Skin parasitism by *Paratrichosoma recurvum* in wild American crocodiles and its relation to environmental and biological factors

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ABSTRACT: *Paratrichosma* spp. are capillarid worms that parasitize the abdominal skin of crocodiles. They are likely not a threat to crocodiles' health, but they affect the skins' commercial value. No successful treatment exists against this parasite, and present knowledge of its life cycle is limited. Herein we report new information on *Paratrichosoma recurvum* occurrence in wild American crocodiles *Crocodylus acutus* from Mexican Caribbean islands and its relation to environmental (water salinity, temperature, climatic events) and biological (body condition) factors. The percentage of parasitized crocodiles (30.3%) is among the highest recorded in wild crocodilian populations. Small (<40.8 cm total length [TL]) and large (>270 cm TL) crocodiles are less parasitized, probably due to the characteristics of their skin or of the parasite life cycle. Two individuals appeared to have eliminated worms naturally between their capture and recapture. The thorax–abdomen is the most parasitized area of the body of crocodiles. The risk of infection is not associated with the sex of the crocodile, but there was a difference in the proportion of parasitized crocodiles between sites, which could be related to different environmental conditions. The body condition of a crocodile does not seem to be affected by the parasite. Climatic events and water temperature show no effect on the parasitism of crocodiles, but salinity could have an effect. The infection of crocodiles by *P. recurvum* could depend more on an individual's behavior than on environmental conditions.

KEY WORDS: Trichosomoididae · *Crocodylus acutus* · Parasite · Nematoda · Skin disease · Capillarid worm · Tropical cyclones · Mexican Caribbean

INTRODUCTION

Paratrichosma spp. are capillarid worms that parasitize the abdominal skin of crocodiles (Moravec & Vargas-Vázquez 1998). There is no evidence that these nematodes affect the crocodiles' health, but they form serpentine tunnels that affect the commercial value of the crocodiles' skin (Hutchzermeyer 2003). To date, no successful treatment exists to cure the lesions or to eliminate these worms, and the development of medical care may be slowed by the limited knowledge existing on the life cycle of those parasites (Hutchzermeyer 2003). Furthermore, the large genetic diversity of *P. recurvum* could give it a high resistance to antiparasitic drugs (Lott et al. 2015).

Currently, 2 species of the genus *Paratrichosoma* Ashford & Muller, 1978, i.e. *P. recurvum* (Solger, 1877) and *P. crocodylus* Ashford & Muller, 1978, are described as occurring in species of the genus *Crocodylus* Laurenti, 1768. These species come from different continents and types of habitat (e.g. mangrove, sea, lagoons, rivers), with contrasting characteristics of vegetation, soil and water (i.e. salinity). To date,

Paratrichosoma spp. have been detected in the following species: *C. acutus* Cuvier, 1807 (Solger 1877, Tellez & Paquet-Durand 2011, Tellez et al. 2016), *C. intermedius* Graves, 1819 (Seijas 2007), *C. johnsoni* Krefft, 1873 (Webb & Manolis 1983), *C. moreletii* Duméril & Bibron, 1851 (Moravec & Vargas-Vázquez 1998, Stafford et al. 2003, Tellez & Paquet-Durand 2011, Padilla & Weber 2016), *C. niloticus* Laurenti, 1768 (Foggin 1987), *C. novaeguineae* Schmidt, 1928 (Ashford & Muller 1978, Montague 1984), *C. palustris* Lesson, 1831 (Whitaker & Andrews 1989) and *C. porosus* Schneider, 1801 (Webb & Messel 1977, Buenviaje et al. 1998, Lott et al. 2015). Very little is known about the parasites' life cycle, but they seem to require soil to complete it (Foggin 1987), and the rainfall regime may have an effect on infection rate (Lott et al. 2015). Moreover, 2 routes of infection have been suggested: a larva may be ingested by the crocodile, develop in the stomach and then migrate to the skin (Solger 1877, Elkan 1974), or free larvae could directly penetrate the skin through the soft tissue between the ventral scales (Hutchzermeyer 2003). Fertilization likely takes place in deeper tissue of the skin, and then females lay unembryonated eggs in the serpentine tunnels formed in the epidermis of crocodiles; the eggs develop there until they contain a fully formed larva (Moravec & Vargas-Vázquez 1998). It has been suggested that these embryonated eggs are then slowly moved to the surface through the growth of the scales and finally released to the environment through abrasion of the keratin (Elkan 1974). Aside from these hypotheses, there is no further information available on these species. Herein we report new information on the occurrence of *P. recurvum* in wild American crocodiles *C. acutus* from the Caribbean coast of Mexico and its relation to environmental (i.e. water salinity, temperature, climatic events) and biological (i.e. body condition) factors.

MATERIALS AND METHODS

Sampling methods

As part of a project assessing the health status of the American crocodile in the Mexican Caribbean, we conducted nocturnal surveys with captures of crocodiles at Cayo Centro in the Banco Chinchorro Biosphere Reserve (BCBR) and at Punta Sur ecological park on Cozumel Island (CI) between June 2003 and August 2015. Both sites are islands located off the coast of Quintana Roo state in the Yucatan Peninsula

(Mexico) and are described in Charruau et al. (2005) and Charruau (2010). Surveys and captures of crocodiles were performed as described in Charruau et al. (2005). We measured water salinity and temperature at the crocodile capture sites with an optical refractometer (0−100 ppt) and a mercury thermometer (°C), respectively. We measured the total length (TL) and snout−vent length (SVL) of each captured crocodile using a flexible measuring tape (±0.1 cm). All captured crocodiles were also marked by removing scales from the tail crests and sex-determined by cloacal examination. Once crocodiles were placed in the ventrodorsal position, we examined ventral scales, searching for trails characteristic of *Paratrichosoma* spp. We recorded the anatomical region where parasite trails were detected, and then we divided the ventral region into 4 areas: throat (from the tip of the snout to the ventral collar), thorax−abdomen (from the ventral collar to the end of the cloaca), tail (from the end of the cloaca to the tip of the tail) and legs. Additionally, on 1 September 2008 we removed a complete ventral scale presenting of *Paratrichosoma* sp. trails from a female crocodile (TL = 160 cm, SVL = 84 cm) in BCBR, and on 13 May 2009 we removed the keratin layer of a ventral scale presenting parasite trails from a male crocodile (TL = 64 cm, SVL = 34 cm) in CI. These samples were preserved in 70% alcohol until their observation in the laboratory.

Analysis

We calculated the percentage of crocodiles with and without parasite trails using TL and SVL classes of 10 cm. We used chi-squared tests to compare the percentages of crocodiles with and without trails of parasites and to investigate differences in trail prevalence between sexes. The percentage of crocodiles presenting trails on each body part and combination of body parts were calculated. We used *t*-tests to investigate possible differences in water salinity and water temperature between the crocodile captures sites with and without parasite trails. The normality of data sets was verified by a Shapiro-Wilk test. A linear regression was performed to assess relationships between the annual percentage of parasitized crocodiles and mean annual body condition of non-hatchlings individuals at BCBR. A logistic regression was used to investigate differences in body condition between parasitized and non-parasitized crocodiles at BCBR and CI. Data on body condition of crocodiles were obtained from a previous study (P. Charruau et al. unpubl. data). Body condition was assessed using
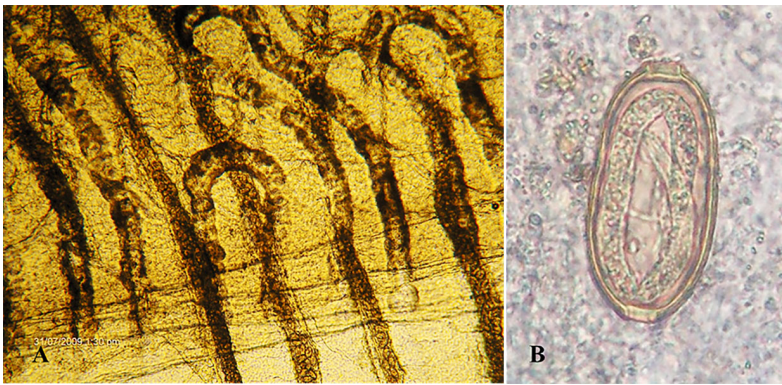
Fig. 1. (A) Serpentine tunnels containing *Paratrichosoma recurvum* eggs in epidermis of an American crocodile *Crocodylus acutus* (magnification ×10). (B) Larvated egg from a tunnel (magnification ×40)
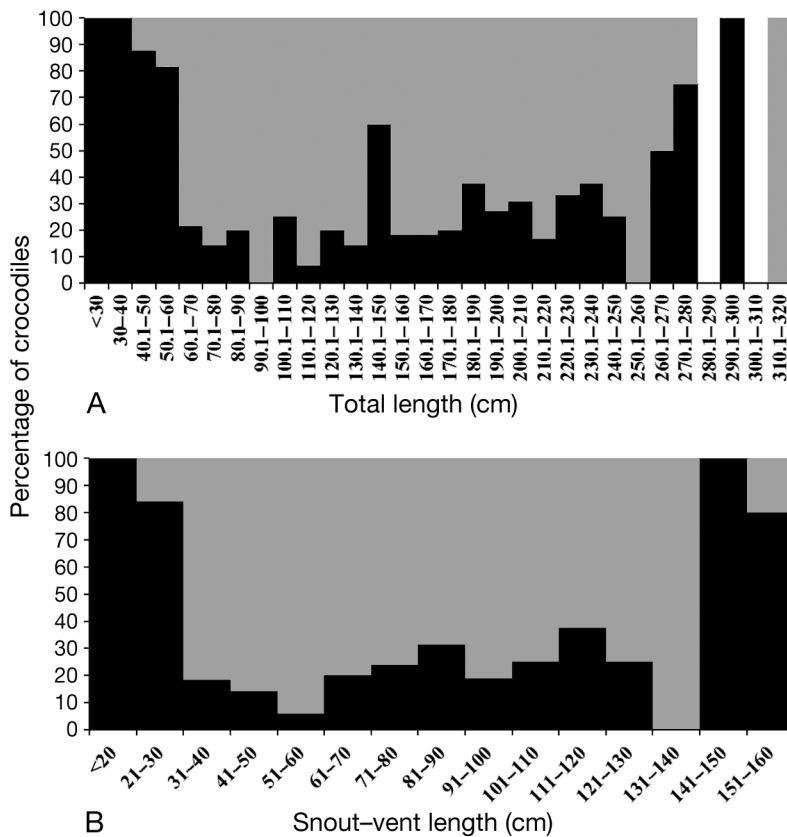

Fig. 2. Proportion of American crocodiles *Crocodylus acutus* with (grey bars) and without (black bars) *Paratrichosoma recurvum* trails, by size classes (10 cm bins) of (A) total length and (B) snout–vent length. White areas: no data available

the Fulton's *K* formula: $K = M/\mathrm{SVL}^3 \times 10^n$, where *M* is the body mass, SVL is the snout–vent length and n is a scaling factor between 0 and 5 used to bring *K* to a value close to one (Nash et al. 2006). A Kruskal-Wallis test was performed to investigate the effect of climatic events (e.g. wave/lows, tropical depressions, tropical storms, hurricanes) occurring each year within a 50 km radius circle from Cayo Centro, Banco Chinchorro, on the percentage of parasitized crocodiles the next year. Information on climatic events was obtained from the tropical cyclone reports of the National Hurricane Center of the National Oceanic and Atmospheric Administration (www. nhc.noaa.gov/data/tcr/). For all statistical analyses, we used the R software version 3.1.2 (R Development Core Team 2014). Results were considered significant at p-value < 0.05.

RESULTS

In serpentine tunnels of the keratin layer and the scale collected from crocodiles at CI and BCBR, we observed *Paratrichosoma* eggs containing single larvae (Fig. 1). These eggs were oval and presented 2 thin layers (Fig. 1B) and correspond to the description of eggs of *P. recurvum* given by Moravec & Vargas-Vázquez (1998). However, egg polar plugs were not protruding as mentioned by Moravec & Vargas-Vázquez (1998), but there may be a number of different reasons for this. One of them is that Moravec & Vargas-Vázquez (1998) observed nonembryonated mature eggs and not embryonated eggs, as in our study. Nonetheless, if we consider the host type and the geographic location of the study (*P. recurvum* was first described in *Crocodylus acutus* in Yucatan Peninsula), there is no doubt that the parasite corresponds to *P. recurvum*.

We captured 482 crocodiles from BCBR (n = 409) and CI (n = 73). Of those 482 crocodiles captured, 48 were recaptures (CI = 11 and BCBR = 37). Crocodile TL ranged from 22.5 to 320 cm, and SVL ranged from 11 to 160 cm. Crocodiles with 60.1 to 270 cm TL and 31 to 140 cm SVL showed higher proportions of individuals with parasite trails (Fig. 2). The minimum size of a crocodile with trails was 40.8 cm TL and 23.5 cm SVL. The percentage of crocodiles with *P. recurvum* trails (30.3%) was significantly lower than the per-

Table 1. Number of American crocodiles *Crocodylus acutus* with a total length >40.0 cm with and without *Paratrichosoma recurvum* trails (infected and not infected, respectively) by sites and sexes, and results of chi-squared test (df = 1). BCBR: Banco Chinchorro Biosphere Reserve; CI: Cozumel Island

	Infected	Not infected	χ^2	p
BCBR females	29	14	5.233	0.0222
BCBR males	83	43	12.698	0.00037
BCBR total	112	57	17.899	0.000023
CI females	7	6	0.077	0.782
CI males	27	25	0.077	0.782
CI total	34	31	0.138	0.7098
Females total	36	20	4.571	0.0325
Males total	110	68	9.910	0.0016
Total	146	88	14.376	0.00015

centage of crocodiles with no trails (69.7%) (χ^2 = 74.896, df = 1, p < 0.0001). However, as none of the hatchlings (i.e. TL <30 cm, n = 218) and crocodiles of 30 to 40 cm TL (n = 30) showed *P. recurvum* trails on their ventral scales (51.4% of the individuals), they were eliminated from the analyses to avoid bias. Without those individuals, the proportion of crocodiles with parasite trails was significantly higher than the proportion of crocodiles without trails (Table 1). In the BCBR there was a significant difference between the numbers of crocodiles with and without *P. recurvum* trails but not on CI (Table 1). At BCBR the number of males and females with *P. recurvum* trails was significantly higher than those without trails (Table 1). There was no effect of sex on the presence of *P. recurvum* trails on crocodiles at BCBR (χ^2 = 0.1261, df = 1, p = 0.7226), at CI (χ^2 = 0.0114, df = 1, p = 0.9151) or in general (χ^2 = 0.1088, df = 1, p = 0.7415).

Two male crocodiles from BCBR showed parasite trails at their first capture and did not show any trails at their recaptures. The first male was captured on 22 August 2006 (195 cm TL) and presented trails on its ventral scales. The crocodile was recaptured 2 times, on 25 August 2010 (225 cm TL) and on 24 August 2011 (230.5 cm TL), 1464 and 1828 d after the first capture, respectively, and no *P. recurvum* trails were observed at these recaptures. The second male was captured on 25 May 2008 (270 cm TL) and presented trails on its abdomen

scales. This crocodile was also recaptured 2 times, on 23 May 2010 (271 cm TL) and on 18 August 2013 (279 cm TL), 706 and 1889 d after the first capture, respectively, and also did not show any *P. recurvum* trails at these recaptures.

We obtained data on the body parts presenting nematode trails from 76 crocodiles. The majority (72.4%) of these crocodiles present parasite trails on more than one part of their body (Fig. 3A). Sixty-nine of the 76 crocodiles had trails on the thorax–abdomen (90.8%), 54 crocodiles had trails on throat (71.1%), 40 had trails on the tail (52.6%) and only one had trails on scales of a leg (1.3%) (Fig. 3).

We obtained water salinity at the capture sites for 310 crocodiles. There was no significant difference in water salinity at capture sites between crocodiles with parasite trails (51.0 ± 15.6 ppt, n = 113) and crocodiles without trails (49.4 ± 14.9 ppt, n = 197) (t = 0.9269, df = 308, p = 0.3547). However, excluding crocodiles <40 cm TL, the mean salinity water at capture sites of individuals with parasite trails (51.2 ± 15.5 ppt, n = 112) was significantly higher than at capture sites of individuals without trails (44.8 ± 14.3 ppt, n = 67) (t = 2.7462, df = 177, p = 0.0067). We obtained water temperature at capture sites for 205 non-hatchling crocodiles. Mean water temperature at capture sites of crocodiles without parasite trails (29.8 ± 1.9°C, n = 82) was not significantly different than at capture sites of crocodiles with trails (30.0 ± 2.0°C, n = 123) (t = −0.6926, df = 203, p = 0.4894).

The percentage of crocodiles with parasite trails is independent of the month (χ^2 = 3.4628, df = 5, p = 0.629). The evolution of the percentage of crocodiles with parasite trails from April to September seems to be stable, showing a unique increase in June, and does not seem to be related to environmental factors
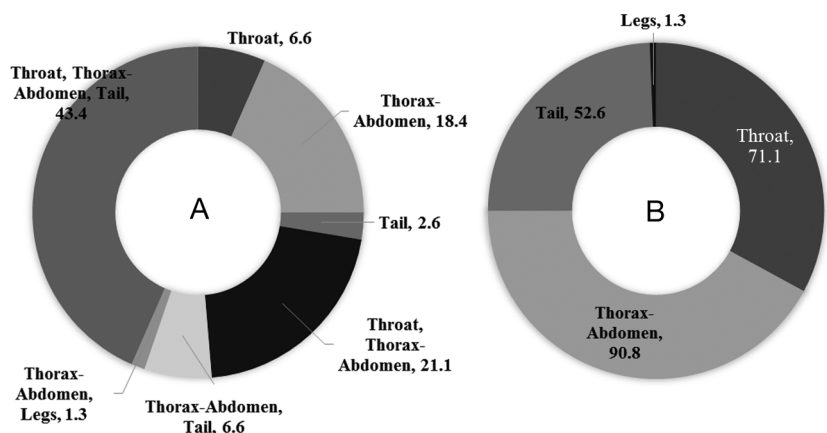

Fig. 3. Percentage of American crocodiles *Crocodylus acutus* presenting *Paratrichosoma recurvum* parasite trails on (A) one or several body parts and on (B) each body part affected
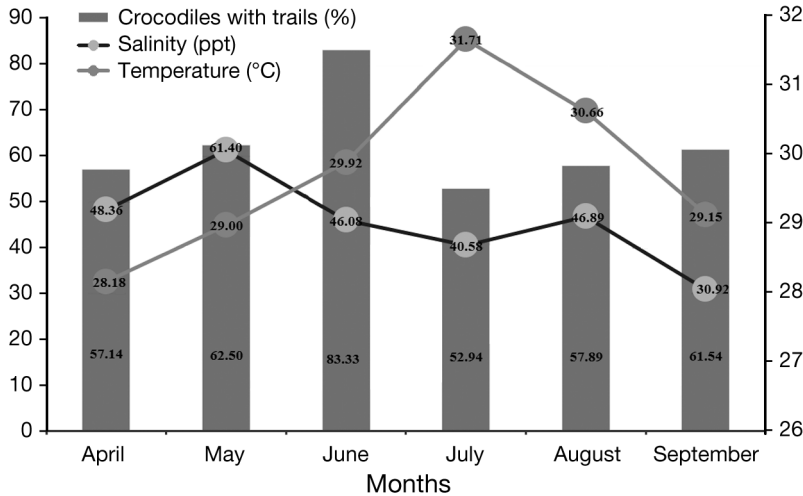
Fig. 4. Monthly evolution of the percentage of non-hatchling American crocodiles with *Paratrichosoma recurvum* trails (left y-axis) and the mean of water temperature (right y-axis) and salinity (left y-axis) at capture sites
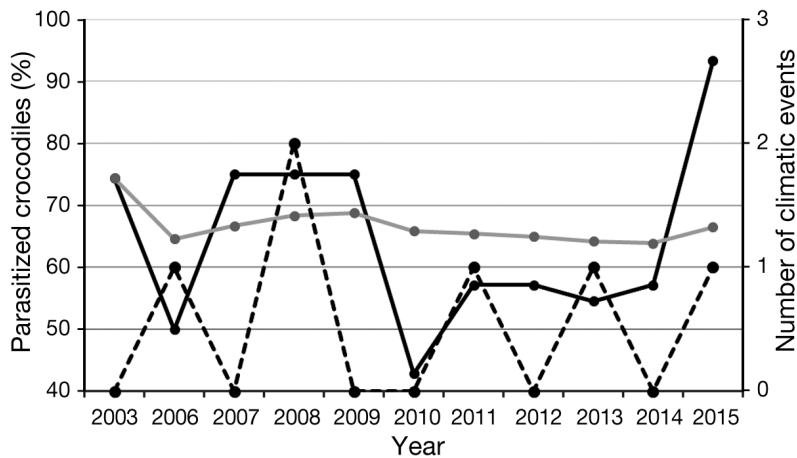

Fig. 5. Number of climatic events occurring during the preceding year (dashed black line) and annual variation in the percentage (black line) and cumulative percentage (grey line) of American crocodiles with *Paratrichosoma recurvum* trails at Banco Chinchorro Biosphere Reserve from 2003 to 2015

(Fig. 4). The cumulative percentage of crocodiles infected by *P. recurvum* at BCBR showed stability over years (Fig. 5). However, annual percentages show variation, with 2 important decreases (2006 and 2010) followed by an increase the next year (2007 and 2011) and a phase of stability (Fig. 5). There was also an important increase in the percentage of crocodiles infected in 2015 (Fig. 5).

The logistic regression did not show any differences in body condition between parasitized and non-parasitized crocodiles at BCBR ($z = -0.093$, $p = 0.926$) nor CI ($z = -1.100$, $p = 0.272$). There was also no relation between the annual percentage of parasitized crocodiles and mean annual body condition of

non-hatchling individuals at BCBR ($r^2 = 0.209$, $F_{1,9} = 2.702$, $p = 0.135$). However, this relation was significant and negative when eliminating data of 2015 from the analysis ($r^2 = 0.529$, $F_{1,8} = 8.988$, $p < 0.02$). Six climatic events occurred within a 50 km radius circle around Cayo Centro (2 wave/low, one tropical depression, one tropical storm, one hurricane Category 1 and one of Category 5 on the Saffir-Simpson scale) from 2002 to 2015. Graphically, the percentage of parasitized crocodiles at BCBR does not seem to be affected by the number of climatic events occurring during the preceding year (Fig. 5). Furthermore, no significant difference exists in the percentage of parasitized crocodiles between years with 2, 1 or no climatic events the preceding year (Kruskal-Wallis, $H = 1.022$, df = 2, $p = 0.588$).

DISCUSSION

Although *Paratrichosoma recurvum* was first discovered and described in young American crocodiles from Yucatan Peninsula (Mexico) by Solger (1877), this is the first detailed study on the prevalence of this skin parasite in *Crocodylus acutus*. Only 7 studies have reported the prevalence of *Paratrichosoma* spp. in wild crocodilian populations: 14.3% (n = 2/14, Stafford et al. 2003) and 44.2% (n = 23/52, Padilla & Weber 2016) for *C. moreletii*, 2.5% for *C. intermedius* (n = 5/199, Seijas 2007), 0.9% for *C. porosus* (n = 12/1345, Webb & Messel 1977), 12.8% for *C. novaguineae* (n = 137/1073, Montague 1984), 71.0% for *C. johnsoni* (n = 566/797, Webb & Manolis 1983) and 92.3% for *C. acutus* (n = 12/13, Tellez et al. 2016). The 30.3% of parasitized crocodiles reported in the present study is then among the highest percent recorded in wild crocodilian populations. Nevertheless, it is lower than the prevalence reported in Belize for the same species (Tellez et al. 2016); this could be attributed to the difference in sample size (482 in this study vs. 13 in Belize). Furthermore, 3 studies present detailed prevalence of *Paratrichosoma* spp. by size classes (Fig. 6). In *C. acutus* the smallest size at which croco-
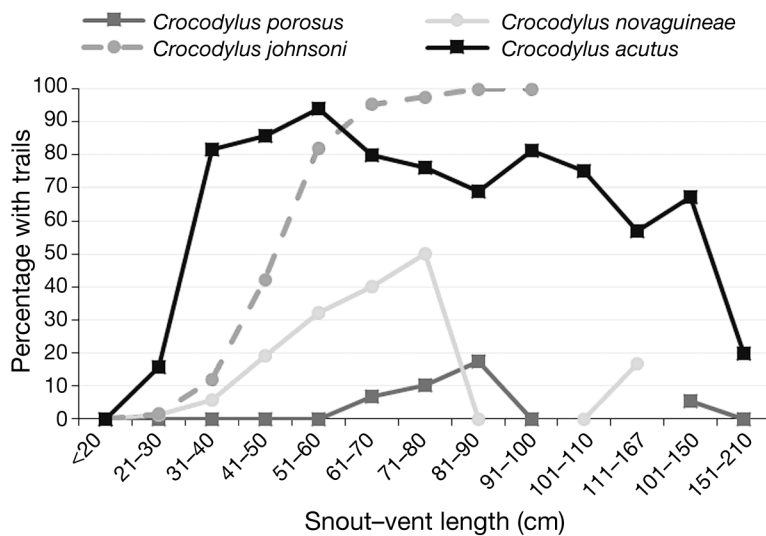
Fig. 6. Proportion (%) of crocodiles presenting *Paratrichosoma* spp. trails by snout–vent length size class (cm) for *Crocodylus acutus* (present study), *C. porosus* (Webb & Messel 1977), *C. johnsoni* (Webb & Manolis 1983) and *C. novaeguineae* (Montague 1984)

diles are infected is likely 40.8 cm TL and 23.5 cm SVL; no crocodiles smaller than this appear to have been parasitized. Then, the percentage of individuals affected by *P. recurvum* increases slightly until 60 cm TL (30 cm SVL); between 60 and 270 cm TL (30–140 cm SVL), 50 to 100% of individuals are parasitized and the proportion decreases drastically (<20%) in crocodiles above 270 cm TL (140 cm SVL) (Figs. 2 & 6). Few data are available for larger size classes in the other studies, but results for smaller size classes (<20 to 100 cm SVL) are similar to our observations (Fig. 6). The hypothesis for this parasitism pattern is that the ventral scales of neonates (<30 cm TL) and yearlings (30 cm < TL < 60 cm) are too thin to be parasitized by *P. recurvum*, and in the case of large adults (>270 cm TL or 140 cm SVL) ventral scales could be too hard to be penetrated by the worms. The single crocodile of more than 3 m TL captured in this study showed a zigzag *P. recurvum* trail, but it was only on one scale and seemed to be old, almost 'erased'. Moreover, the development of all capilariids is generally very slow, and gravid females may take up to ~8 mo until they start to produce their eggs (Worsham et al. 2016). Thus, this can be another reason why the nematode tunnels with eggs are absent from the skin of very small (i.e. young) crocodiles. Juveniles, sub-adults and small adults (60 to 270 cm TL and 30 to 140 cm SVL) are then the most affected classes. However, no signs of crocodile health problems due to *P. recurvum* have been detected in this study. Furthermore, one inter-

esting finding of this study is the disappearance of the parasite tunnels from the ventral scales of 2 crocodiles between their capture and recapture, indicating that crocodiles can eliminate worms naturally. These 2 adult crocodiles measured 225 and 271 cm TL at their recapture, sizes at which crocodiles are less parasitized (Fig. 2).

Our results also showed that the most parasitized body areas are thorax and abdomen, which are more in contact with the substrate when crocodiles move or lay on land. This observation supports the hypothesis that the infection path involves free larvae penetrating the skin through the soft tissue between the ventral scales. However, this infection path is very improbable as only per os infection is known in capilariids (F. Moravec pers. comm.). Infection assisted by leeches, as suggested in Hutchzermeyer (2003), also seems very unlikely due to the absence of such organisms in our study sites because of the high salinity levels. Thus, it is most probable that the path of infection is ingestion of larvae, and future experimental study of the *P. recurvum* life cycle would be very useful to test these hypotheses.

The risk of infection with *P. recurvum* is not associated with the sex of crocodiles, but there was a difference in the proportion of parasitized crocodiles between sites. BCBR presented a higher rate of affected individuals than CI. This difference could be related to different environmental conditions. At both sites, crocodiles presented a good body condition (P. Charruau et al. unpubl. data), and apparently, they were not affected by *Paratrichosoma* infestation. Excluding the 2015 data, the rate of parasitized crocodiles decreases with an increase in body condition. However, this does not mean that there is a direct relation between body condition and parasitism, as both can be correlated with another parameter such as an environmental factor. We know that the body condition of American crocodiles is likely affected by tropical cyclones, water temperature and salinity (P. Charruau et al. unpubl. data). Climatic events and water temperature do not seem to have an effect on the parasitism of crocodiles in our study, but salinity could have one. Lott et al. (2015) found a negative linear relationship between monthly rainfall and incidence of helminthosis in captive *C. porosus*. This supports our results, as salinity increases with a decrease in rainfall, due to evaporation. However, more

data and analyses are necessary to draw conclusions about the effect of these parameters on the infection of crocodiles or about the parasite life cycle. Furthermore, the infection of crocodiles by *P. recurvum* could depend more on the individual's behavior (e.g. habitat use, sunbathing habits, nesting, nest care) than on environmental conditions. The 20% increase in the proportion of crocodiles infected in June (Fig. 4) could be related to a peak in reproduction of the parasite during this month. June also occurs at the end of the dry season, during which time crocodiles are more in contact with land and mud due to the low water level. These conditions could increase the risk of infection. Future studies should determinate the occurrence of *P. recurvum* in water edge substrate used by crocodiles throughout the year.

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