

Diet and Lung Parasites of Swamp Forest Dwarf Crocodiles (*Osteolaemus tetraspis osborni*) in the Northern Congo Republic

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Wild-caught and market-derived adult specimens of the Dwarf Crocodile *Osteolaemus tetraspis osborni*, caught in forests bordering the Congo and Oubangui Rivers in the northern Congo Republic, were examined for food residues in the stomach and pentastomid infections in the lungs. Stomach content analysis revealed that *Osteolaemus* was an opportunistic predator, taking a variety of invertebrates and small vertebrate prey in the dry season. Three species of pentastomids infected the lungs (prevalence 81%), representing three genera (all belonging to the family Sebekidae); every specimen was identified to instar. Two species, *Agema silvaepalustris* and *Alofia parva*, were represented by substantial numbers of infective larvae. Because this instar is also thought to occur in fish intermediate hosts, we postulated that some transmission continued in the dry season. Amphibious catfish (*Clarias* sp.) were common in swamp forest pools and may be the putative intermediate host.

THE Dwarf Crocodile, *Osteolaemus tetraspis* Cope, 1861, inhabits lowland equatorial rain forests of west and central Africa where its range broadly overlaps that of the Slender-Snouted Crocodile *Crocodylus cataphractus* Cuvier, 1824. However, Waitkuwait (1986, 1989) and Kofron (1992) noted that their habitats differ: the former favoring open water of rivers, lakes or lagoons, whereas *O. tetraspis* entered these only occasionally, preferring bordering swamps or pools in periodically flooded forest. Riley and Huchzermayer (1999) confirmed that, by day and at the height of the dry season (Feb. to April), individuals of the Congo subspecies, *O. tetraspis osborni*, were located in small, shallow, patchily distributed permanent pools. Furthermore, dwarf crocodile populations were restricted to a narrow band of swamp forest bordering gallery terra firma forest. Whether crocodiles dispersed in the wet season, when swamp forests in that region of the Congo Republic flooded to a depth of > 0.5 m (Blake, 1993), is unknown.

Schmidt (1919) examined the stomach contents of riverine specimens of *O. t. osborni* and reported that fish were the principal food. According to Waitkuwait (1986), however, *C. cataphractus* preys principally upon fish (and aquatic birds), whereas forest-dwelling *O. tetraspis* favor land-based hunting. Although data were scant, amphibians, reptiles, annelids, crabs, and fish may be taken (Villiers, 1958, in Waitkuwait, 1986).

Prevalence and intensity data for three species of pentastomid parasites in the lungs of crocodiles (Riley and Huchzermayer, 1995; Riley et al., 1997) suggest that fish, the intermediate host in the lifecycles of these parasites, are

likely to be significant items of the diet. We present evidence that adult *Osteolaemus* from swamp forests are opportunistic predators in the dry season, taking a variety of invertebrate and vertebrate prey.

MATERIALS AND METHODS

Adult dwarf crocodiles (overall length 99–140 cm), slaughtered at Ouenze market in the capital Brazzaville (n = 7) and the market in Impfondo (n = 12), were purchased and examined for stomach contents or pentastomid parasites during the dry seasons of 1993–1997 (Tables 1–2; for the geographic location of this and other Congo sites mentioned herein, see Riley and Huchzermayer, 1999). The stomach contents of six of the Impfondo market specimens dissected in 1996 and 1997 (Table 1) were sent to JR by an American missionary. These data were supplemented with data from six wild-caught animals, the only animals whose origins were known, taken in 1995 and 1996. Not all crocodiles yielded both stomach contents and pentastomid parasites; in nine specimens, only the stomach was available (Table 1). Stomachs were either unavailable (i.e., market specimens; n = 3) or contained no recognizable residues in nine additional animals from 1995 in which only lungs were examined (Table 2).

Every *Osteolaemus* that we have seen, either in a market or en route to a market, was muzzled. Furthermore, we know from conversations with hunters that crocodile's snouts are immediately tied at capture (Agnagna et al., 1996). No attempts to feed captives are made, and indeed this notion is totally at odds with the hunter's creed. Thus, data on stomach contents reflected

TABLE 1. STOMACH CONTENTS ANALYSIS OF 16 WILD-CUGHT (*) AND MARKET-DERIVED *Osteolaemus tetraspis* († = LUNGS ALSO EXAMINED FOR PENTASTOMID PARASITES).

Date	Origin	Length (m) Sex	Stomach Contents		Vertebrate
			Invertebrate	Vertebrate	
19/5/93	Ouenze market	0.99	—	fragments of a single insect (1 mandible, 1 limb)	feathers from a small, black bird
22/4/95†	—	1.32	—	17 snail opercula, 7 complete (mean width 26.7 mm; range 18–41 mm) and shell fragments	black/brown hair from a small mammal and 1 claw
22/4/95†	—	1.2 (F)	—	millipede trunk segments (5 mm diam.); a nut (15 × 24 mm)	a small colubrid snake, 25.5 cm long; small mammal (rodent?) incisor, 13 mm long
26/4/95	Impfondo market	—	—	millipede head capsules (×2) with numerous trunk segments (4–5.5 mm diam.); 3 beetles (< 20 mm long); a large cockroach wing covers (?); legs from a large spider (<i>Dolomedes</i> sp.)	2 fish skeletons 3.5 and 5.5 cm long
1/5/95	swamp forest pool, 11 km west of Mobezele	1.15 (F)	—	millipede trunk segments	feathers from a small, black bird
1/5/95†	swamp forest pool, 11 km west of Mobezele	1.2 (F)	—	8 large beetles (length 20 mm)	limbless skink (family Felymidae), entire but in pieces, approx. 13 cm long
9/5/95*	swamp forest pool, 13 km west of Mobezele	1.2 (F)	—	leaf skeletons and leaf fragments, twigs 27 and 45 mm long	small snake scales; ventral 11 mm wide, dorsal 6 mm long
15/5/95†	swamp forest between Impfondo and Eperna	1.3 (M)	—	millipede trunk segments (10 mm diam.), head capsule from at least 3 specimens	small frog remains, semidigested and femurs (?)
24/3/95	Impfondo market	1.2 (F)	—	fragmented millipede limbs and trunk segments; beetle tergum and head capsule; leg fragments and chelicerae from a large spider (<i>Dolomedes</i> sp.)	several fish skeletons (non intact)
28/4/96†	Terra firma forest pool, close to Mbooukou village	1.2 (M)	—	small shell fragment; millipede trunk segments (11–12 mm diam.); beetle elytrum fragment; fragments of a large spider (<i>Dolomedes</i> sp.); leg joint 20 mm long	fish bones
3/5/96	Faecal Analysis	—	—	a large spider (<i>Dolomedes</i> sp.); max. length of leg joint 1.4 mm	
3/5/96	Impfondo market	—	—	scorpion, 13 mm long	
3/6/96	—	—	—	abundant leaf debris; dytiscid beetle	
Jan./Feb. 1997	—	—	—	abundant green leaves and shoot debris; beetle terga; leg fragments and chelicerae of spider (<i>Dolomedes</i> sp.)	
	—	—	—	abundant leaf debris; beetle terga	

TABLE 2. DATA OF THE THREE SPP. OF PENTASTOMIDS IN THE LUNGS OF 16 *Osteoleaemus* FROM OUEZEN (TOP PANEL) AND IMPFONDO (MIDDLE PANEL) MARKETS. Those in the lower panel were wild caught. († indicates concomitant data of stomach contents; see Table 1). Male = male; F = female; Inf = infective nymph; II/III/IV = successive instars (following the infective nymph); Pre-Ad = the instar preceding the adult stage.

Date	<i>Sebekia okavangoensis</i>				<i>Alofia parva</i>				<i>Agema silvaepalustris</i>			
	M		F		M		F		M		F	
	Inf.	Pre-Ad.	Inf.	II/III	IV	Adult	Adult	Adult	Adult	Adult	Adult	
19/4/95	—	—	—	—	—	—	—	—	—	—	—	—
21/4/95	—	—	—	—	—	—	—	—	—	—	—	—
21/4/95	—	—	—	—	1	2	24	—	—	—	—	—
21/4/95	—	—	—	—	—	—	—	—	—	—	—	—
22/4/95†	—	—	—	—	—	—	—	—	—	3	1	—
22/4/95†	—	—	—	—	—	1	—	—	3	—	6	4
26/4/95	—	—	—	—	2	2	17	—	—	—	—	—
26/4/95	—	—	10	7	31	26	101	45	4	—	—	—
26/4/95	—	—	—	—	1	2	—	—	—	—	—	—
26/4/95	—	—	—	—	5	2	21	—	—	—	—	—
26/4/95	—	—	—	—	—	—	—	—	—	—	—	—
1/5/95†	3	—	—	—	—	—	—	—	—	—	—	—
1/5/95†	1	2	—	—	—	—	—	—	—	—	—	—
9/5/95†	—	—	—	—	—	—	—	—	—	—	—	1
10/5/95	—	—	—	—	—	1	—	—	—	—	—	—
15/5/95†	—	—	18	—	—	—	—	—	—	—	—	2
28/4/96†	—	—	—	—	—	—	—	—	—	—	10	8
Total = 357	4	2	28	7	40	36	169	48	5	10	8	—

natural components of the precapture diet. The rectal contents of one wild-caught animal (28/4/96) were also sieved and analyzed. Stomach contents were washed through a 420 µm sieve and preserved in 70% ethanol prior to analysis. Prey items retrieved from the stomach were identified to the lowest taxonomic unit that was feasible. The method of recovery and the specific diagnosis of pentastomids is described in Riley and Huchzermeyer (1995) and Riley et al. (1997). Specimens were cleared by mounting them individually on slides in Hoyer's medium before examination under a light microscope where each specimen was identified to species and instar. Each annulus of the double-hooked infective instars of both *Alofia ginae* and *Agema silvaepalustris* carried a prominent row of chloride cell pore caps whose average diameter was 5 and 10 µm, respectively. This single feature allowed larvae to be easily differentiated.

RESULTS

Stomach contents analysis.—The recognizable residues from the stomachs of 16 dwarf crocodiles are itemized in Table 1. The single animal examined in 1993 contained a mass of feathers, but no other records of stomach contents from animals dissected at that time were kept because the importance of muzzling was not appreciat-

ed. Invertebrate prey were found in 14 crocodiles and vertebrate prey in 10. The stomach of one animal contained only plant debris, and substantial plant remains were present in the three animals examined in 1997 (Table 1).

Lung pentastomids.—Infection data of the three closely related pentastomid genera, all belonging to the family Sebekidae (Riley and Huchzermeyer, 1995; Riley et al., 1997) recovered from 16 crocodiles are summarized in Table 2. Three crocodiles were uninfected, giving a prevalence (percentage of host population infected) of 81%, and the mean number of parasites per host (mean intensity of infection) was 22.3 (Table 2). Distinctive double-hooked, infective larvae of the genera *Alofia* and *Agema* occurred in seven hosts with just one, the most heavily infected specimen, harboring both instars (Table 2). The least common pentastomid, *Sebekia okavangoensis*, was represented only by adults ($n = 6$) whereas the most common species, *Agema silvaepalustris* ($n = 240$), was represented mostly by infective larvae ($n = 169$) and the ensuing two instars ($n = 48$). *Alofia parva* comprised more or less equal numbers of males and females ($n = 76$), but infective larvae ($n = 28$) were found in only two hosts. Sixty three percent (224/357) of the latter two species came from a single host (Table 2).

DISCUSSION

The origins of just six of the animals dissected in this study were known. However, most of the specimens coming to market in Brazzaville also originated in forests bordering the Oubangui and Congo Rivers in the north (Behra, 1990) as did those arriving in Impfondo, most of which were caught in the Likouala swamps prior to transportation along the road from Epena (Blake, 1993; pers. obs.). The Impfondo map (Feuille NA 33 XII-34 VII) confirms that villages along this road are entirely surrounded by extensive tracts of permanently inundated swamp forest. Thus most crocodiles arriving at the Impfondo market (Table 2) probably came from these areas.

Magnusson et al. (1987) analyzed stomach contents from four species of live, wild-caught, deep-forest, South American crocodilians and listed five points that they considered important in the interpretation of their data. We examined only adult crocodiles, and other factors, such as habitat, length of time spent in captivity, and length of time taken to digest the last meal, were unknown for the majority of specimens. Thus no useful inferences can be made concerning the frequency of prey types. However, the stomach contents of deep swamp forest specimens were not too dissimilar to those from markets, except that none contained fish (Table 1).

Adult *Osteoleaemus* emerge as opportunistic predators (sensu Magnusson et al., 1987). These data complement the observations of Waitkuwait (1986, 1989) and Riley and Huchzermeyer (1999) from which it was inferred that at night, in the dry season, *Osteoleaemus* commute from small forest pools to forage along well-defined trails. Congo swamp forests can be extremely dense (Riley and Huchzermeyer, 1999), but the presence of trails suggests that dwarf crocodiles are likely to be very familiar with at least part of their potential territory. Millipedes are crepuscular or nocturnal and presumably are ingested during nightly foraging forays, along with many of the coleopterans and possibly the gastropods. Snakes, the burrowing skink, and the frog also may have been captured at night. Remains of fisher spiders (genus *Dolomedes*) in five stomachs constitute the clearest evidence of an association between *Osteoleaemus* and pools since these spiders run only on still water surfaces (P. D. Hillyard, pers. comm.). Agile prey such as mammals and birds (Table 1) may have been ambushed by submerged crocodiles.

Riley and Huchzermeyer (1999) found that the bulk of the swamp forest *Osteoleaemus* popu-

lation was limited to a narrow (approximately 2.5 km wide) band of forest fringing gallery terra firma forest on the levees of rivers and streams. We postulated that pool availability and the extent to which riverine fish penetrate swamp forests in the wet season may account for this distribution. Pentastomid infection of crocodiles provides additional data on this point.

Development within certain pentastomid taxa, particularly with respect to the number of larval instars, is stereotyped. Thus probably all sebekiids (Winch and Riley, 1986), in common with members of the genus *Porocephalus* (Buckle et al., 1997), have seven instars in their respective intermediate hosts. If their further development mirrors that of *P. crotali*, then three (males) or four (females) molts would be required to attain the adult stage. This appears to be the case with *A. silvaepalustris* (Table 2), even though the separation of two later instars proved difficult (Riley et al., 1997). Had more specimens of these critical instars of *A. parva* also been available, we would have reached the same conclusion. Thus, the double-hooked nymphs of *Alofia* and *Agema*, present in seven hosts (Table 2), almost certainly represent the seventh (infective) instar from fish (Winch and Riley, 1986; Riley et al., 1997; Junker et al., 1998). This pattern agrees with our earlier data which was less rigorous because we did not distinguish between the infective larvae of the two species, and the method used to recover worms was comparatively inefficient (Riley and Huchzermeyer, 1995).

We identified only 94 adult *Agema* and *Alofia* of 351 specimens of these two species (Table 2). Many pentastomids live for several years (Riley, 1986), although *A. silvaepalustris* appears to be atypical in this regard (Table 2; Riley and Huchzermeyer, 1995). Because most specimens of *A. silvaepalustris* are developing stages, clearly it is unlikely that the adult instar is long-lived; otherwise the majority of worms would have been adult. These data indicate that adults probably persist for less than one year, and we conclude that, in this species at least, there is an annual cycle of transmission. Hosts harboring the seventh/eighth instars of both *Agema* and *Alofia* had probably ingested fish within about 2–8 weeks (Buckle et al., 1997). Indeed, three crocodiles had fish remains in their stomachs (Table 1) but only one of these (26/4/95) was examined for pentastomids and was found to be uninfected. We conclude that the transmission of *A. silvaepalustris*, and probably that of *A. parva*, in swamp forests can occur in the dry season (Table 2).

Amphibious catfish (*Clarias* sp.) are common

in swamp forest pools (Riley and Huchzermeyer, 1999), and thus permanent pools may serve as dry season refuges for the three essential elements of the parasite lifecycle, namely crocodiles, pentastomid eggs, and fish. Interestingly, two of the wild-caught *Osteolaemus* (1/5/95 and 15/5/95), which harbored infective nymphs, were captured several kilometers from the nearest flowing water. The role of *Clarias* in transmission awaits clarification.

Agema silvaepalustris and *Sebekia okavangoensis* also infect *C. cataphractus* (Riley and Huchzermeyer, 1995; Riley et al., 1997), suggesting that feeding habits and perhaps part of the ranges of the two host crocodilian species overlap (Schmidt, 1919; Waitkuwait, 1989). Some of the market animals we examined could have come from rivers or streams. In the wet season, when swamp forests are inundated and fish invade from rivers, *Osteolaemus* probably ranges more widely and fish may become an increasingly significant part of the diet. Paradoxically, the transmission of two of the pentastomid parasites of *Osteolaemus* may not be significant at this time.

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LITERATURE CITED

- AGNAGNA, M., F. W. HUCHZERMEYER, AND J. RILEY. 1996. Traditional methods used for hunting African dwarf crocodiles in the Congo, p. 223-226. In: Crocodiles. Proceedings of the 13th working meeting crocodile specialist group, IUCN, World Conservation Union, Gland, Switzerland.
- BEHRA, O. 1990. Sex ratio in African dwarf crocodiles (*Osteolaemus tetraspis* Cope, 1861) exploited for food in the Congo, p. 174-228. In: Crocodiles. Proceedings of the 5th working meeting crocodile specialist group, IUCN, World Conservation Union, Gland, Switzerland.
- BLAKE, S. 1993. A reconnaissance survey in the Likouala swamps of northern Congo and its impli-

- cations for conservation. Unpubl. master's thesis, Univ. of Edinburgh, Edinburgh, Scotland.
- BUCKLE, A. C., J. RILEY, AND G. F. HILL. 1997. The in vitro development of the pentastomid *Porocephalus crotali* from the infective instar, encysted in rat intermediate hosts, to the adult stage, normally resident in the lung of rattlesnakes. Parasitology 115: 503-512.
- JUNKER, K., J. BOOMKER, AND D. G. BOONSE. 1998. Pentastomid infections in cichlid fishes in the Kruger National Park and the description of the infective larva *Subtriquetra rileyi* n. sp. Onderstepoort J. Vet. Sci. 65:159-167.
- KOPRON, C. P. 1992. Status and habitats of the three African crocodiles in Liberia. J. Trop. Ecol. 8:265-273.
- MAGNUSSON, W. E., E. V. DA SILVA, AND A. P. LIMA. 1987. Diets of Amazonian crocodilians. J. Herpetol. 21:85-95.
- RILEY, J. 1986. The biology of pentastomids. Adv. Parasitol. 25:45-128.
- , AND F. W. HUCHZERMEYER. 1995. Pentastomid parasites of the family Sebekidae Fain, 1961 in West African dwarf crocodiles *Osteolaemus tetraspis* Cope, 1851 from the Congo, with a description of *Alafia parva* n. sp. Onderstepoort J. Vet. Res. 62:151-162.
- , AND —. 1999. African dwarf crocodiles in the Likouala swamp forests of the Congo Basin: habitat, density, and nesting. Copeia 1999:313-320.
- , G. F. HILL, AND F. W. HUCHZERMEYER. 1997. A description of *Agema*, a new monotypic pentastomid genus from the lungs of the African dwarf and slender-snouted crocodiles. Syst. Parasitol. 37: 207-217.
- SCHMIDT, K. P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909-1915. Part 1. Turtles, crocodiles, lizards, and chameleons. Bull. Am. Mus. Nat. Hist. 39:385-624.
- WAITKUWAIT, W. E. 1986. Contribution à l'étude des crocodiles en Afrique de l'ouest. Nature et faune (Abidjan), 1.
- , 1989. Present knowledge of the West African slender-snouted crocodile, *Crocodylus cataphractus* Cuvier, 1824 and the West African dwarf crocodile *Osteolaemus tetraspis*, Cope 1861, p. 260-275. In: Crocodiles: their ecology, management and conservation. P. Hall and R. Bryant (eds.). IUCN, World Conservation Union, Gland, Switzerland.
- WINGI, J. M., AND J. RILEY. 1986. The development of *Sebekia oxycephala* (Pentastomida) from the South American crocodilian (*Caiman sclerops sclerops*), in experimentally infected fish. Z. Parasitol. 72:251-264.
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Temporal Variation in Anuran Calling Behavior: Implications for Surveys and Monitoring Programs

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Recent awareness of amphibian declines has raised the need for effective monitoring programs. Call surveys are a standard approach to monitoring populations of most anuran species. Temporal variation in calling activity, however, may result in failure to detect some species. Automated recording systems (ARS) allow consistent sampling for extended periods with little or no disturbance to calling anurans. We used an ARS to measure temporal variation in anuran calling activity during the summer of 1997 at a Carolina bay on the U.S. Department of Energy's Savannah River Site, South Carolina. We documented considerable interspecific variation in calling activity, a phenomenon that, using traditional call survey techniques, would result in failure to detect some species. In particular, we found that Southern Leopard Frogs (*Rana sphenocephala*), thought to breed only in early spring and fall in the region, called consistently from midnight until dawn during July. Because protocols for most call surveys dictate that the listener survey only during early evening hours, most call surveys would not detect the presence of this species. Our results indicate that temporal variation in anuran calling activity warrants further investigation and should be considered when developing anuran monitoring programs.

RECENT concerns over amphibian declines have resulted in the development and standardization of surveying and monitoring methods (Heyer et al., 1994). Techniques used in such programs are based on the supposition that the animals are active during the time of sampling. Because many amphibians are active for limited periods of time during any given day or season, knowledge of amphibian activity patterns should form an essential component of such programs (Peterson and Dorcas, 1992). Volunteer-based call surveys (McDiarmid and Donnelly, 1994) are the primary method for censusing anurans in numerous regional and state monitoring programs. To assist program coordinators, the North American Amphibian Monitoring Program (NAAMP) has developed specific protocols for conducting anuran calling surveys. Volunteers, after listening to identification tapes of anuran vocalizations, proceed to selected wetland areas where they listen for three minutes. Observations begin one-half hour after sunset, and the entire route should be run, including travel time to and from the wetlands, within two hours (U.S. Geological Survey, North American Amphibian Monitoring Program, <http://www.im.nbs.gov/amphibs.html>, accessed 25 June 1999).

Volunteer-based call surveys, while allowing economical coverage of large areas, may fail to detect all species present and result in an inaccurate assessment of anuran populations. Potential problems include misidentification of

anuran calls by inadequately trained volunteers; lack of a permanent sampling record to verify species identification; disturbance to calling anurans; and interspecific, temporal, and environmentally induced variation in calling behavior.

The use of automated recording systems (ARS) can remedy many problems associated with manual call surveys (Dorcas and Foltz, 1991; Peterson and Dorcas, 1992, 1994). These systems provide the ability to sample for extended periods of time, thus increasing the probability of detecting a given species; decreased disturbance to calling anurans, thus decreasing the probability of missing easily disturbed species; a permanent sampling record allowing repeated evaluation by multiple investigators; and the ability to accurately evaluate interspecific and temporal variation in calling behavior. Perhaps most important, data from ARS can be used to develop models to optimize effectiveness of manual call surveys.

We used ARS to quantify and evaluate temporal variation in calling activity of summer breeding anurans at an isolated wetland in South Carolina. We documented considerable interspecific variation in calling activity, a phenomenon that, using traditional call survey techniques, would result in failure to detect some species. In particular, we found that Southern Leopard Frogs (*Rana sphenocephala*), thought to breed only in early spring and fall in the region, called consistently from midnight until dawn during July.