SDR. Prey items grouped into five prey categories: Terrestrial Invertebrates (TI), Aquatic Invertebrates (AI), Molluscs, Fish or Other Vertebrates (OV). See Material and Methods section for detailed information on fresh prey.

Category	Order	Family	Nesting					Non-nesting				
			Occurrence		Frequency		Fresh?	Occurrence		Frequency		Fresh?
			O	%O	N	%N	---	O	%O	N	%N	---
AI	Decapoda	Trichodactylidae	2	0.06	2	0.02	Yes	1	0.06	1	0.01	Yes
AI	Decapoda	Palaemonidae	0	0	0	0	---	1	0.06	1	0.01	Yes
AI	Hemiptera	Belostomatidae	2	0.06	2	0.02	No	4	0.25	4	0.03	Yes
TI	Blattaria	Blaberidae	1	0.03	1	0.01	Yes	0	0	0	0	---
TI	Coleoptera	Carabidae	6	0.18	9	0.11	No	2	0.13	2	0.02	No
TI	Diptera	---	2	0.06	2	0.02	Yes	5	0.31	7	0.06	Yes
TI	Hemiptera	Cicadidae	1	0.03	3	0.04	Yes	4	0.25	20	0.16	Yes
TI	Hemiptera	Cicadellidae	0	0	0	0	---	1	0.06	1	0.01	Yes
TI	Hymenoptera	Formicidae	16	0.48	36	0.44	Yes	7	0.44	51	0.4	Yes
TI	Hymenoptera	Vespidae	2	0.06	2	0.02	Yes	2	0.13	2	0.02	Yes
TI	Isoptera	---	1	0.04	1	0.01	No	0	0	0	0	---
TI	Orthoptera	---	1	0.04	1	0.01	Yes	2	0.13	2	0.02	Yes
TI	Scolopendromorpha	---	1	0.03	1	0.01	Yes	0	0	0	0	---
Mollusc	Gastropoda	Ampullariidae	8	0.24	16	0.20	No	0	0	0	0	---
Fish	Beloniformes	Belonidae	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Characiformes	Anostomidae	0	0	0	0	---	2	0.13	3	0.02	Yes
Fish	Characiformes	Erythrinidae	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Characiformes	Characidae	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Characiformes	Serrasalminae	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Characiformes	Unidentified	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Osteoglossiformes	Osteoglossidae	0	0	0	0	---	1	0.06	1	0.01	No
Fish	Perciformes	Cichlidae	0	0	0	0	---	3	0.19	3	0.02	Yes
Fish	Siluriformes	Auchenipteridae	0	0	0	0	---	1	0.06	1	0.01	Yes
Fish	Siluriformes	Callichthyidae	0	0	0	0	---	6	0.38	6	0.05	Yes
Fish	Siluriformes	Loricaridae	0	0	0	0	---	2	0.13	2	0.02	Yes
Fish	Siluriformes	Pimelodidae	0	0	0	0	---	1	0.06	2	0.02	Yes
Fish	Synbranchiformes	Synbranchidae	0	0	0	0	---	1	0.06	3	0.02	Yes
Fish	Unidentified	---	1	0.04	1	0.01	No	1	0.06	2	0.02	No
OV	Squamata	Amphisbaenidae	0	0	0	0	---	1	0.06	1	0.01	Yes
OV	Unidentified reptile	---	1	0.04	1	0.01	No	1	0.06	1	0.01	No
OV	Primates	Atelidae/Cebidae	1	0.04	1	0.01	No	0	0	0	0	---
Empty	---	---	8	0.24	---	---	---	0	0	---	---	---
Total	---	---	33	1	81	1	---	16	1	125	1	---

Table 2. Summary of analysis of covariance investigating the effects of the independent variables Nest (in attendance or not in attendance) and size (SVL - cm) on diet composition (derived from multidimensional scaling analysis) of nesting and non-nesting female *Caiman crocodilus* in PP-SDR.

Variables	Sum of squares	df	Mean square	F	p	r ²
Diet composition						0.39
Nest	14.698	1	14.698	22.449	0.000	
SVL	0.001	1	0.001	0.001	0.972	
Error	24.880	38	0.655	---	---	

from 6.2 to 13.6 kg (mean=9.4±1.6) and 5.1 to 13.4 kg (mean=9.3±2.4), respectively. While mean SVL of nesting females was higher than non-nesting females ($t=2.29$; $df=47$; $p=0.03$), there was no significant difference in body mass ($t=0.19$; $df=47$; $p=0.84$).

Total mass of stomach contents in nesting and non-nesting females was 208 g (mean=8.5±11.6) and 207 g (mean=13.3±11.4), respectively. Plant material occurred in stomach contents of 62% of nesting females and 72% of non-nesting females, representing about 27% and 2% of the total mass, respectively. About 24% of stomachs of nesting females were empty (Fig. 2A), while stomachs of all non-nesting females contained at least one food item ($U=234.0$; $p<0.05$). The number of food items in nesting females ranged between 1 and 8 (mean=3.2±1.9), and

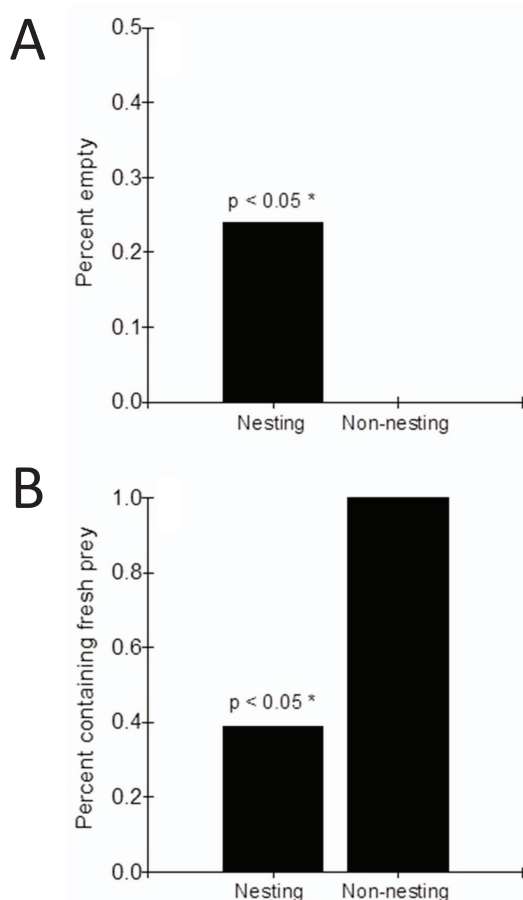


Fig. 2. Incidence of empty stomachs (A) and fresh food items (B) in *Caiman crocodilus* nesting ($n=33$) and non-nesting females ($n=16$) in PP-SDR.

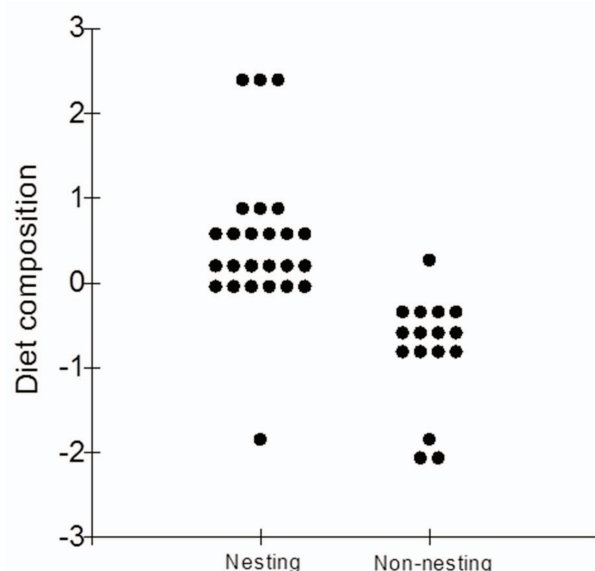


Fig. 3. Diet composition (represented by score values derived from multidimensional scaling analysis) between nesting and non-nesting females of *Caiman crocodilus* in PP-SDR. Each point represents a female.

was significantly less ($U=112.5$; $p<0.02$) than the number encountered in non-nesting females (ranging between 1 and 26 (mean=7.9±7.5)).

Recently ingested food items were found in only 39% of stomach contents of nesting females (Fig. 2A), whereas all non-nesting females had recently ingested prey items in their stomachs ($U=84$; $p<0.05$). A total of 206 prey items were identified, 70% of which were terrestrial invertebrates, 15% were fish, 8% were molluscs, 5% were aquatic invertebrates and 2% were other vertebrates (Table 1).

The proportion of terrestrial invertebrates did not differ significantly ($U=205.6$; $p=0.82$) between nesting and non-nesting females. Aquatic invertebrates were more often found in stomachs of non-nesting females, however with no significant difference between the two female groups ($U=157$; $p=0.12$). Molluscs only occurred in stomach contents of nesting females ($U=205.5$; $p<0.05$). Fish comprised a larger part of the diet in non-nesting females ($U=33$; $p<0.05$), and fish remains were found in 88% of non-nesting females and 4% of the nesting females. No significant difference ($U=191$; $p=0.64$) was found in the proportion of other vertebrates. The NMDS revealed a significant difference between nesting and non-nesting females (Fig. 3). Diet composition of individual females was affected by nesting status (nesting or non-nesting, ANCOVA, $F_{1,1}=22.449$; $p<0.001$), but not by female size ($F_{1,40}=0.001$; $p=0.972$, Table 2).

DISCUSSION

Crocodilians are generalist opportunistic predators and their diet may vary according to species, habitat, prey availability, and environmental conditions such as temperature and water levels (Ross, 1989; Da Silveira & Magnusson, 1999; Richardson et al., 2002). Our study demonstrates that nest attendance is another

important factor to influence the dietary composition and feeding frequency of female *C. crocodilus* during egg the incubation period. Relatively low metabolic demands (Coulson & Hernandez, 1983) and high food conversion rates (Webb et al., 1991) suggest that crocodilians feed infrequently and often at lengthy intervals (Coulson et al., 1989). However, although nesting females of *C. crocodilus* may endure periods of food deprivation associated with nest attendance (see Neill, 1971; Mrosovsky & Sherry, 1980; Webb et al. 1983; Whitaker & Whitaker, 1984 for other crocodilians and Mrosovsky & Sherry, 1980 for birds), they occasionally ingest food. However, reports of crocodilians with empty stomach contents in dietary studies are generally common (e.g. Taylor, 1979; Da Silveira & Magnusson, 1999; Platt et al., 2006), and a more reliable index of relative feeding frequency than the proportion of empty stomachs found is the prevalence of fresh prey (Thorbjarnarson, 1993a; Platt et al., 2013). Only about 40% of nesting females stomachs contained fresh food remains, whereas all non-nesting females had fresh prey in their stomachs, suggesting that these females are able to feed more often than those attending nests.

Most prey categories that we encountered have previously been recorded for this species in the Amazon (Magnusson et al., 1987; Da Silveira & Magnusson, 1999; Laverty & Dobson, 2013) and in the Llanos of Venezuela (Stanton & Dixon, 1975; Thorbjarnarson, 1993a). However, for the first time we also found primate remains, based on hair cuticular and medullar patterns (Quadros, 2002; Ingberman & Monteiro-Filho, 2006; Quadros & Monteiro-Filho, 2006) probably an Atelidae (*Alouatta puruensis*) or Cebidae (*Sapajus apella* or *Saimiri sciureus*). *Sapajus apella* is responsible for about 80% of depredation events on nests of *C. crocodilus* and *Melanosuchus niger* in our study area (Marioni et al., 2007; Barão-Nóbrega et al., 2014). Species of the genus *Saimiri* have also been mentioned as potential predator of eggs and/or emerging hatchlings of *C. crocodilus* elsewhere (Barboza et al., 2012).

The high incidence of fish in the diet of non-nesting females is in accordance with previous information (Stanton & Dixon, 1975; Da Silveira & Magnusson, 1999). The low occurrence of fish in nesting *C. crocodilus* could be related to nest attendance combined with differential habitat use. While nesting females were found in the forest (Marioni et al., 2007), non-nesting females usually occur in the canals (Thorbjarnarson, 1994; Ayarzagüena & Castroviejo, 2008).

The presence of aquatic prey items such as molluscs and aquatic beetles in the stomachs of nesting females suggests some food intake in nearby water bodies, although differential digestion is a common source of bias in studies of crocodilian diet (Jackson et al., 1974; Garnett, 1985; Magnusson et al., 1987). Molluscs (*Pomacea*) chitinous opercula were found only in stomachs of nesting females, but tend to accumulate in the stomach of crocodilians for long periods of time (Diefenbach, 1975; Garnett, 1985). However, the occurrence of crustaceans in the stomachs of nesting females further suggests occasional feeding by nesting females in nearby water

bodies. Females might also leave the nest unattended to feed in nearby water bodies (*A. mississippiensis*: Joanen & McNease, 1989; *C. porosus*: Webb et al., 1983; captive *A. sinensis*: Wang et al., 2011). Future studies should attempt to combine more detailed information on nesting female movements using techniques such as radio-telemetry.

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