Climbing behaviour in extant crocodilians

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Abstract. Although arboreality in extinct crocodilians is frequently suggested, the climbing abilities of extant crocodilians have never been discussed in any detail in scientific literature. We present an overview of published and anecdotal information on climbing in extant crocodilians, as well as original observations on four species representing two crocodile genera. These data suggest that climbing behaviour is common among crocodilians and might have multiple functions. The fact that at least some extant crocodilians are capable of climbing arboreal vegetation despite lacking any obvious morphological adaptations for arboreality must be taken into account by paleontologists trying to elucidate behavioural clues from the morphology of fossil taxa.

Keywords: arboreality, Crocodylus, Mecistops, Australian freshwater crocodile, Nile crocodile, American crocodile, slendersnouted crocodile, American alligator.

Introduction

Extant crocodilians are generally considered to be predominantly or semi-aquatic. And, although the role of terrestrial activity in their natural history is increasingly recognized (see, for example, an overview of terrestrial hunting in crocodilians in Dinets, 2011), they are virtually never thought of as animals capable of climbing. Their non-arboreality is often taken for granted in various analyses of tetrapod limb evolution and behaviour of extinct Archosauria (see Birn-Jeffery et al., 2012, for a discussion of the subject and a bibliography). Climbing behaviour in extant crocodilians has never been described in detail in the scientific literature, though it was briefly mentioned by Tarsitano & Hecht (1980), Frey (1988), and, earlier, Guggisberg (1972) who wrote that baby crocodiles "can climb into bushes, up trees and even hang on reeds like chameleons."

Despite this limited documentation, the ability of crocodilians (mostly juveniles) to climb trees is well known to local residents in some locations. They reported routinely observing basking in mangrove trees by juvenile American crocodiles (Crocodylus acutus) near Tulum (Quintana Roo, Mexico, Jason Cleinsten pers. comm.), in mangrove trees up to 10 m above ground by juveniles of the same species in Isla de Salamanca National Park (Barranquila, Colombia, Juan Cabrera pers. comm.) and by juvenile estuarine crocodiles (C. porosus) near Sorong (West Papua, Indonesia, Benyamin Syatfle pers. comm.). A photo of a Nile crocodile (C. niloticus) climbing a low tree trunk was obtained in March 2012 by Grant and Dimari Oliver in Okavango Delta, Botswana (Larien Spies pers. comm.). Photos of a juvenile New Guinea crocodile (C. novaeguineae) basking on a tree trunk growing at an angle were taken at Elevala River (Papua New Guinea) by Michael Lech (pers. comm.). A photo of a Philippine crocodile (C. mindorensis) in a tree can be seen in van Weerd & van der Ploeg (2012). Crocodiles (presumably Central African slendersnouted crocodile Mecistops cataphractus, see notes on taxonomy below) are reportedly often observed in Odzala-Kokoua National Park (Republic of Congo) as they bask in trees in very dense rainforest (Jackie Appleton unpubl. obs.). Juvenile Siamese crocodiles (C. siamensis) in Laos (Octávio Mateus pers. comm.) and American alligator (Alligator mississippiensis) in USA (Shawn Heflick pers. comm.) have been observed

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Fig. 1. A sub-adult American alligator (*Alligator mississippiensis*) perching on a tree branch in Pearl River Delta, Mississippi. Photo by Kristine Gingras, used with permission.

on tree branches 0.5-1 m above the water. A photo of a sub-adult American alligator perched on a tree branch 2-3 above the water (Fig. 1) was obtained at Pearl River Delta, Mississippi (Kristine Gingras pers. comm.). Captive dwarf crocodiles (*Osteolaemus* sp.) often climb tree branches (Ralf Sommerlad pers. comm.). One adult dwarf crocodile escaped from its enclosure at the Bristol Zoo (UK) by climbing up a tree growing at an angle and then over the barrier (John Dickson pers. comm.).

In most of these cases, crocodilians are observed low above the water surface. But, as the following observations show, they are capable of climbing higher, sometimes into tree crowns.

Materials and Methods

All observations were conducted opportunistically in the course of unrelated research. Sizes and distances were estimated visually. Details on locations, dates and sample sizes are provided in relevant chapters below.

Results

Tree climbing in the Australian freshwater crocodile

A.B. has observed Australian freshwater crocodiles climbing steep riverbanks on many occasions, and even attempting to climb chain-link fence up to 1.8 m tall. Although estuarine crocodiles also climb up steep slopes, their climbing abilities appear to be inferior to those of Australian freshwater crocodiles. The ability to climb decreases with increasing size and mass. Hatchlings of both species are lightweight and with their relatively strong claws can even climb vertical brickwork (the cause of occasional crocodile farm escapes). In the wild, Australian freshwater crocodiles frequently climb into low branches above the water, either by climbing directly onto the tree close to the water, or by climbing onto the tree from the bank and then along a branch projecting above the water, typically to a height of 1-2 m. Such crocodiles may be concealed by fringing vegetation or fully exposed. Crocodiles in this position

that were approached by boat readily fell into the water as a means of escape. Crocodiles observed basking or resting in branches were rarely larger than 1.5 m total length. They were observed in trees by day and night, across a variety of creeks and water bodies within their range including the Daly and Douglas Rivers (13°50'S, 131°08'E), Mary River and McKinlay Rivers (12°57'S, 131°38'E) in the Northern Territory, Chamberlain River (15°58'S, 127°55'E) in Western Australia, and Mitchell River (15°15'S, 141°42'E) in Queensland.

Tree climbing in the American crocodile

On many occasions, V.D. observed American crocodiles up to 1 m long (by visual estimate) lying on aerial roots and low branches of mangrove trees during the day. Such observations were made at the following locations: Santa Rosa National Park (Costa Rica, 10°47'N, 85°40'W, May 1995, N > 30), Lago Enriquillo (Dominican Republic, 18°30'N, 71°35'W, February 2008, N = 4), Isla de Salamanca National Park (Colombia, 11°56'N, 74°42'W, January 2007, N=4), and Everglades National Park (USA, 25°07'N, 81°04'W, N = 1). All of these "roosts" were in well-concealed places above the water, usually in red mangroves (Rhizophora mangle), up to 1 m above the water surface. Some were in black mangroves (Avicennia germinans), and on one occasion a crocodile visually estimated to be 45 cm long was observed approximately 3 m above the water at high tide. Climbing to some of these roosting sites apparently required the crocodiles to scale tree trunks, aerial roots and/or branches growing at more than 45° angle. Despite extensive night-time observations, American crocodiles were never seen in trees at night. The process of climbing was never observed. All crocodiles seen in trees were extremely wary, and jumped or fell in the water when the approaching observer was still more than 10 m away. This shyness might explain why treeclimbing behaviour in crocodilians remains relatively little known despite being relatively common.

Tree-climbing in the Central African slender-snouted crocodile

Of all the crocodilians, tree-climbing behaviour is most discussed for the slender-snouted crocodiles of Central Africa, particularly in Gabon. M.H.S. has observed slender-snouted crocodiles 0.40 - 2.0 m total length (by visual estimate) basking on fallen trees over river courses both during the day and at night. Observations were made along the N'gowe and Echira Rivers of

Loango National Park (Gabon, S2.225/E9.679, N > 50), Dji Dji River of Ivindo National Park (Gabon, N0.16/E12.74, N >10), Bongo River of Moukalaba-Doudou National Park (Gabon, S2.53/E10.14, N = 3), and the Epulu River in the Okapi Faunal Reserve (DRC, N1.50/E28.68, N = 2). The day "roosts" tended to be in more exposed portions of the trees than night "roosts," presumably due to the use of emerged trees as basking sites along closed canopy rivers where terrestrial sites are not readily available. Night "roosts," however, were just as open about 50% of the time, making it difficult to say whether the crocodiles sought out these roosts at night or simply remained there after daytime basking. The frequency of daytime versus nighttime basking on trees was approximately equal, and the frequency of the behaviour is so great that crocodiles and African darters (Anhinga rufa) are equal candidates for glimpses of animals jumping off trees into the water throughout this area. Tree-basking crocodiles were significantly warier during the daytime, usually dropping off the basking site on first sight of the survey crew (> 50 m), than crocodiles tree-basking at night, which could often be approached and hand-grabbed or noose captured off the trees. The tree "roost" sites ranged from 0.25 - 3.0 m above the surface of the water, though on one occasion a 1.4 m individual was seen basking at the end of a fallen tree about 5 m out from the bank and 4 m above the surface of the water - to reach this site the crocodile would have had to scale a 4 m completely vertical bank and then walk amongst the branches to reach the end of the tree. A photo series taken of a smaller crocodile walking down a tree trunk shows how they navigate the branches (Fig. 2). Interestingly, while abundant anecdotal information and pictures exist of slendersnouted crocodiles tree basking throughout Central Africa (e.g., largely from tourists and NGO employees), there are no records or anecdotal accounts of this behaviour in West Africa. West and Central African slender-snouted crocodiles are in the process of being recognized as distinct species (Shirley et al., 2014) and this could reflect interspecies behavioural divergence despite ecological niche convergence. No observations have been made by M.H.S. of Osteolaemus sp. or Crocodylus sp. in West or Central Africa exhibiting tree-climbing behaviour despite individuals of these two species often occupying elevated bank sites ranging from 0.25 to even 10 m above the surface of the water where banks ranged from gradual to vertical slopes.



Fig. 2. A juvenile (+/- 0.7 m total length) Central African slender-snouted crocodile (*Mecistops cataphractus*) on a tree branch. Loango National Park, Gabon.

Tree-climbing in the Nile crocodile

A. B. observed a Nile crocodile approx. 2 m in total length basking on a tree in the panhandle region of the Okavango Delta, Botswana (S18°38', E22°07'), which then dropped into the water as the observers passed it in a boat. The branch was approximately 0.5 m above the water surface. The crocodile likely climbed onto it from the point where it dipped into the water nearer to the bank. V. D. observed juvenile Nile crocodiles basking on tree branches less than 1 m above the water in Mahango Game Reserve, Namibia (S18°13' E21°45' N>5), in South Luangwa National Park, Zambia (S12°46' E31°56', N=2), and in Liwonde National Park, Malawi (S14°51', E35°18', N=1), always during the daytime.

Interestingly, all photos of Nile crocodiles basking on tree branches that the authors could find on the Internet also come from the southern part of the species' range (South Africa, Zambia, Zimbabwe and Botswana), rather than from East Africa, where the species is equally common and frequently observed, or from other parts of the continent where this species, and the West African crocodile (*C. suchus*), occur. In all cases, climbing abilities seem to be less developed than in Australian freshwater, American and Central African slender-snouted crocodiles.

Discussion

Despite lacking any morphological adaptations for climbing trees, crocodilians are capable of entering arboreal environments within the limits of their locomotory abilities, and in some cases might spend considerable time high above ground. The factors driving such behaviour can only be postulated upon, but our observations support it is likely driven by two predominant conditions: 1) thermoregulation, and 2) surveillance of the habitat. The most frequent instances of tree climbing occur with species or populations that are living in areas with few terrestrial basking sites (e.g., heavily forested or mangrove coastlines) implying that individuals must seek alternatives for adequate thermoregulation. This, however, does not explain the more interesting observation of high frequency nighttime "basking" amongst these tree climbing species, or rather the frequency of nighttime arboreal basking compared to nighttime terrestrial basking.

differences in diurnal versus nocturnal The approachability in crocodilians is well known - and a large factor in why crocodilian population surveys are largely nocturnal, for example. Our observations show that arboreal basking individuals during the day are much more skittish, fleeing at further distances, than their terrestrial basking or resting in the water counterparts but that approachability does not seem to change with arboreal nighttime basking individuals compared to other individuals at night. This suggests that one key role of arboreal basking is, in fact, site surveillance and increased individual security through longer distance observation of potential threats from a vantage point where escape is as easy as falling off a log. A secondary benefit may be increased detectability of prey under such conditions.

Climbing behaviour in extant crocodilians

The difficulty of climbing something is proportional to the steepness of the slope, the smoothness of the surface being climbed, the agility of the animal to help direct the body upwards and secure a grip, and the strength of the animal relative to its weight. Climbing a steep hill and climbing a tree branch are mechanically similar assuming the branch is wide enough to walk on, and especially if that branch grows at an angle, as those of certain tree species tend to be when overhanging water. In theory a wide range of animals can climb trees if the branches are wide enough and the angle is shallow enough. Juvenile crocodilians can do not just that, but also climb on relatively thin, vertical branches that have to be gripped from the sides, or even across multiple branches using them as a ladder and lifting the body vertically. The ability to climb vertically (as long as footholds are available) is a measure of crocodilians' spectacular agility on land and their ability to pull the body along an angled surface. This demonstrates that the degree of arboreality of extinct crocodilians and many other Archosaurian taxa cannot always be ascertained from fossil material. Any small, highly terrestrial crocodilian, such as the recently extinct Trilophosuchus rackhami (Willis, 1993), could be arboreal to some extent.

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