On terrestrial hunting by crocodilians

VLADIMIR DINETS

Dept. of Biology, P.O. Box 249118, University of Miami, Coral Gables, Florida, 33124 USA. dinets@gmail.com

CROCODILIANS are generally considered to be specialised predators hunting in the water or at the water edge (Neil, 1971). Their terrestrial activities such as nesting, migrating, aestivating/hibernating and basking are well known and documented in most overviews of crocodilian biology. Despite abundant anecdotal evidence of terrestrial hunting (mostly in the form of scary campfire stories), this aspect of crocodilian behaviour has never been studied nor scientifically described. Observations made during a study of crocodilians in the wild in 2006-2010, mostly on American alligator (*Alligator mississippiensis*), Nile crocodile (*Crocodylus niloticus*), and to a lesser extent on other species, suggest that terrestrial hunting may be more common than previously thought.

American Alligator (*Alligator mississippiensis*)

Alligator attacks on humans sometimes occur away from water. At least 3 of 13 fatal attacks recorded in the US in the last 10 years happened on land. A 28-year-old woman was apparently attacked by a 3 m alligator while jogging at night along a trail atop a 2 m high dyke parallel to a canal (Harding & Wolf, 2006). An 81-year-old man was attacked by a 3.5 m alligator while walking his dog on a trail at night (Florida Fish and Wildlife Conservation Commission, 2009). A 54 year old woman was attacked by a 4 m alligator while working in her garden 25 m away from a pond (Yarrow, 2008).

During night time observations in southern Florida in April-October of 2006-2010, American alligators 1.5-3.5 m (all sizes were visually estimated) were occasionally observed lying motionless for many hours at the edges of forest roads and public trails (Fig. 1). In some cases the alligator's snout protruded 30-70 cm onto the road, and in one case a 2 m alligator was lying across a narrow trail, completely blocking it. During approximately 200 hours of walking and driving along trails and backcountry roads, such behaviour was observed in Big Cypress National Preserve (n=25), Everglades National Park (n=30) and adjacent private lands (n=13), Fakahatchee Strand National Preserve (n=9), Arthur R. Marshall Loxahatchee National Wildlife Refuge (n=7) and Picayune State Forest (n=1). One such observation was made just 20 minutes after sunset, but on all other occasions animals were observed by roadsides at night. The longest distance from the water edge to the road/trail was 50 m, but in most cases the animals were less than 10 m from water.

When approached by foot, most alligators remained motionless until the observer or the car was 1-2 m. At closer than 1-2 m, they slowly moved into surrounding vegetation or the water. Although the attacks mentioned above might seem to indicate otherwise, American alligators, especially those less than 3 m long, very rarely display predatory behaviour toward people, and tend to avoid close contact (Neil, 1971). However, approximately one quarter of the animals in this study did not move away and thus it was sometimes necessary to walk or drive around them in a circle. One large (>3 m) alligator made a swift turn towards the observer when approached to about 1-1.5 m, and slapped its jaws. One 2 m long animal held and then consumed a Virginia opossum (*Didelphis virginianus*).

On October 7 and 8, 2006, twelve alligators were counted along the edge of a 24 km road (Shark Valley Road, Everglades National Park) on a clear night with full moon, between 21:30-06:00. Ten animals were positioned at an angle to the road edge in such a way that only their heads and sometimes chests were on the pavement. The other two were lying parallel to the road just off the pavement. No alligators were located entirely on the pavement or more than 1 m outside the pavement. The distance from the edge of pavement

Figure 1. American alligator (*Alligator mississippiensis*) on a roadside at night. Everglades National Park (Florida, USA).

to a canal located parallel to the road was mostly 2-3 m (up to 10 m at some locations). This road was closed to vehicles at night and there was no foot or bicycle traffic at the time of observation.

In May-June of 2008-2009, alligators were observed lying on roadsides at night in other parts of American alligator's range: twice in Ocala National Forest (northern Florida), twice in Aransas National Wildlife Refuge (Texas), and once in Cat Island National Wildlife Refuge (Louisiana).

My initial assumption was that this behaviour was possibly performed by individuals either migrating from dried-up ponds and channels, or using warm road surfaces for thermoregulation. However, many alligators moved to the roads from lakes and channels >1 m deep. Some animals spent hours lying near a road/trail and never attempted to cross it, but instead returned to the water before dawn. This behaviour was recorded on both warm (25-30^{o}C) and cool (17-25^{o}C) nights. Alligators were almost always observed on roadsides, not on the pavement where the surface would likely be warmest.

To check if thermoregulation was the reason for such behaviour, temperatures were measured at night during April 17, 2010 on a narrow paved road with no night time traffic at Merritt Island National Wildlife Refuge (Florida). A 2.5 m alligator, that apparently had emerged from a brackish lagoon 3 m from the road, was found at 23:05 lying in low, sparse grass on the roadside, with its head on the gravel-covered road shoulder. Temperatures of the water in the lagoon, the air, the pavement, the gravel road shoulder and the soil under the grass were taken using a Rayteck™ RAYMT6 infrared thermometer and a mercury thermometer every hour until the animal returned to the water. The results (Table 1) showed that when the animal was found, the temperatures of all land surfaces were not greatly different from the air temperature, and

	Thermometer Type	**Time of day**			
		23:10	00:10	01:10	02:10
Air 1 m above the road	mercury	21	20.6	20.1	19.7
Water surface in the lagoon	infrared	23	23	22	22
Lagoon water at 5 cm depth	mercury	23.5	23.2	22.8	22.2
Road pavement	infrared	22	21	21	20
Gravel on the road shoulder	infrared	21	21	20	20
Soil near the road	infrared	21	20	20	20

Table 1. Temperature readings (^{o}C) recorded when an American alligator was observed lying near a paved road 3 m from the shore of a brackish lagoon. Infrared thermometer - accurate to 1^{o}C and a mercury thermometer - accurate to 0.1^{o}C. Merritt Island National Wildlife Refuge (Florida, USA).

lower than water temperature. They also showed that the pavement was warmer than the gravel or soil on which the animal had positioned itself.

Crocodilians need to dry their skin regularly to get rid of parasites and algal growth (Huchzermeyer, 2003). Interestingly however, Alligators were frequently observed on roadsides during nights characterised by high relative humidity and abundant dewfall, conditions that arguably may have promoted algal or fungal growth on skin. Alligators at all sites were basking for many hours in late morning and early afternoon, at which time all or almost all adult animals would be out of water. These basking times could be sufficient for skin care. A reasonable alternative explanation is that alligators lying on roadsides and trails are attempting to ambush terrestrial vertebrates. All observed animals were >1.5 m, possibly because smaller alligators would risk predation if they moved further from water at night. Note that two of three aforementioned fatal attacks on humans occurred on trails during the night.

Nile Crocodile

Pooley (1982) mentioned his observation of two Nile crocodiles carrying a recently killed Nyala (*Tragelaphus angasii*) overland, but it was not clear if the animal had been killed on land.

In September 2008 in South Luangwa National Park (Zambia), at 02:15, I observed a 2.5 m Nile crocodile unsuccessfully chase a juvenile Bushbuck (*Tragelaphus sylvaticus*) for 5-6 m across a dry, elevated river terrace at least 100 m from the water edge. Interviews with local hunters, safari guides and game rangers suggested that Nile crocodiles are occasionally seen on roadsides during night drives in South Luangwa and Lower Zambezi National Parks (Zambia), Mudumu and Mamili National Parks (Namibia), Chobe and Moremi National Parks (Botswana), Lilongwe National Park (Malawi), and Murchison Falls National Park (Uganda).

I have observed terrestrial behaviour at the Oromo River Delta, Ethiopia (n=1 in 44 hours of nocturnal searching), Mahango Game Reserve, Namibia (n=2 in 56 hours of nocturnal searching and driving), and at Simangaliso Wetland Park, South Africa (n=1 in 6 hours of nocturnal searching). Terrestrial behaviour on these occasions was always by crocodiles of between 2-3.5 m. In the latter case, a 2.5 m long crocodile was observed catching and swallowing a large toad (Bufonidae) as it was moving along the trail. Once located, each crocodile was observed for 20-30 min to see if it would start moving, but no attempts to change location were ever seen. The fact that predation attempts were seen twice in less than 2 hours of observing Nile crocodiles on land at night suggests that terrestrial hunting is possibly an effective alternative hunting strategy.

Other Crocodilian Species

In August 2009, local residents in a suburb of Sorong (West Papua Province, Indonesia) reported that a dog had been taken during previous night by a large saltwater crocodile (*Crocodylus porosus*) from a trail 25 m from the water edge. The witnesses claimed that the dog had been following a group of people, who passed by the crocodile and did not notice the reptile until it attacked the dog.

Mugger crocodiles (*Crocodylus palustris*) were observed far from water twice in 68 hours of night time observations. In January 2007 in Kateraniaghat Wildlife Sanctuary (Uttar Pradesh, India), a 3 m *C. palustris* remained on the side of a game trail 30 m from a forest pond for 3 hours during the second half of a night, while the air temperature dropped to 12^{o}C. In the same month in Sasan Gir National Park (Gujarat, India), two 2-2.5 m animals were observed on the side of a trail following a small permanent river, also on a cold (14-16^{o}C) night. They were approximately 100 m apart.

A 2.5 m American crocodile (*Crocodylus acutus*) was observed on three consecutive nights in March 2006 at Everglades National Park, lying just outside the pavement of a parking lot, where its tail and body were concealed by mangrove vegetation. It was approximately 12 m away from the water edge.

A nocturnal observation of an Orinoco crocodile (*Crocodylus intermedius*) near a trail far from water was made at Rio Capanaparo, Venezuela (J. Thorbjarnarson, pers. comm.).

In August 2007 at Caranambu Ranch (Rupununi, Guyana), a 2.5 m black caiman (*Melanosuchus niger*) was observed for 2 hours as

it was lying at the side of a trail 15 m from water, in a location frequently used for river access by domestic and wild animals.

However, such behaviour has never been observed during hundreds of hours of night time observations of three smaller species: Yacare caiman (*Caiman yacare*), spectacled caiman (*Caiman crocodilus*), and broad-snouted caiman (*Caiman latirostris*) in South America. On a few occasions when these animals were seen at night >5 m from water, they were actively moving in the direction of a nearby body of water.

During a study in Costa Rica, Grant et al. (2008) observed spectacled caimans of all sizes frequently moving overland between temporal ponds in the forest, apparently in pursuit of fish trapped in those ponds, but with no evidence of hunting terrestrially.

Magnusson & Lima (1991) found that radiocollared Cuvier's dwarf caimans (*Paleosuchus trigonatus*) spent considerable amounts of time away from water. These animals apparently used shelters deep in the forest rather than hunted on land.

According to hunters in Okoyo (Congo) and rangers in Korup National Park (Cameroon), central African dwarf crocodiles (*Osteolaemus tetraspis*) also use den sites in the forest far from water. None of the interviewed claimed any knowledge of dwarf crocodiles hunting on land.

Unsurprisingly, there seems to be a lack of data on terrestrial hunting by specialised piscivorous species – slender-snouted crocodile (*Mephistops cataphractus*), false gharial (*Tomistoma schlegeli*) and Indian gharial (*Gavialis gangeticus*). The latter is not as agile on land (Neil, 1971).

It appears that terrestrial hunting is a regularly occurring behaviour in large omnivorous species of crocodilians. Other species leave water to nest, den, bask, or move between aquatic habitats, but there are no observations yet that prove they hunt on land.

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