LIFE IN THE WATER: ECOLOGY OF THE JACARERANA LIZARD, *CROCODILURUS AMAZONICUS*

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The semi-aquatic teiid lizard *Crocodilurus amazonicus* (local name jacarerana) inhabits lakes and rivers throughout Amazonia. Although it is a common species in many areas, very little information is available on its biology. I provide information on the ecology of *C. amazonicus* in areas of flooded forests in central Amazonia, Brazil. Most field observations were made at two igapó (blackwater swamp) forest in the Negro River basin, from 1992 to 1995. Lizards were found accidentally or during time-constrained searches by boat or on foot. More than 100 individuals were observed in both areas. Lizards were either swimming in shallow waters or exposed on the ground or on low vegetation. During low water, when large expanses of shoreline became exposed, *C. amazonicus* foraged and basked on these margins. When the water began to rise and several ponds were formed in the igapó forests, the lizards moved into the flooded forest. They were much easier to find during low water. The jacarerana feeds on several prey types, but eats more crustaceans and other aquatic animals than terrestrial teiids. I found 85 prey items in 26 stomachs. Arthropods (insects, shrimps, crabs and spiders) comprised about two thirds of total prey volume and vertebrates (fish and frogs, including tadpoles) about one third. Because most prey were aquatic, *C. amazonicus* probably forages mainly in the water. The jacarerana may be the only Neotropical lizard that feeds frequently on fish (23% of total prey volume) and crabs (16%). The occurrence of *C. amazonicus* in many protected areas in Brazil and adjacent countries may offset population declines associated with development in the future.

Key words: Amazonia, aquatic lizard, piscivory, swamp forest, Teiidae

INTRODUCTION

Teiid lizards are conspicuous elements of Neotropical habitats. Although most species of teiids are terrestrial (mainly those in the speciose genera *Cnemidophorus* and *Ameiva*), species in two genera (*Crocodilurus* and *Dracaena*) are semi-aquatic and at least *Tupinambis teguixin* and four species of *Kentropyx* occasionally enter water (see review in Vitt *et al*., 2001). Indeed, besides *Crocodilurus* and *Dracaena*, *Kentropyx altamazonica* is closely associated with water courses in Amazonia (Vitt *et al*., 2001). In the last decade, the ecology of many Amazonian teiid lizards that inhabit forests have been studied in detail (e.g. Vitt *et al*., 1995, 1997, 2000, 2001; Sartorius *et al*., 1999). However, the ecology of species that are found almost exclusively along large rivers and lakes, especially *Dracaena* and *Crocodilurus*, is still largely unknown (see review in Ávila-Pires, 1995). Because the water level of these lakes and rivers varies considerably during the year, these lizards should respond to fluctuating shorelines in an observable manner.

The jacarerana, *Crocodilurus amazonicus* (Fig. 1), inhabits the margins of rivers, creeks and lakes in the Amazon basin (Goeldi, 1902; Crump, 1971; Vanzolini, 1972, 1993; Hoogmoed & Lescure, 1975; Gasc, 1990; Ávila-Pires, 1995; Bartlett & Bartlett, 2003) and occurs from Peru eastwards to Belém, Pará, Brazil, and from the Orinoco in Venezuela southwards to the upper Madeira River, Amazonas, Brazil (Ávila-Pires, 1995).

FIG. 1. An adult *Crocodilurus amazonicus* from Tartarugalzinho, Amapá, Brazil (G. R. Colli).

Published data on the feeding habits of *C. amazonicus* are scarce. Vanzolini & Valencia (1965) described its dentition as being of the insectivore pleurodont type. Ávila-Pires (1995), quoting M. Martins, reports on a stomach of an adult from Cuieiras River that contained 10 juvenile *Bufo marinus*, a dragonfly and a hemipteran. Bartlett & Bartlett (2003) stated that *C. amazonicus* feeds on fish, amphibians, insects, worms and spiders, but without supporting data.

Here I provide information on the ecology of populations of *C. amazonicus* from central Amazonia, Brazil.

MATERIALS AND METHODS

Field observations were made at Miratucu Lake (1°57'08"S, 61°49'20"W, elevation approx. 100 m), Jaú River, and Jaradá Lake (2°8'34"S, 60°21'26"W),

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Cuieiras River, Amazonas, Brazil; both lakes are large basins of still water connected to blackwater rivers of the Negro River basin. Three field trips were made in 1995 to Miratucu Lake (24 March to 15 April; 7 June to 3 July; 9–29 November). Two field trips were made to Jaradá Lake (12–19 August, 1992; 31 March to 5 April, 1993). Additional observations of *C. amazonicus* were made by other researchers doing fieldwork at Jaradá lake in 1992 and 1993.

Lizards were found accidentally or during time-constrained searches. In both Miratucu and Jaradá lakes, I searched for *C. amazonicus* by boat or on foot along the margins of the lake and of ponds of various sizes and flooded streambeds in the igapó forest.

At Jaú River, 31 lizards were collected by hand, killed by a lethal injection of Nembutal®, measured (snout-vent length and tail length) and weighed. These specimens were deposited in the collection of Instituto Nacional de Pesquisas da Amazônia (INPA) at Manaus, AM, Brazil. Stomach contents were examined under a dissecting microscope and measured (length, width and height) with callipers. Prey volume was calculated with the formula for an ellipsoid ($V = 4/3\pi \times$ length $\times$ width $\times$ height). Linear regression analysis was used to test whether lizard body size influences mean and maximum prey volume. To compare the degree of generalization in the diet of *C. amazonicus* with that of other teiids, niche breadth values for numerical and volumetric diet data were calculated as in Vitt *et al.* (2000). Prey categories used herein are similar to those in the studies used to compare the niche breadth of *C. amazonicus* (Howland *et al.*, 1990; Vitt & Colli, 1994; Vitt & Ávila-Pires, 1998; Vitt *et al.*, 2001).

At Cuieiras River, ten Tomahawk mammal traps (six of them approx. $65 \times 23 \times 23$ cm and four $40 \times 15 \times 15$ cm) were left on the ground along the margins of the lake for four days (40 trap-days). Traps were baited with fish and banana (to attract flies). Data gathered during accidental observations made in other areas in Amazonia are also provided.

RESULTS

At Miratucu and Jaradá lakes, about 110 individuals of *C. amazonicus* were observed within the igapó margins, mostly on sunny days. Most observations were made during low water (October through January), when large extensions of unvegetated, leaf-litter-covered margins became exposed. Lizards were either swimming in shallow waters or exposed on the ground or on low vegetation (mainly on slender branches of fallen trees, sometimes over the water). No lizard was observed in areas of deep water. When approached, *C. amazonicus* fled by swimming distances of up to 20 m, most often parallel to the lake or river bank. They also submerged and concealed themselves inside the leaf litter of the bottom or sought retreat in burrows in the margin, mostly under fallen tree trunks; juveniles also sought retreat in hollows inside fallen tree trunks.

During the first trip to Miratucu Lake (24 March to 15 April), the water level was rising and only some narrow stretches of the lake margins were exposed. Several large, shallow ponds were forming within the igapó forests inland. The streambeds inside igapó forests were also becoming flooded. I searched for *C. amazonicus* by boat or on foot through the few exposed margins of the lake and the margins of flooded streambeds and ponds of various sizes inside the igapó forest. Six *C. amazonicus* were observed during 23.5 man-hours of diurnal visual searching (0.25 *C. amazonicus*/man-hour), most of them inside the partially flooded igapó forest (mainly on the margins of large ponds). An additional individual was found at night, apparently asleep within the leaf litter in the shallows of a large pond in the igapó forest, several metres from the flooded lake margins.

During the second field trip to Miratucu Lake (7 June to 3 July), the water level was very high (the peak of flooding) and all the lake margins were flooded. Only the highest portions of the igapó forest (tree crowns) were exposed; I failed to find the lake margins inside the igapó (it became a labyrinth of water and tree trunks). I visually searched for *C. amazonicus* by boat through the flooded lake margins and streambeds. No *C. amazonicus* was found during 41.5 man-hours of diurnal visual searching.

During the third field trip to Miratucu Lake (9–29 November) the water level was very low and large extensions of lake margins were exposed. Fifty-five *C. amazonicus* were observed on this trip, during 76.6 man-hours of visual searching (0.72 *C. amazonicus*/man-hour). Most of these individuals were juveniles 220–300 mm in total length. No *C. amazonicus* was found in the streams that cut through the unflooded igapó forests.

In addition to the Miratucu Lake observations above, additional individuals were seen along the margins of the Jaú River proper on all field trips, although these sightings were not quantified. Most of them were basking either on fallen tree trunks or on rocks, and fled by jumping into the water. Apparently, *C. amazonicus* is far less common along rivers than it is along lake margins.

About 30 *C. amazonicus* were observed along the margins of the Jaradá Lake and the Cuieiras River proper during low waters of 1992 and 1993. Most were either in still or slow-moving waters. Behaviour and microhabitat use by these lizards were identical to those observed at Jaú River (see above). One individual (total length about 50 cm) observed at Jaradá Lake, Cuieiras River, in August 1992, basked on the emerging leafless twigs of a partially submerged tree about 20 m offshore for one hour (1030 hrs to 1130 hrs). It then swam slowly about 60 m towards an emerging tree trunk (diameter ca. 50 cm) about 10 m offshore, where it hid inside a large hollow. The mammal traps failed to catch *C. amazonicus* at the margins of Jaradá Lake; only a small *Ameiva ameiva* was caught with a trapping effort of 40 trap-days.

At the Anavilhanas archipelago (Negro River, north of the mouth of the Cuieiras River), *C. amazonicus* was also found to be common in igapó forests (R. Silveira, pers. comm.). In February 1993, at Janauari Lake, a whitewater lake on the right bank of the Amazonas River, near its confluence with the Negro River, also in central Amazonia, a large *C. amazonicus* (total length ca. 60 cm) was basking by day at the top of a standing dead tree trunk (2 m high) in the middle of a stream (ca. 10 m wide) that cuts through floodable várzea forests. One specimen at Oriximiná, Pará, Brazil (MZUSP 52513), attempted to hide in a hollow log in the middle of a 2 m wide forest stream, 300 m from its confluence with the Trombetas River (M. T. U. Rodrigues, pers. comm.).

Additional lizard species commonly observed on the margins and associated igapó forests of both Jaradá and Miratucu lakes were the teiids *Ameiva ameiva*, *Kentropyx altamazonica* and *Tupinambis teguixin*, and the tropidurid *Uranoscodon superciliosus*. As with *C. amazonicus*, the three teiids were far easier to observe during low rather than high water. *Ameiva ameiva* was found mainly in sunspots inside the igapó forest, while *K. altamazonica* and *T. teguixin* were both relatively common in the lake margins. During high water, *Uranoscodon superciliosus* was very common in the tree trunks of the flooded lake margins, but it was uncommon during low water.

Thirty-one specimens of *C. amazonicus* collected at Jaú River were examined for stomach contents. Five stomachs were empty; a total of 85 prey items were found in the 26 remaining stomachs (Table 1). In general, arthropods (insects, crustaceans and spiders)

represented about two thirds (69%) of total prey volume, the remaining one third (31%) being vertebrates (fish and frogs; Table 1). The main food types (with over 5% of total prey volume) were: fish (22.7%), crustaceans (17.9%), hemipterans (17.1%), dipterans (12.2%), coleopterans (12.0%) and frogs (including tadpoles, 8.0%). Hemipterans, coleopterans, fish and spiders occurred in at least 30% of the stomachs (Table 1). As with the vertebrates, almost all invertebrates found in the stomachs of *C. amazonicus* were aquatic. Niche breadths for numerical and volumetric data in Table 1 were 8.1 and 7.5, respectively.

In general, the major food types of juveniles (SVL 74–101 mm, n=20) were similar to those of subadults and adults (SVL 158–218 mm, n=6), although our sample is too small for adults to allow a detailed analysis. Lizard SVL seems to determine mean and maximum volume of the prey ingested by *C. amazonicus* (all variables log transformed; n=23 for both analyses, R^2=0.289 and 0.278, F=8.523 and 8.078, P=0.008 and 0.010, respectively). Furthermore, mean and maximum prey volume increased proportionally to lizard SVL, since the slopes of the regression lines were not significantly different from one (b=2.093 and 2.010, t=1.524 and 1.427, respectively, P>0.05 in both analyses); i.e. there was no ontogenetic shift in the relative volume of prey ingested in *C. amazonicus*.

None of the three adult females (SVL 173, 179 and 222 mm) collected at the Jaú River in November, 1995 were reproductive. However, the largest one apparently had already reproduced (wrinkled oviduct walls), while the smaller ones were apparently non-reproductive (smooth oviduct walls). Five juveniles (SVL 73–88

TABLE 1. Stomach contents (n=85 prey items) of 26 *Crocodilurus amazonicus* from Jaú River, central Amazonia, Brazil. Results for major taxonomic groups are in boldface. Abbreviations are: n=number of prey; stm = number of stomachs in which a given prey type occurred; vol = volume (cm³) of prey. Anurans include two tadpoles.

Prey type	n	stm	vol	% n	% stm	% vol
Crustaceans (total)	**5**	**4**	**2.69**	**5.9**	**15.4**	**17.9**
crab	3	2	2.45	3.5	7.7	16.4
shrimp	2	2	0.24	2.3	7.7	1.5
Insects (total)	**51**	**17**	**7.27**	**60.0**	**65.4**	**48.8**
dipteran	14	1	1.82	16.5	3.8	12.2
coleopteran						
hydrophiliid	5	3	0.41	5.9	11.5	2.7
staphylinid	1	1	0.22	1.2	3.8	1.5
other	5	4	1.17	5.9	15.4	7.8
ephemeropteran	1	1	0.18	1.2	3.8	1.2
hemipteran						
belostomatid	16	9	2.33	18.8	34.6	15.6
other	2	2	0.22	2.3	7.7	1.5
hymenopteran (pupae)	6	1	0.60	7.0	3.8	4.0
orthopteran grillotalpid	1	1	0.32	1.2	3.8	2.1
Spiders	**12**	**8**	**0.33**	**14.1**	**30.1**	**2.1**
Fish	**13**	**8**	**3.38**	**15.3**	**30.1**	**22.7**
Anurans	**4**	**3**	**1.20**	**4.7**	**11.5**	**8.0**

mm) collected in November, 1995 at Jaú River had evident umbilical scars, indicating that they were born in the previous few weeks, at the onset of the low waters.

DISCUSSION

During over seven years of fieldwork around Manaus, central Amazonia (see, for example, Martins & Oliveira, 1998), *C. amazonicus* was never observed in streams that cut terra firme (=non-floodable) forests, where the gymnophthalmid *Neusticurus bicarinatus* and the tropidurid *Uranoscodon superciliosus* were always common (pers. obs.). Thus, at least in central Amazonia, *C. amazonicus* is apparently always associated with streams, rivers and lakes in areas of igapó and várzea forests. Furthermore, it seems to be restricted to areas of still or slow moving water.

The variation of water level in igapó seems to be an important environmental factor in the life of *C. amazonicus*. My observations at the Jaú and Cuieiras rivers show that during low water, when large expanses of shoreline become exposed, *C. amazonicus* individuals concentrate on these margins where suitable microhabitats for foraging and basking become abundant. When the water begins to rise and several ponds are formed in the low igapó forests, it seems to gradually move into the forest, probably seeking stretches of margins of inland ponds where sunspots or clearings are available; during this period, foraging may occur in the shallows of these ponds. Only one *C. amazonicus* individual was found during high water, although during this period I failed to find the igapó margins where individuals could have been. If sunspots and clearings are scarce in the flooded igapó margins during high water, *C. amazonicus* may even decrease or interrupt activity until the water level goes down again. In an area south of Manaus, *C. amazonicus* individuals were observed sitting 10–15 m off ground on top of the ends of branches over the edges of a lake (L. J. Vitt, pers. comm.); thus, alternatively, this species may become more arboreal during high water. A radio-tracking study of *C. amazonicus* would certainly contribute significantly to our knowledge of its seasonal activity cycle. The biology of populations of the tropidurid *U. superciliosus* that inhabits areas of floodable forests also seems to be affected by the variation in water level; individuals seem to follow the margins of waterbodies as water level fluctuates (Howland *et al.*, 1990).

The swimming behaviour of *C. amazonicus* has been described as "strong, undulating movements of body and tail" (Hoogmoed & Lescure, 1975), or as "lateral movements of tail, while limbs are kept adpressed along body" (Ávila-Pires, 1995, quoting M. Martins). Additional observations of several swimming individuals corroborate the quotation in Ávila-Pires (1995), which was based on a single individual. The long (about twice as long as body length), laterally compressed tail of *C. amazonicus* (Fig. 1) may facilitate this serpentine swimming method, which resembles that of a caiman (suggestively, the local name of *C. amazonicus* in Bra-

zilian Amazonia, jacarerana, means false caiman; see also Gasc, 1990). Vanzolini & Valencia (1965) suggested that the fringed toes of *C. amazonicus* could indicate that it walks on the water. However, I never observed this behaviour in *C. amazonicus*.

Besides the long, laterally compressed tail, other morphological traits in *C. amazonicus* seem to be associated with its swimming style: the relatively long neck (that makes it similar to varanids; Fig. 1; Goeldi, 1902), which could help in keeping a larger portion of the head outside the water while swimming; and the nostrils apparently closer to the tip of the snout than in other teiids (Goeldi, 1902). On the other hand, the evident dorsal crests and large convex scales found in *Dracaena*, which makes this species very similar to a caiman and seem to be adaptations for swimming, are not present in *C. amazonicus* (Fig. 1). An ecomorphological study of teiids would certainly reveal additional adaptations for aquatic habits in *Crocodilurus* and *Dracaena*.

It has been suggested that *C. amazonicus* may be non-heliothermic (Vanzolini, 1993), although this is not corroborated by the data presented herein. However, body temperature may drop significantly when basking lizards move into the water, although the water surface may reach relatively high temperatures (ca. 35°C) during the hottest hours of a sunny day in central Amazonia.

Crocodilurus amazonicus in the Jaú River feeds mostly on aquatic invertebrates (insects and crustaceans), but also on aquatic vertebrates (mainly fish), and shows wide food niches (8.1 and 7.5 for numerical and volumetric diet data, respectively). Wide food niches are widespread among teiids (Greene, 1982; Vitt, 1991; Vitt & Carvalho, 1992; Vitt & Colli, 1994) and *C. amazonicus* is no exception. For instance, the numerical and volumetric niche breadths of *C. amazonicus* were similar to or higher than those calculated by Vitt *et al.* (2000) for sympatric *A. ameiva* (8.9 and 4.1), *Kentropyx pelviceps* (2.4 and 2.2) and *K. altamazonica* (4.7 and 3.7) in western Amazonia (see similar results for *A. ameiva* and *K. altamazonica* in Vitt *et al.*, 2001, and Vitt & Colli, 1994). Despite their phylogenetic affinities, other aquatic or semiaquatic Amazonian lizards have relatively wide food niches: 15.2 and 8.6 (for numerical and volumetric data, respectively) in the gymnophthalmid *Neusticurus ecpleopus* (Vitt & Ávila-Pires, 1998) and 10.8 and 8.0 in the tropidurid *Uranoscodon superciliosus* (Howland *et al.*, 1990).

Although the food niche of *C. amazonicus* is relatively wide, both genera of primarily aquatic teiids, *Crocodilurus* and *Dracaena*, are specialized on aquatic prey to some degree. Although poorly studied, both species of *Dracaena* are considered mollusc specialists (Amaral, 1950; Vanzolini, 1961; Rand, 1964; Dixon & Soini, 1986). On the other hand, another teiid that inhabits aquatic habitats in Amazonia, *Kentropyx altamazonica* (rivers, igapós and várzeas; pers. obs.; Ávila-Pires, 1995; Vitt *et al.*, 2001), neither swims like *C. amazonicus* and *Dracaena* (instead, it runs over the water; Martins, 1996) nor feeds frequently on aquatic or

vertebrate prey (Vitt *et al.*, 2001; W. Y. Oda, pers. comm.).

Vertebrates form a considerable part of the diet in a few relatively unspecialized teiids (e.g. lizards in *Callopistes flavipunctatus*, Greene, 1982; frogs in *Kentropyx striatus,* Vitt & Carvalho, 1992, pers. obs.). Other teiids like *A. ameiva*, *Callopistes maculatus*, *Cnemidophorus lemniscatus*, *K. calcarata* and *Tupinambis* spp. may occasionally feed on small vertebrates (e.g. Greene, 1982; Vitt, 1991; Vitt & Carvalho, 1992; Vitt & Colli, 1994; Pianka & Vitt, 2003; M. Martins, pers. obs.). Vertebrates (fish, frogs and tadpoles) comprised about one third of the diet of *C. amazonicus.*

Piscivory is extremely rare in lizards (see review on lizard diets in Pianka & Vitt, 2003), being well known only in large aquatic monitors (e.g. Shine, 1986; Losos & Greene, 1988). *Crocodilurus amazonicus* is perhaps the only Neotropical lizard in which fish are important prey in the diet (23% of prey volume).

Feeding on aquatic prey occurs in some lizards that are associated with water bodies, but not in others. The tropidurid *U. superciliosus*, which is closely associated with river banks and forest streams, seems not to feed frequently on aquatic prey (Howland *et al.*, 1990; Gasnier *et al.*, 1994), although it may feed on prey floating on the surface film of rivers (Howland *et al.*, 1990). On the other hand, the gymnophthalmid *N. ecpleopus* feeds frequently on larvae of aquatic insects (Vitt *et al.*, 1998) and both species of *Dracaena* seem to feed heavily on aquatic molluscs (Amaral, 1950; Vanzolini, 1961; Rand, 1964; Dixon & Soini, 1986). The ingestion of fish, tadpoles, crabs, shrimps and several different species of aquatic insects indicates that *C. amazonicus* forages mainly in water. The ease with which *C. amazonicus* dives and the transparency of shallow water in igapó and várzea margins may facilitate underwater foraging. Furthermore, most of the prey eaten are nocturnal, indicating that prey may be disturbed by the lizard's movements by day. Alternatively, prey may be detected chemically, as teiids are characterized by a highly developed chemosensory system (see, e.g, Schwenk, 1995). In any case, how *C. amazonicus* manages to grasp fast moving prey like fish and shrimps remains to be studied.

Juvenile recruitment in *C. amazonicus* seems to occur early in the low water season in central Amazonia. If prey availability is higher during low water (when the igapó margins become exposed), recruitment at the onset of this period would guarantee a good food supply for juveniles. At least in captivity, growing is rapid in *C. amazonicus* (fed with meat): three juveniles with SVL ca. 80–100 mm, collected in November 1995, at Jaú River, attained ca. 180–230 mm in about two years (October 1997; A. S. Abe, pers. comm.).

Although the present study provides new information on the ecology of *C. amazonicus*, it was conducted in a very small portion of its geographical distribution. Thus, further studies in other areas, especially in várzea regions, would certainly provide important new information on this interesting species. The occurrence of *C. amazonicus* in many preserved areas in Brazil (the entire Jaú river basin, for instance, lies within one of the largest Brazilian parks, with over two million hectares) and adjacent countries may facilitate its preservation in the future, when inevitably most unprotected areas in Amazonia will be clear cut or at least highly disturbed.

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