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## THE ROLE OF PREDATION IN SHAPING CROCODYLIAN NATURAL HISTORY

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**ABSTRACT:** Although adult crocodylians have few predators (mostly humans and other crocodylians), hatchlings and eggs are killed and consumed by a diverse array of invertebrates, fishes, anurans, reptiles, birds, and mammals. We review published literature to evaluate the incidence of predation in crocodylian populations, and the implications of that mortality for crocodylian life-history evolution. Presumably because predation is size-dependent, small-bodied crocodylian taxa appear to be more vulnerable to predation (across a range of life stages) than are larger-bodied species. Several features of crocodylian biology likely reflect adaptations to reducing vulnerability to predation. For example, the threat of predation may have influenced the evolution of traits such as nest-site selection, maternal care of eggs and hatchlings, crèche behavior in hatchlings, and cryptic coloration and patterning. Even for such large and superficially invulnerable taxa such as crocodylians, the avoidance of predation appears to have been a significant selective force on behavior, morphology, and ecology.

*Key words:* Alligator; Caiman; Crocodile; Ontogeny; Vulnerability

AN ORGANISM'S vulnerability to predation can play a central role in its biology. For many kinds of animals, predation is a major source of mortality, and hence can influence patterns of distribution and abundance (Sih et al., 1998; Ormerod, 2002). On an evolutionary level, vulnerability to predation can impose selection on traits that influence an organism's rate of encounter with potential predators (e.g., diel patterns of activity, habitat selection [Holomuzki, 1986; Turner and Mittelbach, 1990; Turner, 1996]), its ability to detect the presence of predators (e.g., via visual or olfactory cues [Petranka et al., 1987; Magurran and Seghers, 1990; Lehtiniemi, 2005]), and its ability to escape from a predator's attack (e.g., toxin tolerances, locomotor speeds [Snell et al., 1988; Husak and Fox, 2006]). Although many antipredator tactics clearly have evolved in response to the selective forces imposed by interactions with predators, most of these examples involve species that occupy relatively low positions within trophic webs (e.g., Matsuda et al., 1996; Finke and Denno, 2004; Kondoh, 2007; Carey and Wahl, 2010). In such animals, vulnerability to

predation is likely to explain a high proportion of variation in lifetime fitness. However, even adult top predators may occasionally serve as prey (Pienaar, 1969; Hoelzel, 1991). Has the threat of predation acted as a significant selective force even in large and well-armed species?

In the present review, we collate published records of predation on crocodylians. Although some species attain relatively small mean maximum sizes (<2 m in *Paleosuchus* spp., *Caiman* spp., *Osteolaemus tetraspis*: Alderton, 1998), others grow to >4.5 m in length (e.g., *Crocodylus porosus*, *Crocodylus niloticus*, *Tomistoma schlegelii*: Alderton, 1998). Crocodylians are exclusively carnivorous, and occupy the role of top predator in many tropical food webs (Mazzotti and Brandt, 1994; Lang, 2002) with the prey of adults including animals as large as wallabies, cattle, water buffalo, zebra, wildebeest, deer, and giraffe (Pye, 1976; Webb and Manolis, 1998; Shoop and Ruckdeschel, 1990; Shield, 1994; Alderton, 1998; Doody et al., 2007). The formidable armament of crocodylian skins is thought to render them invulnerable to most predators (Garrick and Lang, 1977). Many studies have evaluated the role of crocodylians as predators (e.g., Delany and Abercrombie, 1986; Tucker et al.,

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1996; Platt et al., 2007; Wallace and Leslie, 2008; Borteiro et al., 2009), but less is known about the role of crocodylians as prey. Their mobile, semiaquatic and cryptic nature makes it difficult to observe them, especially during juvenile life (Lang, 1987).

Our aims in the present review were to (1) collate field records of predation on crocodylians and (2) explore the degree to which distinctive phenotypic traits of crocodylians may have arisen as antipredator adaptations. We have not attempted to review the numerous records of predation on crocodylians by humans, and discuss this topic only briefly (see also Magnusson, 1982, 1986; Cuc, 1994; Lamarque et al., 2009; Crocodile Specialist Group (CSG) newsletters; proceedings of the CSG meetings, etc. for further information on this topic).

#### MATERIALS AND METHODS

To identify species that prey upon crocodylians, we reviewed literature from a wide range of sources. We examined peer-reviewed literature on ecological, behavioral, and natural history studies on crocodiles in indexed journals using online search engines. We focus primarily upon references that include direct behavioral observations of actual or attempted predation incidents, or of crocodile stomach contents. Because such evidence-based records are rare in peer-reviewed literature, however, we also include reliable records from "grey literature." These include studies published in scientific and technical reports, field guides, and newsletters. Such records typically comprise anecdotal observations, often based upon small sample sizes, but merit inclusion as long as they exhibit the same levels of methodological rigor as does published literature (Conn et al., 2003). By ignoring such reports, we would fail to include a rich source of field observations (Simkhada et al., 2005). To ensure that the reports came from qualified people, however, we only included those from professional biologists and members of the International Union for the Conservation of Nature Crocodile Specialist Group; we omitted reports by other individuals unless they contained objective data.

#### RESULTS AND DISCUSSION

##### *Field Records of Predation on Crocodylians*

A search of published literature (including anecdotal observations of predation events and stomach content analyses) and communication with colleagues revealed 279 cases, involving 184 species of predators preying on 19 crocodylian taxa (see Supplementary Material; Figs. 1 and 2). Most predators are species that naturally co-occur with crocodylians, but several are invasive species.

Among invertebrates at least three species of ants have been observed to prey upon hatchling crocodylians. One of these, the Fire Ant (*Solenopsis* spp., native to Central and South America) has been widely identified as a predator of hatchling crocodylians (*Caiman yacare*, *Crocodylus moreletii*, etc.), often colonizing crocodylian nests (Cintra, 1985; Platt et al., 2008). When the crocodiles hatch, the ants swarm and attack hatchlings, inflicting painful bites and consuming weaker individuals. In some cases, *Solenopsis* ants have consumed almost entire clutches of hatchlings (Platt et al., 2008). Introduced to the United States between 1930 and 1940 (Callcott and Collins, 1996), *Solenopsis invicta* also has been reported killing and consuming hatchlings of *Alligator mississippiensis* and *Crocodylus acutus* as well as reducing growth rates and increasing morbidity in survivors (Joanen, 1969; Goodwin and Marion, 1978; Taylor, 1984; Platt et al., 1995). Alligator hatchlings exposed to fire ant bites showed higher plasma corticosteroid levels, decreased total leukocyte counts, and decreased heterophil/leukocyte ratios, signifying that ant attacks may have an immunosuppressive effect in hatchlings (Falconi et al., 2013). Ants have destroyed entire clutches of *Osteolaemus tetraspis* eggs (Kofron and Steiner, 1994), discouraged female crocodylians from opening nests, and killed hatchlings (Reagan et al., 2000). Staton and Dixon (1977) interpreted the presence of ants (species not given) in *Caiman crocodylus* nests in the Venezuelan Llanos as beneficial, with the ants ridding the nest of fungal growth and cracked eggs that might otherwise emit odors that attract nest predators. The presence of ants in nests may deter some nest predators (Riley et al., 1985). However, the effects of ant predation on the

population dynamics of crocodylians have never been quantified.

Crustaceans occasionally consume reptiles (including turtles, lizards, and snakes: e.g., McCormick and Polis, 1982; Voris and Jeffries, 1995), but the only reports of them preying on crocodylians involve Blue Crabs (*Callinectes sapidus*) and Land Crabs (*Cardisoma guanhumi*) consuming *Crocodylus acutus* hatchlings (e.g., Lang, 1975; Ogden, 1978; Kushlan and Mazzotti, 1989). Crabs are opportunistic predators and tend to target newly hatched crocodiles during their most vulnerable stage.

Predation by fish on crocodylians is difficult to observe, and mortality rates due to fish predation may be underestimated as a consequence. Webb (1979) considered it likely that Black Bream (*Hephaestus fuliginosus*) and Saratoga (*Scleropages leichardti*) prey on hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*, explaining low densities of hatchlings in some waterways. Hatchling and juvenile *C. porosus* (and *C. johnstoni*) inhabiting tidal reaches of large rivers in northern Australia are consumed by several fish species, including Barramundi (*Lates calcarifer*), Tiger Sharks (*Carcharhinus taurus*), Pig-eye Sharks (*Carcharhinus amboinensis*) and River Sharks of the genus *Glyphis* (G. Allen, personal observation). Tail amputations of hatchling *C. porosus* in northern Australia have been attributed to shark attack (Webb and Messel, 1977).

Invasive freshwater fish have affected many aquatic organisms worldwide (e.g., Ogutu-Ohwayo, 1990; Crowl et al., 1992; Englund, 1999; Jang et al., 2006), and Pacu (*Piaractus brachipomum*), introduced into the Sepik (Papua New Guinea) in the 1980s and 1990s, attack *C. porosus* and *Crocodylus novaeguineae* hatchlings and juveniles and also damage the floating mats of vegetation used for *C. porosus* nesting (Cox et al., 2006). Pacu sometimes sever limbs and tails of young crocodylians (Fig. 1).

Records of amphibians preying on crocodylians are rare and limited to American Bullfrogs (*Lithobates* [formerly *Rana*] *catesbeianus*), and Southern Leopard Frogs (*Lithobates* [formerly *Rana*] *sphenocephalus*), both of which were reported to consume week-old

*A. mississippiensis* hatchlings in captivity in Florida, USA (Springer, 1938; Wettstein, 1954, cited by Cott, 1971).

The highly toxic Cane Toad (*Rhinella marina* [formerly *Bufo marinus*]), introduced to Australia in 1935, has not been reported preying upon hatchling *C. johnstoni* or *C. porosus*. Nonetheless, the toads have caused massive mortality of crocodiles through toxic prey ingestion, causing a population decrease of up to 77% in the *C. johnstoni* population at Victoria River, Northern Territory (Letnic et al., 2008), and Boodjamulla National Park in northwestern Queensland (White, 2008). Cane Toads also indirectly affect crocodile population dynamics by poisoning egg predators, such as varanid lizards (Doody et al., 2006) thus increasing crocodile egg survivorship (C. Manolis, personal observation).

Among reptiles, lizards (14 species), snakes (seven species), turtles (~10 species), and crocodylians (12 species) have been reported to consume crocodylians and their eggs (Supplementary Material; Figs. 1 and 2). In northern India, hatchling *Gavialis gangeticus* are eaten by Soft-shelled Turtles (*Nilssonina gangeticus*) soon after hatching (R. Whitaker, personal observation). In Australia, adult Northern Long-necked Turtles (*Chelodina rugosa*) kill and eat young *C. johnstoni* in captivity (Webb et al., 1983a), and the same turtle species and Northern Snapping Turtles (*Elseya dentate*) have been commonly observed near crèches of hatchling *C. johnstoni* in the wild; some of the hatchlings in those crèches exhibited injuries consistent with attempted predation by turtles (Webb et al., 1983a; Chibeba, 2003; G. Webb, personal observation).

Predation of hatchling and adult crocodylians by large constricting snakes has been widely reported (Cintra, 1989; Magnusson, 1989; Rivas et al., 1999; Platt et al., 2004; Snow et al., 2007b). In South America, Anacondas (*Eunectes* spp.) prey upon juvenile and subadult caimans (e.g., Rivas, 2000), and in Africa, large [ $>2.5$  m in total length] Rock Pythons (*Python sebae*) prey upon African Dwarf Crocodiles (*Osteolaemus tetraspis*; Luiselli et al., 2001; see also the review by Reed and Rodda, 2009). The invasive population of Burmese Pythons (*Python molurus*



FIG. 1.—A diverse array of predators kill and consume crocodilians at all life stages. (A) A hatchling New Guinea Crocodile (*Crocodylus novaeguineae*) after being attacked by the invasive Pacu (*Piaractus brachipomum*) at Sepik in Papua New Guinea (photo: J. Cox). (B) Rufescent Tiger Heron (*Tigrisoma lineatum*) ingesting a Caiman (*Caiman*

*bivittatus*) in Everglades National Park, Florida (Snow et al., 2007a) preys on *A. mississippiensis*: 11 sets of remains were identified from regurgitation, stomach contents and/or feces of *P. m. bivittatus* (M. Rochford, personal observation; S. Snow, personal observation). Anecdotal reports that Australian Water Pythons (*Liasis fuscus*) may prey on young *C. porosus* and *C. johnstoni* (Worrell, 1963; Gow, 1976) have not been confirmed despite detailed ecological research on these snakes in regions where both *C. porosus* and *C. johnstoni* are abundant (e.g., Madsen and Shine, 2000; Madsen et al., 2006).

Monitor lizards, or goannas (family Varanidae), are a major predator of crocodylian eggs in Africa, Asia, and Australia. In southeastern Zimbabwe, 80% of Nile Crocodile (*C. niloticus*) nests not attended by females were destroyed by Nile Monitors (*Varanus niloticus*) within 2.5 mo of laying (Kofron, 1989). *Varanus niloticus* also may prey on hatchlings during the first few days after they hatch (Modha, 1967; Root, 1989). Steel (1989) suggested that Nile Monitors work in pairs, with one decoying the female crocodile (if she is attending the nest) and the other raiding the nest. In Australia, monitor lizards destroyed up to 85% of *C. johnstoni* nests in the McKinlay River area of the Northern Territory (Smith, 1987; Chibeba, 2003). The Asian Water Monitor (*Varanus salvator*) is the most widely distributed varanid species (Koch et al., 2007) and is a predator of nests of *C. porosus*, *Crocodylus palustris*, *G. gangeticus*, and *T. schlegelii* (R. Whitaker, personal observation).

Cannibalism potentially took place among prehistoric crocodylians such as dyrosaurids (Martin, 2013) and is common among extant crocodylians (e.g., Stevenson-Hamilton, 1957; Cott, 1961; Pooley, 1969; Staton and Dixon,

1975; Messel and Vorlicek, 1987; but Magnusson, 1986 states that members of their own species are not important items in the diets of most crocodylians). Though cannibalism may take place at any life stage (e.g., Webb et al., 1983a), in the population models introduced by Nichols et al. (1976) and Blomberg et al. (1982), it was considered a major process only for the first 3 yr of life.

Crocodyles sometimes feed on the eggs of their own species both in the wild (e.g., in *C. niloticus*: Modha, 1967; Root, 1989) and under captive conditions (e.g., in *Caiman yacare*: Walkowich, 2009). Larger crocodyles are major predators of both hatchlings and juveniles, both within and between species (Hippel, 1946; Cott, 1961; Graham, 1968; Webb and Manolis, 1998). Cannibalism on hatchlings also may take place both in the wild (e.g., in *A. mississippiensis*: Rootes and Chabreck, 1993) and in captivity (e.g., in *C. palustris*: Reddy, 1978; *C. niloticus*: Hutton, 1984). Cannibalism on smaller animals appears to be common among Nile Crocodyles. Hippel (1946) reported that 11% of the stomachs of "large" Nile Crocodyles contained the remains of other crocodyles and Cott (1961) gives four anecdotal reports of cannibalism, all of large juveniles and intermediates by adults and, in addition, reports evidence of cannibalism in the stomach contents of 17 of 851 animals. Pooley (1969) reports a 2-m adult Nile Crocodile catching and eating a 1-m conspecific. Nonetheless, several studies that examined large numbers of *C. niloticus* stomach samples did not reveal any evidence of cannibalism (e.g., Graham, 1968; Blomberg, 1977; Taylor, 1979; Webb et al., 1982).

Smaller individuals tend to lead a more secretive life style, inhabiting fringe habitat away from larger animals: Cott (1961) attributed this secretive behavior of young (2- to 5-

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*crocodylus crocodylus*) hatchling at Tambopata National Reserve, Peru (photo: D. Johnston). (C) A Painted Stork (*Mycteria leucocephala*) preying on a baby Muggler (*Crocodylus palustris*) at Yala National Park, Sri Lanka. (photo: G. Rajapakse). (D) An Asiatic Lion (*Panthera leo persica*) with a young Muggler (*Crocodylus palustris*) at Gir Lion Sanctuary, Gujrat, India (photo: B. Pandya). (E) A Leopard (*Panthera pardus*) killing an adult Nile Crocodile (*Crocodylus niloticus*) at Kruger National Park, South Africa (photo: H. Brindley). (F) The highly acclaimed photograph of a ~3.9-m Burmese Python (*Python bivittatus*) split open after swallowing the ~1.8-m American Alligator (*Alligator mississippiensis*) at south Miami-Dade, Florida (photo: Everglades National Park rangers). (G) A Bengal Tiger (*Panthera tigris*) with a Muggler (*Crocodylus palustris*), which it killed after a 13-h fight at Ranthambhore Tiger Reserve, Rajasthan, India (photo: M.D. Parashar). All photographs reprinted with permission.

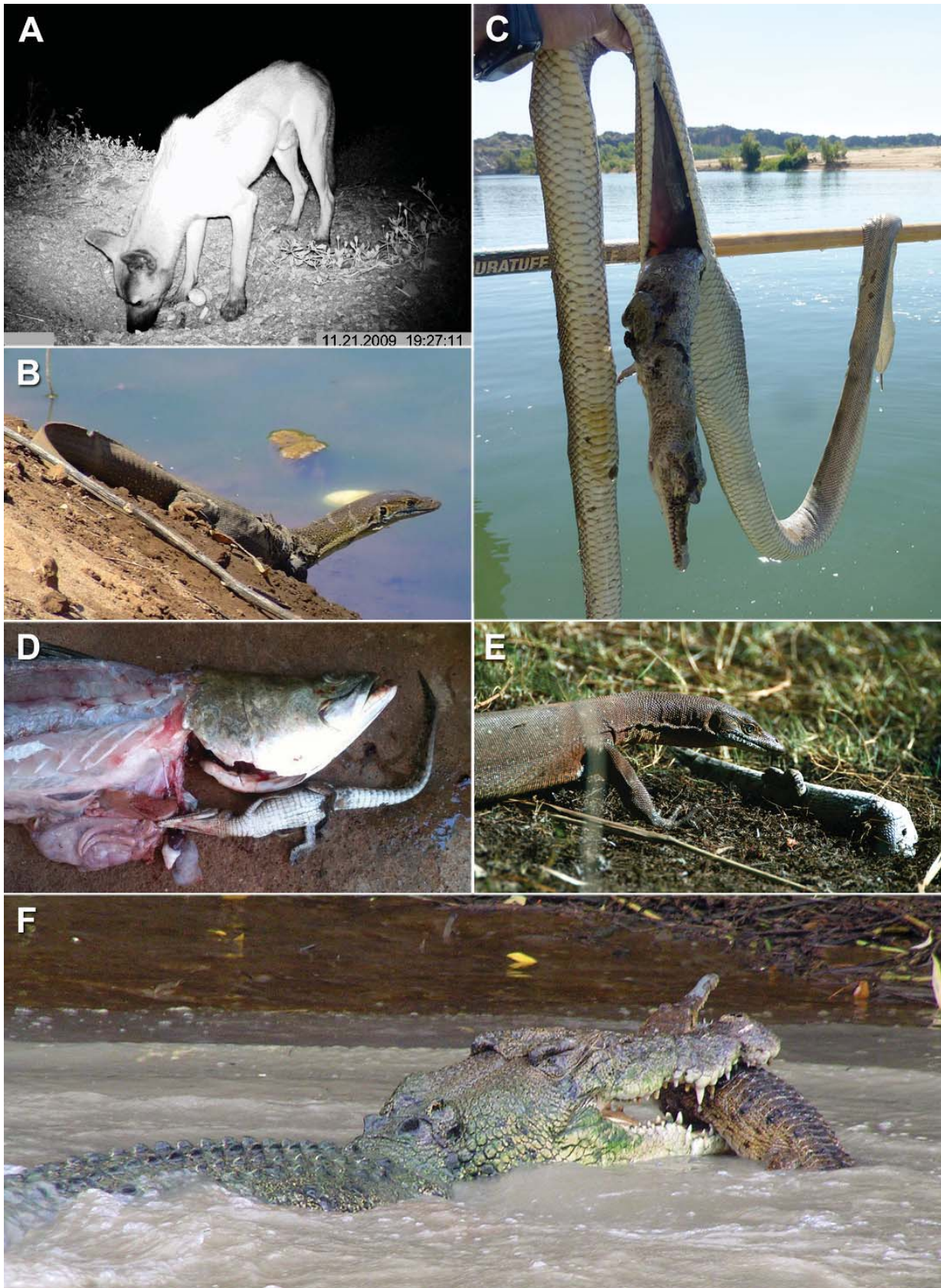


FIG. 2.—The smaller of the two Australian crocodylians, the endemic Australian Freshwater Crocodile (*Crocodylus johnstoni*), is vulnerable to predation at all life stages. (A) A Dingo (*Canis lupus dingo*) excavating a newly laid *C. johnstoni* nest at Lake Argyle, Western Australia (photo: R. Somaweera). (B) Merten's Water Monitors (*Varanus*

yr-old) Nile Crocodiles in Zululand to the threat posed by cannibalistic adults. In some instances, especially at high population densities, cannibalism may regulate crocodilian population densities. Large American Alligators (>2.73 m) in Louisiana preyed heavily on large juveniles and small adults (total lengths 1.22 to 2.12 m: Rootes and Chabreck, 1993).

When two or more species of crocodilian are sympatric, the larger species is likely to dominate the smaller through predation (Fitch, 1975). Predation by larger crocodilian species may also affect the spatial distribution of smaller species. For example, small caiman taxa (*Caiman crocodilus*) are most common in areas where populations of the larger Black Caiman (*Melanosuchus niger*) and Orinoco Crocodile (*Crocodylus intermedius*) have been depleted through hunting (Webb and Manolis, 1998). Medem (1971a) described a similar situation, in which selective hunting of *Crocodylus acutus* allowed the smaller *Caiman crocodilus* to spread into areas from which it was previously excluded. In areas of northern Australia containing both *C. porosus* and *C. johnstoni*, a negative correlation between numbers of the two species may be due to competitive exclusion and predation of *C. johnstoni* by *C. porosus* (Webb et al., 1983b; note that adult *C. johnstoni* also prey on hatchling *C. porosus*: Supplementary Material). Saltwater crocodiles also may limit the distribution of freshwater crocodiles in Asia, with the distribution of *C. palustris* in Sri Lanka and *T. schlegelii* in Borneo being shaped partly by interactions with *C. porosus* (R. Whitaker, personal observation).

The level of cannibalism may change seasonally, with high rates in warmer and drier seasons when crocodilians concentrate in the remaining waters (Webb and Smith, 1984; Woodward et al., 1987).

Most avian predators of crocodilians have been observed preying upon hatchlings (Supplementary Material; Fig. 1). Birds also consume crocodilian eggs, but usually do so only after other predators have opened the nest. In Everglades National Park, Florida, Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) scavenge *C. acutus* eggs after raccoons have opened the nest (M. Brien, personal observation), and at Australia's Lake Argyle, Torresian Crows (*Corvus orru*) consumed *C. johnstoni* eggs after the nests were opened by Dingoes (*Canis lupus dingo*; Somaweera et al., 2011a). In Africa, Marabou Storks (*Leptoptilos crumeniferus*) may feast on *C. niloticus* hatchlings when nests are opened by Nile Monitors (Cott, 1961). However Marabou Storks also use their large bills to probe through sand to gain access to crocodile eggs (Pooley and Ross, 1989). In northern Santa Fe in Argentina, Crested Caracaras (*Polyborus plancus*) open the nests of *Caiman latirostris* and consume the eggs (Larriera and Piña, 2000). Although most avian predators of crocodilians are diurnal, nocturnal avian predators include owls and night herons that prey upon hatchlings (e.g., Pooley, 1969; Ayarzagüena, 1980).

An array of diurnal raptors and other large waders take hatchling and juvenile crocodilians (Supplementary Material; Fig. 1) but most of these records are based on brief opportunistic observations.

Over 50 species of mammal have been identified as predators of crocodilians. Rodents and larger mammals of the families Suidae, Canidae, Viverridae, Procyonidae, and Herpestidae account for most egg predation, whereas predation on young crocodilians appears to be mainly by the Felidae and Canidae (Supplementary Material; Figs. 1 and 2). Olfactory cues seem to attract mammalian

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*mertensi*) rarely excavate nests themselves but often raid eggs from already open *C. johnstoni* nests at Ord River, Western Australia; a raided egg is in the background (photo: B. Dempsey). (C) An Olive Python (*Liasis olivaceus*) found dead at Geike Gorge, Western Australia, with a hatchling *C. johnstoni* as its last meal (photo: B. Scoble and D. Woods). (D) A *C. johnstoni* hatchling found inside a Barramundi (*Lates calcarifer*) at Katherine, Northern Territory (photo: D. Forder). (E) A Merten's Water Monitor with its prey (freshly killed hatchling *C. johnstoni*) at Lake Argyle, Western Australia (photo: R. Somaweera). (F) A large Saltwater Crocodile (*Crocodylus porosus*) seizing an adult *C. johnstoni* at Adelaide River, Northern Territory (photo: A. Bowman). All photographs reprinted with permission.



predators to crocodile eggs, and factors that increase the concentration of such cues—such as the nearby presence of turtle nests (Deitz and Jackson, 1979) and human visitation (Deitz and Hines, 1980)—may attract more mammalian predators.

Large cats are capable of tackling an adult crocodile, with reports of such attacks by the Ocelot (*Leopardus pardalis*), Puma (*Puma concolor*), Jaguar (*Panthera onca*), Leopard (*Panthera pardus*), Tiger (*Panthera tigris*) and Lion (*Panthera leo*) including the Asiatic Lion (*P. l. persica*; e.g., Cott, 1961; Pienaar, 1969; Gorzula, 1978; Emmons, 1989; Alvarez del Toro and Sigler, 2001; Scognamillo et al., 2003; Cavalcanti and Gese, 2009; Da Silveira et al., 2010; Azevedo and Verdade, 2012; Fig. 1). Among the canines, feral and native species also may cause predation in certain areas (e.g., Feral Dogs attacking young *C. palustris* in Baluchistan area in Iran [A. Mobaraki, personal observation]; Dingoes preying on *C. johnstoni* nests at Lake Argyle in Australia [Somaweera et al., 2011a]). However, larger crocodiles may be a major part of mammalian predator diets only when crocodilians are abundant and other prey items are rare (Da Silveira et al., 2010). In lowland Florida Everglades 11.1% of Puma kills were *A. mississippiensis* (Dalrymple and Bass, 1996), whereas in the uplands and in Peruvian Amazon, the importance of crocodilians was reduced and mammals dominated the diet (Emmons, 1987; Maehr, 1997). Similarly, the predation rate of caimans by Jaguars in the southern Pantanal in Brazil peaked during the dry season when caimans congregate in high densities and are more easily captured (Azevedo and Verdade, 2012).

Human predation (hunting crocodilians as a source of food) persists in many countries, especially among rural and tribal communities (Brazaitis et al., 1996; Alderton, 1998; Pauwels et al., 2003). Predation by humans can focus on all stages of crocodilians, from eggs (e.g., Whitaker and Whitaker, 1984; Webb and Manolis, 1998) to hatchlings (e.g., Wilson, 1978), subadults (e.g., Heydt, 1744), and adults (e.g., Abercrombie, 1978; Gramentz, 1999). Some species are sold as food in open markets (e.g., *Crocodylus cataphractus* in Gabon [Steel, 1994]; *C. palustris* in Sri Lanka

[Whitaker and Whitaker, 1979]). Aboriginal people of northern Australia have been harvesting *C. porosus* eggs for thousands of years, and may thus have shaped population dynamics of crocodiles in some areas (Webb and Manolis, 1998). Subadult and adult crocodilians are typically killed for other reasons (e.g., reduction of danger to people or livestock; skins for commercial trade [Parker and Watson, 1970]) but meat is a by-product in many incidents (even when the mortality is unintentional, as when crocodiles drown in fishing nets [Lawson, 1993]).

### *Biases and Quality of Evidence*

The above reports (and see Supplementary Material) suggest that the incidence of predation is not distributed randomly among the different subfamilies or life stages of crocodilians. The numbers of records are highest for crocodilian species that (1) have been well studied (either for longer durations or in numerous locations), (2) are relatively abundant, and (3) occupy more easily accessible habitat. There is a paucity of field data for some species (e.g., *Alligator sinensis*, *Crocodylus mindorensis*, *Crocodylus rhombifer*, *Crocodylus siamensis*, *Crocodylus intermedius*) and some life stages (Table 1). Incidents of predation and mortality are more easily recorded at the egg and hatchling stage for most species, as juveniles and larger size classes are harder to study.

Quantifying rates of predation on different species of crocodiles is virtually impossible with the available data. Most observations of predation are opportunistic and either unpublished or published as anecdotal reports. Thus, in the following section we examine the biases in a qualitative fashion only.

### *Patterns in Crocodilian Vulnerability to Predators*

Predation has been reported on 11 species of crocodilids (161 records), seven species of alligatorids (107 records), and the sole gavialid (10 records). Based on reported predation incidents (Supplementary Material), the life-history stage of a crocodilian affects the type of predators to which it is vulnerable. Eggs were predominantly consumed by terrestrial

TABLE 1.—Field mortality rates of crocodilians due to predation (numbers in parenthesis refer to the total sample size in the study).

Crocodilian species	Mortality (%)	Predator(s) involved	Location	Source
<b>Eggs</b>				
<i>C. gangeticus</i>	10.8% (n = 5623)	<i>Canis lupus</i>	National Chambal Sanctuary, India	Hussain, 1999
<i>M. niger</i>	0.47%	Unidentified mouse	Northeastern Ecuador	Villamarin-Jurado and Suarez, 2007
<b>Nests</b>				
<i>A. mississippiensis</i>				
	6.60%	<i>Procyon lotor</i>	Florida Everglades, USA	Kushlan and Jacobsen, 1990
	16.5 (n = 266)	<i>Procyon lotor</i>	Louisiana, USA	Joanen, 1969
	26.9% (n = 26)	<i>Procyon lotor</i>	Florida, USA	Ogden, 1978
	31% (n = 13)	<i>Procyon lotor</i>	North-central Florida, USA	Goodwin and Marion, 1978
	45% in dry years	<i>Procyon lotor</i>	Louisiana, USA	Fleming et al., 1976
	56.3 (n = 96)	Mammals	North-central Florida, USA	Dietz and Hines, 1980
	16.1% (n = 31)	<i>Procyon lotor</i> , <i>Sus scrofa</i>	Florida, USA	Ruckel and Steele, 1984
	69% but could be as high as 90%	<i>Procyon lotor</i> , <i>Ursus americanus</i> , <i>Oryzomys</i> sp.	Okefenokee Swamp, USA	Hunt and Odgen, 1991
	86.4% (n = 110)	<i>Ursus americanus</i>	Georgia, USA	Metzen, 1977
<i>C. acutus</i>	14.50%	<i>Procyon lotor</i>	Southern Florida, USA	Kushlan and Mazzotti, 1989
	29% (n = 222)	<i>Procyon lotor</i> ?	Everglades National Park, USA	Mazzotti et al., 2007
	35% (n = 40) partially	<i>Procyon lotor</i>	Florida, USA	Ogden, 1978
<i>C. johnstoni</i>	64% (n = 88)	Varanids, <i>Sus scrofa</i>	McKinlay River, Australia	Webb et al., 1983a
	25% (n = 117)	<i>Varanus gouldii</i>	McKinlay River, Australia	Smith, 1987
	85.3% (n = 61)	<i>Varanus panoptes</i>	McKinlay River, Australia	Chibeba, 2003
	72.1% but could be high as 100% (n = 111)	<i>Canis lupus dingo</i>	Lake Argyle, Australia	Somaweera et al., 2011a
<i>C. moreletii</i>	27.1% (n = 59)	<i>Procyon lotor</i> , <i>Tayassu tajacu</i> , <i>Oryzomys</i> sp.	Northern Belize	Platt et al., 2008
<i>C. niloticus</i>				
	34%	<i>Varanus niloticus</i>	St. Lucia, South Africa	Pooley, 1969
	17.1% (n = 152)	<i>Varanus niloticus</i>	Lake Rudolf, Kenya	Graham, 1968
	3.6–31.4%	<i>Varanus niloticus</i> and birds	Lake Rudolf, Kenya	Modha, 1967
	38.8% (n = 18)	<i>Varanus niloticus</i>	Southeastern Zimbabwe	Kofron, 1989
	up to 20%	<i>Varanus niloticus</i>	Ndumu, Zululand	Pooley, 1969
<i>C. niloticus</i>		<i>Varanus niloticus</i>	Zimbabwe	Blake and Loveridge, 1975
		<i>Varanus niloticus</i>	Uganda	Cott, 1961, 1971, 1975
<i>C. novaeguineae</i>	13.3% of which 6% from non-human predation (n = 83)	Varanids, <i>Sus scrofa</i>	Lake Murray, PNG	Hall and Johnson, 1987
<i>C. palustris</i>	5% (n = 59)		India and Sri Lanka?	Whitaker and Whitaker, 1984
<i>C. porosus</i>	76.9% (52)	<i>Varanus indicus</i>	Liverpool and Tomkinson River systems, Australia	Magnusson, 1982

TABLE 1.—Continued.

Crocodilian species	Mortality (%)	Predator(s) involved	Location	Source
<i>Caiman crocodilus</i>	69%	<i>Tupanambis teguixin</i>	Venezuela	Staton and Dixon, 1977
	12.5% (n = 32)	<i>Procyon lotor</i>	Cano Negro, Costa Rica	Allsteadt, 1994
	50% (n = 2)		Northern Surinam	Ouboter and Nanhoe, 1997
<i>Caiman latirostris</i>	41%	<i>Sus scrofa</i> , <i>Polyborus plancus</i> , <i>Conepatus chinga</i>	Northern Santa Fe, Argentina	Larriera and Pina, 2000
<i>Caiman yacare</i>	35%		Pantanal, Brazil	Campos, 1993
	73.80%	<i>Nasua nasua</i> , <i>Cerdocoion thous</i>	Brazil	Crawshaw and Schaller, 1980
	48.5		Pantanal, Brazil	Cintra, 1988
<i>M. niger</i>	28% (may include other sources of mortality)	<i>Tupanambis teguixin</i>	Rupununi Savannah, Guyana	Taylor, 2006
<i>P. palpebrosus</i>	50% (n = 2)		Amazon region, Brazil	Campos et al., 2006
Hatchlings (<1 yr)				
<i>A. mississippiensis</i>	71% (n = 1676)		Central Florida, USA	Temsirpong, 1999
<i>A. mississippiensis</i>	35%		Louisiana, USA	Nichols et al., 1976
<i>C. johnstoni</i>	~98% (n = 204)		McKinlay River, Australia	Webb et al., 1983a
<i>C. johnstoni</i>	7–17%		McKinlay River, Australia	Smith, 1987
<i>C. porosus</i>	54%		Northern Australia	Webb et al., 1984

mammalian and reptilian predators (86.2%), whereas hatchlings were consumed by a wider taxonomic array of predators (invertebrates to humans). Similar numbers of aquatic, aerial, and terrestrial predators were reported to take hatchlings and juveniles (37.1%, 30.9% and 32%, respectively). Adult and subadult crocodilians are vulnerable to terrestrial (51.7%) and aquatic (48.3%) predators such as large constrictors, larger crocodilians, felids, and humans.

Hatchling crocodilians are vulnerable to a range of bird, mammal, fish, reptile, and invertebrate predators during the first year of life. After this first year, individuals of most species have doubled in size and the number of predators declines dramatically (Webb and Manolis, 1998). Many female crocodilians survive until senescence, whereas males often are killed in territorial disputes, especially in high-density populations (Gallegos et al., 2008).

#### *Adaptations Due to Predation on Crocodilian Eggs*

The level of predation on crocodilian eggs varies among and within species, and is influenced by the mode of nesting, nest site selection, and the existence of nest protection by adults. High rates of nest predation may have favored a range of adaptations, as noted below.

*Mode of nesting.*—Female crocodilians form nests either by digging a hole in the substrate or by mounding up soil, sand, and vegetation (Alderton, 1998). These two modes of nesting are phylogenetically conservative, but also may be adaptive to local habitat conditions (Greer, 1970, 1971; Campbell, 1972; Thorbjarnarson, 1996). Hole-nesters are more likely to nest communally and this may have both advantages and disadvantages (*C. niloticus*: Cott, 1961, 1975; *C. acutus*: Garrick and Lang, 1977; *C. johnstoni*: Webb et al., 1983a; Doody et al., 2009). At McKinlay River in Australia, predation by monitor lizards was greater at colonial nesting sites of *C. johnstoni* than where only one or two crocodiles nested (Webb et al., 1983a; Webb and Smith, 1984); however, the nest density did not affect the predation latency of nests of the same crocodile species at Lake Argyle in

Australia where the main nest predators were Dingoes (Somaweera et al., 2011a). Concentrations of eggs or adults (mothers) may attract predators to nest sites (Christian and Tracy, 1981; Graves and Duvall, 1995). Although nesting near conspecifics might potentially reduce the per-capita probability of predation (of mothers, eggs, or neonates) through prey saturation or satiation, larger predators could return in a few days to consume the remainder of the eggs (especially in species such as crocodylians in which development is prolonged). Also, consumption of just one egg can compromise the entire clutch by destroying the nest cavity (see review by Doody et al., 2009). Conversely, communal nesting may improve hatchling survival (both at nest and nursery stages) due to the larger number of parents attending (and thus, nest-guarding); and also, larger number of hatchlings may enable better social communication (Rao and Singh, 1993).

Maternal nest defense and territoriality are more common in mound-nesting crocodylian species (e.g., *C. porosus*, *A. mississippiensis*) than in hole-nesters (e.g., *C. acutus*, *C. johnstoni*), although some hole-nesting species (e.g., *C. niloticus*) defend their nests also (Modha, 1967; but see Kofron, 1989 for a counterexample). However, there are no robust data to test the prediction that the common association between mound-nesting and maternal defense results in lower levels of predation in mound-nesting species (despite mound nests being more obvious to predators).

*Nest site selection.*—Crocodylian nesting sites are nonrandomly distributed, apparently reflecting factors that influence egg development (e.g., temperature, humidity), egg survival rates (e.g., flooding, predation), and maternal costs (Webb et al., 1983a; Ouboter and Nanhoe, 1988; Somaweera and Shine, 2012a). Oviposition site selection affects vulnerability of the nest to predation, with nests in more exposed sites or sites with easier access to predators experiencing higher levels of predation. For example, forest nests of *C. yacare* in the Brazilian Pantanal were raided by predators more frequently than were nests built by the same species on floating grass mats (Campos, 1993). Mound-nesting species sometimes select swamp areas rather than

riparian habitats for nest construction; being surrounded by water on all sides is likely to reduce egg predation (see Webb et al., 1983a; Ouboter and Nanhoe, 1997). However, for hole-nesters, the distance of a nest from permanent water may be based on availability of suitable, friable substrates (Chibeba, 2003; Somaweera and Shine 2012a) rather than protection from predators. When suitable substrates are common, nesting farther away from water may reduce the risk of nest flooding (Modha, 1967; Allsteadt, 1994) but increase the risk of nest predation (Kofron, 1989; but see Somaweera et al., 2011a for counterexample). Nesting farther from water also may reduce the likelihood of nest attendance by the female (Larriera and Piña, 2000). For example, at a study site in Runde River in southeastern Zimbabwe, female Nile Crocodiles attended 100% of the nests that were laid within 20 m of water, but only 20% of those more than 20 m away from water (Kofron, 1989).

Islands can provide protected nesting habitat for crocodiles because insular areas often have fewer nest and egg predators than do mainland habitats (Rand, 1968; Rand and Robinson, 1969). Despite being laid at similar distances from the lakeshore, survival rates of *C. johnstoni* nests on offshore islands at Lake Argyle are higher than on mainland nest sites (Somaweera et al., 2011a). Similarly, nesting success of *C. moreletii* in northern Belize was higher on natural islands than on man-made islands or shoreline sites (Platt et al., 2008). Islands in Lake Rudolf, northern Kenya, had none of the mammalian predators that heavily predate *C. niloticus* eggs in other parts of its range (Modha, 1967), and in the National Chinese Alligator Reserve in China, *A. sinensis* used small islands set in agricultural ponds as nesting grounds since these islands received little human use (Thorbjarnarson et al., 2001).

*Parental defense.*—Some individuals in most species of crocodylians actively defend their nests (Shine, 1988; Brazaitis and Watanabe, 2011). Maternal defense can deter nest predators, and the intensity of maternal defense among crocodylians differs according to species, location, density of nests, habitat, past experience with humans, and levels of

human disturbance (Kushlan and Kushlan, 1980; Smith, 1987; Thorbjarnarson, 1989). Nest defense by female crocodylians can range from all-out attack to simple presence (e.g., Modha, 1967; Cott, 1971; Deitz and Jackson, 1979; Lang, 1987); secretions from the female's gular or cloacal glands at the nest may also deter smaller predators (Kofron, 1989).

Aggressive nest protection and attacks towards intruders (sometimes including humans) have been reported for most crocodylian species (e.g., Hartwig, 1873; McIlhenny, 1934; Neill, 1946; Darmakumarshinji, 1947; Pooley, 1969; Cott, 1971; Bustard and Singh, 1981; Magnusson, 1982: see Table 2). In *C. niloticus*, the male and female form a pair bond after courtship and the male defends the nesting territory (Pooley, 1977). Kushlan and Kushlan (1980) found that nest-attending *A. mississippiensis* showed progressively intense behaviors toward intruders. Female *O. tetraspis* showed a marked increase in aggressiveness after oviposition (Tryon, 1980). Female *C. niloticus* were present close to the nests by day (Modha, 1967) and night (Pooley, 1977), apparently to guard the nest (Modha, 1967). In other areas, maternal presence may aid egg incubation by compacting the soil on top of the nest (Pooley, 1962). However, female *C. porosus* do not remain at the nest site throughout the incubation period; instead, they move between the river and the nest (Choudhury and Bustard, 1980; Webb et al., 1983d). In *C. palustris*, an older female fasted and guarded the nest throughout incubation while younger females were less attentive to their nests and did not fast (Whitaker and Whitaker, 1984). However, other species such as *C. johnstoni* lack nest defense behavior in the wild (Smith 1987), perhaps reflecting the lack of mammalian egg predators in Australia over evolutionary time (Webb et al., 1983a; but see Somaweera et al., 2011a for a counterexample).

Attacks by brooding females may be aimed selectively at potential predators. In Lake Rudolf, nest-guarding *C. niloticus* females chased away egg scavengers such as Grey Herons (*Ardea cinerea*), Sacred Ibises (*Threskiornis aethiopicus*), Fan-tailed Ravens (*Corvus rhipidurus*), and potential hatchling predators such as Little Egrets (*Egretta garzetta*), and Great White Egrets (*Ardea alba*) from the

nests. However, the same females did not attack nonpredatory species such as Egyptian Geese (*Alopochen aegyptiacus*), Spur-winged Plovers (*Vanellus spinosus*), Black-winged Stilts (*Himantopus himantopus*), and Stone Curlews (*Burhinus* spp.) near nest sites (Modha, 1967). In one study on *A. mississippiensis*, the frequency of predation (by raccoons (*Procyon lotor*) and bears) on unguarded nests was 88% compared with 17% for guarded nests (Hunt, 1987). Low predation rates on alligator nests in the Everglades may reflect a high frequency of nest guarding by females (Kushlan and Kushlan, 1980).

*Environmental effects.*—Nesting during drier seasons or drier years, or later in the season, has been linked to increased rates of nest predation (Thorbjarnarson, 1991; Larriera and Piña, 2000). For mound-nesting species such as *A. mississippiensis* and *C. crocodylus* that rely on surrounding water for protection, lower water levels enable greater access to nests for predators such as raccoons, tegu lizards and foxes (Joanen, 1969; Fleming et al., 1976; Staton and Dixon, 1977; Hunt and Odgen, 1991; but see Goodwin and Marion, 1978 for a counterexample of raccoon predation not depending on water level). Hunt and Odgen (1991) also proposed that female *A. mississippiensis* might be less able to defend their nests during dry years. Availability of alternative food resources also could influence level of nest predation; for example, Fleming et al. (1976) concluded that intensity of raccoon predation on *A. mississippiensis* nests was dependent on the availability of alternate foods, with nest predation being lowest when crayfish were most abundant.

#### *Adaptations Due to Predation on Hatchling Crocodylians*

The concept of r and K selection has provided a useful framework to compare life history strategies (Pianka, 1970) but crocodylians do not fit the classical r/K continuum: although individuals are large and long-lived, they produce a large number of small, "inexpensive," and expendable young, rather than a few large offspring (Magnusson, 1986).

Predation on crocodylians is high during the first year of life (Webb et al., 1983a). Survival of *C. niloticus* is size-related partly due to

TABLE 2.—A summary of parental care behaviors shown by each species of crocodylian (modified and updated from Shine, 1988). The records include observations at all natural, seminatural, and captive conditions. Parental care is primarily by females (F), with a few cases of biparental and paternal care.

Species	Nest type	Form of parental care <sup>1</sup>							References <sup>2</sup>
		Attends nest	Defends nest	Opens nests	Carries young	Defends young			
<i>Alligator mississippiensis</i>	Mound	F	F	F	F	F	F	1–11	
<i>A. sinensis</i>	Mound	F	F	F	F	F	F	12 as cited by 13	
<i>Caiman crocodilus</i>	Mound	F	F, M	F, M	M (?)	F, M	F, M	14–18	
<i>C. latirostris</i>	Mound	F	F (?)	Yes	—	Yes	Yes	19–21	
<i>C. yacare</i>	Mound	F	F (?)	F	—	F	F	22	
<i>Crocodylus acutus</i>	Mound and hole	F	F	F	F	F	F	23–26	
<i>C. cataphractus</i>	Mound	F	—	F	F (?)	F (?)	F (?)	27, 28	
<i>C. intermedius</i>	Hole	F	—	—	—	F	F	29	
<i>C. johnstoni</i>	Hole	F	F (mostly under captivity)	F	F	F	F	30–33	
<i>C. mindorensis</i>	Mound	—	F	—	—	—	—	28	
<i>C. moreletii</i>	Mound	F	F	F	F	F, M	F, M	34–37	
<i>C. niloticus</i>	Hole	F	F	F, M	F, M	F, M	F, M	38–44	
<i>C. noronae</i>	Mound	F	F	F	F, M	M	M	45, 46	
<i>C. palustris</i>	Hole	F	F	F, M	F, M	F, M	F, M	47–51	
<i>C. porosus</i>	Mound	F	F	F	F	F, M	F, M	47, 52–59	
<i>C. rhombifer</i>	Mound	—	—	—	—	—	—		
<i>C. siamensis</i>	Mound	F (?)	—	—	—	Yes (?)	Yes (?)	60, 61	
<i>Gavialis gangeticus</i>	Hole	F	F	F	F	F, M	F, M	62–67	
<i>Melanosuchus niger</i>	Mound	F	F	F	—	F	F	68–70	
<i>Osteolaemus tetraspis</i>	Mound	F	F	F	F, M	F, M	F	71–74	
<i>Palaeosuchus palpebrosus</i>	Mound	F	F	—	—	—	—	29	
<i>P. trigonatus</i>	Mound	—	—	Yes	—	—	—	28	
<i>Tomistoma schlegelii</i>	Mound	F (?)	No (?)	F	No (?)	—	—	20, 75, 76	

<sup>1</sup> F indicates female; M, male; —, lack of records, (?), uncertainty.

<sup>2</sup> (1) Clarke, 1888; (2) Devenish, 1893; (3) Reese, 1907; (4) Joanen, 1969; (5) Kushlan, 1973; (6) Fogarty, 1974; (7) Metzger, 1977; (8) Goodwin and Marion, 1978; (9) Dietz and Hines, 1980; (10) Kushlan and Kushlan, 1980; (11) Kushlan and Simon, 1981; (12) Huang and Watanabe, 1986; (13) Thorbjarnarson et al., 2001; (14) Alvarez del Toro, 1974; (15) Alvarez del Toro, 1969; (16) Staton and Dixon, 1977; (17) Gorzula, 1978; (18) Staton, 1978; (19) Larriera and Pina, 2000; (20) Richardson et al., 2002; (21) Larriera et al., 2004; (22) Crawshaw and Schaller, 1980; (23) Descourtiz, 1809; (24) Ogdén and Singletary, 1973; (25) Ogdén, 1978; (26) Dugan et al., 1981; (27) Waitkuvait, 1989; (28) Alderton, 1998; (29) Medem, 1958; (30) Worrell, 1952; (31) Compton, 1981; (32) Somaweera et al., 2011b; (33) Somaweera and Shine, 2012b; (34) Hunt, 1974; (35) Hunt, 1975; (36) Platt et al., 2008; (37) Rainwater et al., 2000; (38) Cott, 1971; (39) Modha, 1967; (40) Pooley, 1969; (41) Pooley, 1974; (42) Pooley, 1977; (43) Hadley, 1969; (44) Pooley and Gans, 1976; (45) Neill, 1946; (46) Shine, 1988; (47) Deraniyagala, 1939; (48) Dharmakumarsingh, 1947; (49) David, 1970; (50) Whitaker and Whitaker, 1984; (51) Lang et al., 1986; (52) Biswas, 1977; (53) Webb, 1977; (54) Choudhury and Bustard, 1980; (55) Bustard and Choudhury, 1980; (56) Magnusson, 1980; (57) Acharyo and Mishra, 1981; (58) Bustard and Kar, 1981; (59) Jelden, 1981; (60) Thorbjarnarson, 2003; (61) Platt et al., 2006; (62) J. Lang, personal observation; (63) Singh and Bustard, 1977; (64) Whitaker and Whitaker, 1977; (65) Bustard, 1980; (66) Basu and Bustard, 1981; (67) Bustard and Singh, 1981; (68) Hartwig, 1873; (69) Medem, 1971b; (70) Medem, 1980; (71) Schmidt, 1919; (72) Cansdale, 1955; (73) Tryon, 1980; (74) Magnusson et al., 1985; (75) Bezuijen et al., 1998; (76) Mathew et al., 2011.

predation pressure at different life stages (Hutton, 1984), and hatchling mortality of *C. niloticus* appears to be related to predator densities (Watson et al., 1971). The susceptibility of a hatchling crocodylian to predation may be influenced by its size, species, environment, individual behavior, and parental protection.

*Size and morphology.*—Hatchling size is correlated with egg size in crocodylians (e.g., Webb et al., 1983a,c; Larriera et al., 2004), but the effects of hatchling body size on fitness remain unclear (Webb and Cooper-Preston, 1989). Unlike some other reptile species (Congdon and Gibbons, 1985; Sinervo, 1990; Stearns, 1992; Janzen, 1993), larger body size at hatching may not actually lead to increased growth and survival in crocodylians. In fact, average-sized hatchlings may exhibit higher rates of growth and survivorship than do either small or larger hatchlings (Webb and Cooper-Preston, 1989). Hatchling crocodylians that are compromised in some way at hatching (e.g., congenital defect, twinning) may quickly succumb to predators (Steel, 1989).

*Environment.*—The duration of incubation varies between crocodylian species, and is influenced by environmental conditions. Temperate-climate species such as *A. mississippiensis* have relatively short incubation times, compared to species such as *C. porosus* that occupy tropical areas (Webb et al., 1983d). As a result, *A. mississippiensis* emerge from the egg at an earlier developmental stage than do species such as *C. porosus*; whether or not this makes them more vulnerable to predation is unknown.

The timing of egg deposition is influenced by environmental conditions. For example, *C. porosus* lays eggs during the wet season and after heavy rains. Egg laying also occurs at a time that enables hatching to occur during favorable environmental conditions (Webb et al., 1983d). Therefore, nests that are deposited too late, or too early, may encounter adverse conditions. In *C. johnstoni*, nesting is delayed under higher temperatures (Webb et al., 1983a) or rainy and cool conditions (Somaweera and Shine, 2012a), but if nesting is delayed too long, flooding during the subsequent wet season may reduce embryo survivorship (Webb et al., 1983a).

Survival of hatchling crocodylians may be affected by the proximity of the nest to suitable nursery habitat: that is, areas with adequate cover (riparian vegetation, etc.), protected from wave exposure (Ogden, 1978; Mazzotti, 1983), and experiencing low salinity (Thorbjarnarson, 1989; Brandt et al., 1995; Mazzotti et al., 2007) and little to no tidal or current action (Magnusson, 1979). In *A. mississippiensis* that typically nest in inland swamps, females modify conditions around the nest to create better nursery habitat (known as “gator holes”; Steel, 1989).

Hatchling crocodylians seek secluded shallow waters (Garrick and Lang, 1977) and the hatchlings’ exposure to predators in these habitats may depend on terrain, shade and vegetation cover, and turbidity and depth of water. Predation on hatchlings may increase with greater water clarity (Webb and Messel, 1977; Magnusson, 1978; Webb and Manolis, 1998). Floating vegetation mats are important habitat for young crocodylians (Cox et al., 2006; Somaweera et al., 2011b). In the absence of floating vegetation, hatchlings seek shelter in densely vegetated shoreline areas (Platt and Thorbjarnarson, 2000a,b). In lotic waters, where floating vegetation is scarce, fallen trees, root systems, rock outcrops, and riparian vegetation may be used as nursery habitat (Steel, 1989). In “gator holes,” broken grass stems blend with the dorsal yellow bars and light-colored ventral scales of *A. mississippiensis* hatchlings. The striped coloration of *C. porosus* hatchlings also matches the surrounding weedy environments (Biddell and Stringer, 1988). Camouflaged hatchlings in such habitats may be afforded a higher degree of protection from aquatic and aerial predators (Hunt and Watanabe, 1982). Hatchlings dive and remain at the bottom of water bodies as a response to predation attempts (R. Somaweera, personal observation). Thus, the depth of water may determine which predators (especially waders and aerial predators) could reach them at the bottom.

Depending on the availability of food, the environment may also determine growth rates of hatchling crocodylians. Jacobsen and Kushlan (1989) suggest that if an alligator grows more slowly, it will take longer to reach maturity, and increase its susceptibility to predation, disease, and cannibalism.

Droughts in nursery habitats cause hatching pods to travel significant distances in search of suitable habitats (Temsiripong, 1999). This behavior may increase hatchling mortality because of desiccation and predation (Nichols et al., 1976). Fluctuating water levels also concentrate crocodylian populations and increase conflicts, with consequent injuries and death (Deitz, 1979).

*Parental care.*—Records of parental care behaviors shown by each species of crocodylian are summarized in Table 2. Hatching can occur during either the day or night, depending on female behavior (because hatchlings of most species of crocodylians rely upon the female to unearthen them). Most, and probably all, crocodylians open their nests at hatching time and Pooley and Gans (1976) have discussed the life history and evolutionary correlates of such behavior. Parental assistance is required in most emergences and if the nests are unattended, hatchlings may be susceptible to predation (Cott, 1971; Pooley and Gans, 1976; Webb et al., 1983a).

When presented with prehatching calls, female *C. niloticus* attending their nest react by digging (Vergne and Mathevon, 2008). This adult intervention is critical for hatchling survival (Magnusson, 1980). At Lake Argyle in Australia, *C. johnstoni* nests that were not dug up by adults contained hatchlings that either were deformed (e.g., with kinked tails) or were dead (Somaweera and Shine, 2012b). Grunting prenatally in the egg potentially stimulates synchronous hatching and may enhance survival by eliciting parental nest-opening and egg release (Burghardt, 1977). Synchronous hatching may also serve to dilute predation risk by promoting synchronous emergence or reducing the period in which smells associated with hatching can attract predators to unhatched eggs (Doody, 2011). Nevertheless, the impact of prehatching calls on predator attraction is unknown (Campbell, 1973; Vergne et al., 2009).

An open nest with its attendant odors also may attract predators (Hunt, 1987). Male and female *C. niloticus* eat the eggshells and membranes from hatched eggs, removing this potential predator attractant as well as contributing to parental nutrition (Pooley, 1977).

Parental transport of hatchlings from the nest to water undoubtedly protects the

newborn from predators, especially when drought increases the distance between nest and water (Hunt, 1987). Transport of the young to water by the females occurs in several crocodylian taxa (e.g., Alvarez del Toro, 1969; Kushlan, 1973; Ogden and Singletary, 1973; Hunt, 1974, 1987; Herzog, 1975). In *Caiman crocodilus*, *Crocodylus palustris*, *C. niloticus*, *C. novaeguinae*, and *O. tetraspis*, adult males have been recorded opening the nest and transporting hatchlings to water (Alvarez del Toro, 1969; Pooley, 1977; Burgin, 1980; Tryon, 1980), sometimes without the assistance of the female (Lang et al., 1986). Parents sometimes transport the young in their gular pouches, on the snout, on the head, or on the back (Pooley, 1974), but may sometimes merely lead them to water (Whitaker and Whitaker, 1984). The ability to transport many neonates at one time would enable hatchlings to be protected from opportunistic predators and if the pod is quickly formed, the mother can focus on its defense (Hunt, 1987). Although adults of some species only carry one or two hatchlings at a time, *C. moreletii* transports up to 12 neonates at a time, whereas *C. niloticus* has been observed transporting 19 at once (Pooley, 1974; see Somaweera and Shine, 2012b for a review on factors determine the number of hatchlings transported).

In the Pantanal of Pocone in Brazil, hatchling *Caiman yacare* congregate during the day and disperse away from the mother during the night, a behavior that may reduce the risk of predation by adult caiman and other diurnal predators (Cintra, 1989). Similar behavior has been reported in family groups of *A. mississippiensis* (Deitz, 1979). Female *C. niloticus* at Lake Rudolf constantly guarded hatchlings during the day and may compromise feeding as a result; the adult crocodiles were rarely observed feeding during this period (Modha, 1968). Given that female *C. porosus* do not remain at the nest site throughout the incubation period (Choudhury and Bustard, 1980) it could be assumed that they feed and remain in good condition (Webb, 1977; Webb et al., 1983d). However, some female *C. porosus* found at nests had empty stomachs (Deraniyagala, 1939) or were emaciated (Webb et al., 1983d).



Most reptiles lack extended parental care, such that the only maternal provisioning to developing embryos involves the quality and quantity of yolk (Shine, 1988). Postnatal maternal provisioning of hatchling crocodylians has long been suggested (McIlhenny, 1935), but most reports of extended parental care (e.g., feeding neonates) have been only made under captive conditions (e.g., *O. tetraspis*: Anonymous, 1977; *C. intermedius*: Blöhm, 1982; *C. siamensis* and *C. palustris*: Whitaker, 2007).

Maternal protection decreases the vulnerability of hatchlings to predation (Staton, 1978; Magnusson, 1980). At Lake Rudolf, *C. niloticus* females attacked and chased potential predators such as Goliath, Grey, and Purple Herons (*Ardea goliath*, *A. cinerea*, and *A. purpurea*) whenever they came close to nurseries (Modha, 1967). In India, *C. palustris* chased Black-necked Storks (*Ephippiorhynchus asiaticus*), herons, and egrets that approached hatchlings (Darmakumarshinhji, 1947). Captive *O. tetraspis* attacked turtles (*Pelomedusa* sp. and *Pelusios* sp.) if they swam close to the hatchlings (within 1 m; Tryon, 1980). Adult *C. moreletii* threatened and occasionally attacked young (40–75 cm in total length) conspecifics, when these young were in contact with or approached small hatchlings in the pod (Hunt, 1977).

During the first days after hatching, female crocodylians are strongly reactive to hatchling vocalizations and will actively chase other crocodiles away from the hatchlings (Modha, 1967; Hunt, 1975; Hunt and Watanabe, 1982). Adults are attracted to distress calls by young (e.g., Modha, 1967; Kushlan, 1973; Pooley, 1974) and can be lured by playing back recorded distress calls (Pooley, 1977). In *A. mississippiensis*, vocal signaling between mother and young, and among the young, likely aids maternal care and promotes group cohesion (McIlhenny, 1935; Campbell, 1973). However, species differ in the vigor of protection by parents following distress calls by young (Campbell, 1973). Male crocodylians also may respond to hatchling calls (Lang, 2002), but mothers may actively discourage the presence of large males, possibly reflecting the risk of cannibalism (Root, 1989).

The duration of parental care for hatchlings varies among species and can encompass ~7 d

in *Paleosuchus trigonatus* (Magnusson, 1989), over 12 wk in *C. niloticus* (Cott, 1975; Pooley and Gans, 1976), the first few weeks (over 5 wk) in *C. acutus* (Alvarez del Toro, 1974), almost 12 mo in *C. latirostris* (Penny, 1991) and *C. yacare* (Campos et al., 2006), and to 1–3 yr in *A. mississippiensis* (Fogarty, 1974; Garrick and Lang, 1977). As predicted by theory (Trivers, 1974), maternal *A. mississippiensis* direct their vigilance to younger, more vulnerable, offspring (Hunt and Watanabe, 1982). Hatchling *C. crocodilus* from northern Surinam stayed together (sometimes associated with yearlings) for up to 18 mo, but parental guarding was only present for 7 mo, until the beginning of the rainy season (Ouboter and Nanhoe, 1997).

*Hatchling behavior.*—Soon after they hatch, most crocodylians seek shelter under a nearby object such as an overhanging bank, dead vegetation on a bank, or logs and branches; in rock crevices; or among riparian vegetation (Modha, 1967; R. Somaweera, personal observation). In areas such as canal systems, where the vegetation has been stripped and the banks are relatively bare, the level of predation on hatchlings and juveniles can be much higher than in more densely vegetated sites (e.g., *A. mississippiensis* in Florida [Rootes and Chabreck, 1993]). Lack of adequate cover in captivity may disrupt normal behavior patterns of young crocodiles and induce stress responses (Lang, 1987). In the wild, a lack of adequate cover may lead hatchlings to travel in search of suitable habitat, further increasing exposure to predators.

Hatchlings of most species form social groups as pods (sibling groups) or crèches, mostly near and around the nest site (Platt et al., 2002; Campos et al., 2006). In one study, each *C. moreletii* pod comprised neonates from a single nest (Platt, 1996) but some pods include hatchlings from several clutches (e.g., Modha, 1967; Reagan, 2000). Hatchling *C. crocodilus* are sedentary within the first month of life (Da Silveira et al., 1997) and in the Brazilian Pantanal, *C. yacare* hatchlings remained within 200 m of their nests for 6 mo and were attended by females (Cintra, 1989). Hatchling *C. palustris* individuals may follow their mother into tunnels on the banks and may also dig their own burrows off the main

tunnel (Shekher, 1993). Sometimes these groups are formed even in the absence of an adult guardian and this group-living behavior may reduce risk of predation (Lang, 1987). In captivity, *A. mississippiensis* hatchlings prefer to group with other hatchlings rather than remain solitary or seek cover, and these hatchlings are not necessarily kin (Passek and Gillingham, 1999). Group living may enhance survival of hatchlings by increasing the probability of predator detection and by revealing the presence of food (grunts emitted by hatchlings during feeding attract nearby individuals to the food: Deitz, 1979). However, some populations do not show strong pod-forming behaviors (e.g., true pod formation occurs only briefly after hatching or not at all among *C. acutus* in Belize [Platt and Thorbjarnarson, 2000b]; hatchlings of some *A. mississippiensis* populations in Louisiana disperse soon after hatching [Reagan, 2000]).

Vocalization by hatchlings may have several functions, including defense against predation (Britton, 2001; Vergne et al., 2009). In the presence of a predator or when seized, juvenile crocodylians emit calls (Vergne et al., 2009) that may correspond to the "screech" given when a bird is held by a predator (Marler and Slabbekoorn, 2004). Calls range from a grunt of mild apprehension to a louder distress cry if threatened and a loud screech if actually seized (Herzog and Burghardt, 1977). Though not substantiated, Steel (1989) argues that the unusually loud distress calls of young *C. cataphractus* may be adaptive to their relatively weak jaws (compared to most other crocodile species); a louder call may induce a startled assailant to drop the victim. Distress calls produced by hatchlings also may act as alarm signals for nearby conspecifics (siblings from the same pod and hatchlings from other nearby pods) and induce them to swim away from the caller (Romero, 1983) or dive (R. Somaweera, personal observation). Vulnerability to capture of an aquatic creature increases with proximity to the water surface for both aerial and aquatic predation (Rahel and Kolar, 1990; Heithaus and Frid, 2003); hence, diving in the presence of a predator or during an alarm may be of survival value. However, it is also possible that any benefits of the calls for

related and nonrelated individuals may be a fortuitous effect rather than an adaptation (Staton, 1978).

The duration of group persistence may be influenced by environmental factors as well as intrinsic behaviors of the members of the pod. In seasonal habitats (e.g., billabongs, seasonal pools, gator holes, etc.) where space and resources are limited, hatchlings may congregate for long periods. However, in drying water holes in tropical Australia, predation (cannibalism) pressure from adults may force *C. johnstoni* hatchlings to seek shelter on land (rather than in water; Kennett and Christian, 1993). In contrast, dispersal tends to occur sooner in habitats where water is available throughout the year (e.g., Kar, 1993; Ouboter and Nanhoe, 1997). Webb (1977) considered survival of *C. porosus* hatchlings to be high during the first 3 mo posthatching, once they had moved from nest sites to the main river channel. In large flowing water bodies, small *C. johnstoni* tend to stay in the shallows (Webb et al., 1982; Cooper-Preston, 1991), thereby avoiding cannibalistic adults (Tucker et al., 1997). In a large, permanent, stagnant water body, *C. johnstoni* hatchlings disperse from their natal pods within 1 mo of hatching (more or less the same time the guarding adult leaves the pod), and move to sheltered habitats that provide abundant food and lower predation risk (Somaweera et al., 2011b).

#### *Adaptations Due to Predation on Posthatching Crocodylians*

*Predation on juveniles, subadults, and adults of smaller crocodylian species.*—For most crocodylian species, mortality due to predation is very high for eggs and hatchlings, and then declines as the young grow (Lang, 2002; Vergne et al., 2009). The main predators for smaller crocodylians are other crocodylians (both interspecific and intraspecific), large constrictors, humans, felids, raptors, and large fish (especially sharks; see Supplementary Material). Young of most crocodylian species enter a dispersal phase and become solitary (Lang, 2002). Shelter-seeking behavior to reduce risk of predation is pronounced in young crocodylians (e.g., *C. latirostris*: Borteyro et al., 2008) and young of some species such as *C. niloticus* may construct earthen

TABLE 3.—Body sizes of crocodylian hatchlings and adults of different species, and the number of records of predation on hatchlings, juveniles, and adults.

Species	Size category <sup>1</sup>	Average size of adult male (m) <sup>1</sup>	Average total length of hatchling (cm)	Average mass of hatchling (g)	No. of predation records on adults or subadults	No. of predation records on hatchlings or juveniles	No. of predation records on eggs
<i>Alligator mississippiensis</i>	Large	3.5–4.3	28.2 <sup>2</sup> –31.6 <sup>3</sup>	62.29 <sup>2</sup> –81.7 <sup>3</sup>	3	20	4
<i>Caiman crocodilus</i>	Small	1.5–2.5	22.8 <sup>4</sup>	41.9 <sup>4</sup>	5	26	12
<i>Caiman latirostris</i>	Small–medium	2	23.6 <sup>5</sup>	42.4 <sup>5</sup>	—	2	3
<i>Caiman yacare</i>	Small–medium	3	25.1 <sup>6</sup>	50.5 <sup>6</sup>	1	5	12
<i>Crocodylus johnstoni</i>	Small–medium	1.5–3	24.4 <sup>7</sup>	42.0 <sup>7</sup>	1	15	6
<i>Crocodylus moreletii</i>	Small–medium	2–3	21.5 <sup>8</sup>	46.2 <sup>9</sup>	3	14	4
<i>Crocodylus niloticus</i>	Large	4	31.0 <sup>10</sup>	76.8 <sup>10</sup>	2	23	14
<i>Crocodylus porosus</i>	Large	5–5.5	29.3 <sup>11</sup>	72 <sup>11</sup>	—	10	5

<sup>1</sup> Richardson et al. (2002).<sup>2</sup> Temsiripong (1999), from central Florida lakes, USA.<sup>3</sup> Neal et al. (2004), from southeast Arkansas, USA.<sup>4</sup> Allsteadt (1994), from Cano Negro, Costa Rica.<sup>5</sup> Pina et al. (2007), from Santa Fe Province, Argentina.<sup>6</sup> Cintra (1988), from Brazilian Pantanal.<sup>7</sup> Webb et al. (1983a), from McKinlay River, Australia.<sup>8</sup> Review by Ferguson 1985.<sup>9</sup> Pérez-Higareda et al. (1995), from Tabasco, Mexico.<sup>10</sup> Modha (1967), from Lake Rudolf, Kenya.<sup>11</sup> Webb and Manolis (1998), from Northern Territory, Australia.

tunnels during the winter in which they seek shelter (Lang, 1987). This life stage is poorly understood, because these highly dispersive individuals are difficult for researchers to access and study.

Adults of smaller crocodylian species are likely to be more vulnerable to predators than are adults of larger species (see Table 3). The adults of smaller crocodylian species, such as caimans, are vulnerable to predators such as larger crocodylians, sharks, felids, and constrictors (e.g., Green Anacondas [*Eunectes murinus*]; Emmons, 1989; Scognamiglio et al., 2003). In seasonally flooded habitats in South America, caimans (*C. yacare*, *C. crocodilus*, and *M. niger*) represented 51% of the reptilian prey of Jaguars, and in habitats where terrestrial mammalian prey are absent, Jaguars prey extensively on caimans (Da Silveira et al., 2010). However, *M. niger* adults (which grow much larger than the sympatric *C. crocodilus*) are less susceptible to Jaguar predation (Da Silveira et al., 2010). This interspecific difference in vulnerability to felid predation also may be facilitated by the fact that *C. crocodilus* individuals spend more time on land than *M. niger*, both during basking and nesting, which in turn makes them more vulnerable to terrestrial predators (Da Silveira et al., 2010).

Smaller species of crocodylian tend to be more heavily armored than their larger

counterparts, affording them greater protection from predators (Ross and Mayer, 1983). For example, the skin of the small *A. sinensis* is more heavily armored than the superficially similar but larger *A. mississippiensis* (Richardson et al., 2002). Members of the genus *Paleosuchus* are among the smallest and the most heavily armored of all crocodylians (Alderton, 1998). *Paleosuchus trigonatus* and *C. rhombifer* both forage largely on land, and have heavily ossified dermal armor, which may protect them in this exposed habitat (Magnusson et al., 1987; Steel, 1989). However, the level of armor also may reflect selective pressures on level of movement (e.g., a reduced armor may facilitate long-distance swimming of *C. porosus*) and feeding (a heavy armor like that of *C. latirostris* may facilitate feeding on mollusks at the bottom of the water body).

Some small crocodylian species are highly cryptic, which may reduce exposure to predators. Indeed, *P. trigonatus* is so cryptic in behavior that it cannot be studied by standard survey methods (Magnusson and Lima, 1991). Some *C. crocodilus* nests are found inside forests, sometimes up to 1 km from permanent water, and females guarding their nests usually hide near the nest, frequently under leaf litter, and rely primarily on crypsis (Marioni et al., 2007). In the Likouala Swamp

Forests of the Congo Basin, *O. tetraspis* rarely ventures away from pools with burrows (Riley and Huchzermeyer, 1999). Inhabiting these flooded burrows may enable the crocodilians to escape Leopards (*P. pardus*) that hunt in the swamps even at the height of the wet season (Blake, 1993).

*Predation on adults of larger crocodilian species.*—The adults of larger crocodilian species such as *A. mississippiensis*, *C. acutus*, *C. niloticus*, *C. palustris*, and *C. porosus* have few predators other than man and larger crocodiles. The risk posed by conspecifics increases at high population densities, when larger individuals prey upon smaller and weaker ones (Lang, 2002). However, Great White Sharks (*Carcharodon carcharias*) prey upon adult *C. acutus* in Colombia (Medem, 1981), and large sharks may kill subadult and adult crocodilians in other areas (Webb and Messel, 1977). Occasionally, felids such as the African Lion (*P. leo*), Asiatic Lion (*P. leo persica*) and Bengal Tiger (*P. tigris*) kill and consume adult *C. niloticus* and *C. palustris* (Supplementary Material; Fig. 1), generally during extreme drought conditions in which water holes have dried up, or when competing for the same prey item. Invasive Burmese Pythons (*P. m. bivittatus*) have also been reported preying upon adult *A. mississippiensis* in the Florida Everglades (S. Snow, personal observation).

Most large adult crocodiles are solitary and inhabit less-sheltered sections of water bodies (e.g., Ouboter and Nanho, 1988). However, individuals inhabiting areas that have been hunted extensively are more wary of human presence than are conspecifics that have not been exposed to hunting (e.g., Webb and Messel, 1977; Montague, 1983).

In conclusion, adult crocodiles exhibit large body sizes, formidable weaponry, and heavy armor. Unsurprisingly, the highest rates of predation on crocodiles are on the least effectively defended individuals, both within a species (e.g., eggs rather than hatchlings, and hatchlings rather than adults) and among species (i.e., smaller rather than larger species). Vulnerability of the life-history stages least able to protect themselves (eggs and hatchlings) is reduced by the frequent display of parental protection for periods of months

(and occasionally, years) during the high-risk phase. Many aspects of crocodilian behavior (from secretive and aggregative behaviors of hatchlings, through to prolonged maternal protection of offspring) are likely to have evolved as adaptations to predation risk. Other behavioral and morphological traits (e.g., camouflage coloration; heavy dermal armor) may reflect selection for effective predation (to allow close approach to prey and prevent damage from a struggling prey item) as well as the reduction of predation risk. Teasing apart such influences will be a difficult task, but our review clearly indicates that (1) even an apex predator may be at substantial risk of becoming a prey item, especially early in its life, and (2) such vulnerabilities may have imposed significant selective forces on phenotypic traits of even these large and formidable creatures.

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## SUPPLEMENTARY MATERIAL.—Reported incidents of predation on crocodylians.

Predator taxon	Crocodylian spp.	Stage of crocodile*	Location	Evidence	Reference
<b>INSECTS</b>					
<i>Crematogaster</i> sp. Cocktail Ant	<i>C. niloticus</i>	E	Africa	mentioned	Pooley and Ross, 1989
<i>Solenopsis invicta</i> Fire Ant	<i>A. mississippiensis</i>	H	North America	mentioned	Allen et al., 1997; Reagan et al., 2000
	<i>C. acutus</i>	E	Florida, USA	observed in wild	Wasilewski and Enloe, 2006
	<i>Caiman latirostris</i>	H	Argentina	assumed	Marco et al., 2012
	<i>Caiman yacare</i>	H	South America	mentioned	Cintra, 1985
<i>Solenopsis saevissima</i> Fire Ant	<i>A. mississippiensis</i>	E	South Carolina, USA	mentioned	Wilkinson, 1983
Unknown ant species	<i>C. moreletii</i>	H	Belize	observed in wild	Platt et al., 2008
	<i>Osteolaemus tetraspis</i>	E	Liberia, Africa	observed in captivity	Kofron and Steiner, 1994
	<i>C. porosus</i>	H	Australia	observed in wild	G. Webb, personal observation
<b>CRUSTACEANS</b>					
<i>Callinectes sapidus</i> Blue Crab	<i>C. acutus</i>	H	Florida, USA	observed in wild	Kushlan and Mazzotti, 1989; M. Cherkiss, personal observation
<i>Cardisoma guanhumi</i> Land Crab	<i>A. mississippiensis</i>	H	Florida, USA	observed in wild	Lang, 1975; Ogden, 1978; Kushlan and Mazzotti, 1989
	<i>C. acutus</i>	H	Banco Chinchorro atoll, Mexico	observed in wild	G. Acosta, personal observation
<b>FISH</b>					
<b>Catfish</b>					
<i>Arius midgleyi</i> Silver Cobbler	<i>C. johnstoni</i>	H	Western Australia	stomach contents mentioned	Somaweera et al., 2011c
<i>Bagarius</i> spp. Catfish	<i>Gavialis gangeticus</i>	H, J	India	stomach contents mentioned	Whitaker and Basu, 1983
<i>Clarias lazera</i> African Catfish	<i>C. niloticus</i>	H	Lake Rudolf, Africa	stomach contents mentioned	Modha, 1968
<i>Hoplias macrophthalmus</i> Giant Trahira Catfish	Caiman	H	South America	mentioned	Medem, 1983
<i>Ictalurus punctatus</i> Channel Catfish	<i>A. mississippiensis</i>	J	North America	mentioned	Levy, 1991

<i>Pseudoplatystoma fasciatus</i> Catfish	<i>C. acutus</i>	H	Colombia	mentioned	Medem, 1981
<b>Garfish</b>					
<i>Atractosteus tropicus</i> Tropical Garfish	<i>Caiman crocodilus chitapasius</i>	H	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
	<i>C. moreletii</i>	H	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<i>Lepidosteus tropicus</i> Garfish	<i>A. mississippiensis</i>	H	North America	mentioned	Levy, 1991
	Caiman	H	South America	mentioned	Alvarez del Toro, 1974
	<i>C. acutus</i>	H	Nicaragua	mentioned	Camacho, 1983
<b>Sharks</b>					
<i>Carcharodon carcharias</i> Great White Shark	<i>C. acutus</i>	A	Isla de Fuerte, Colombia	mentioned	Medem, 1981
<i>Carcharhinus leucas</i> Bull Shark	<i>C. niloticus</i>	H	Africa	mentioned	Pooley and Ross, 1989
<i>Negaprion brevirostris</i> Lemon Shark	<i>C. acutus</i>	H	Florida, USA	assumed	Mazzotti, 1983
<b>Other fish</b>					
<i>Centropomus undecimalis</i> Snook	<i>C. acutus</i>	H	Florida, USA	assumed	Mazzotti, 1983
<i>Hephaestus fuliginosus</i> Black Bream	<i>C. johnstoni</i>	H	Liverpool River, Australia	assumed	Webb, 1979
<i>Hydrocynus</i> sp. Tigerfish	<i>C. niloticus</i>	H	Africa	mentioned	Steel, 1989
<i>Lates calcarifer</i> Barramundi	<i>C. johnstoni</i>	H	Australia	stomach contents	D. Forder , personal observation; D. Morgan, personal observation
<i>Lates niloticus</i> Nile Perch	<i>C. niloticus</i>	H	Africa	observed in wild	Root, 1989
	<i>Osteolaemus tetraspis</i>	H	Germany	observed in captivity	F. Schmidt , personal observation
<i>Megalops atlantica</i> Tarpon	<i>C. acutus</i>	H	Florida, USA	assumed	Mazzotti, 1983
<i>Micropterus salmoides</i> Largemouth Bass	<i>A. mississippiensis</i>	H	South Carolina, USA	assumed	Brisbin et al., 1996
<i>Micropterus</i> sp. Bass	<i>A. mississippiensis</i>	J	North America	mentioned	Allen and Neill, 1952
<i>Piaractus brachipomu</i> Pacu	<i>C. novaeguineae</i>	H, J	PNG	observed in wild	J. Cox, personal observation



<i>Sclerophages leichardti</i> Saratoga	<i>C. johnstoni</i>	H	Liverpool River, Australia	assumed	Webb, 1979
<i>Serrasalmus</i> sp. Piranhas	Caiman	H	South America	mentioned	Blohm, 1973; Ayarzagüena, 1980
<b>AMPHIBIANS</b>					
<i>Rana catesbeiana</i> American Bullfrog	<i>A. mississippiensis</i>	H	North America	stomach contents	Wettstein, 1954
<i>Rana sphenoccephala</i> Southern Leopard Frog	<i>A. mississippiensis</i>	H	Florida, USA	observed in captivity	Springer, 1938
<b>REPTILES</b>					
<b>Crocodylians</b>					
<i>A. mississippiensis</i> American Alligator	<i>A. mississippiensis</i>	H, J	South Carolina, USA; Sabine National Refuge, USA; Louisiana, USA	mentioned; stomach contents	Giles and Childs, 1949; Valentine et al., 1972; Nichols et al., 1976; Delany and Abercrombie, 1986; Brisbin et al., 1996; Chabreck, 1966; Chabreck and Wright, 2002
<i>C. acutus</i> American Crocodile	<i>A. mississippiensis</i>	SA	Florida, USA	observed in wild	M. Brien , personal observation
	<i>C. acutus</i>	H, SA	Florida, USA; Lago Ticamaya, Honduras	mentioned; observed in wild	Schmidt, 1924; M. Cherkiss , personal observation
	<i>Caiman crocodilus crocodilus</i>	H, A	South America	mentioned	Medem, 1981
<i>C. intermedius</i> Orinoco Crocodile	<i>Caiman crocodilus</i>	H, A	Colombia	mentioned	Medem, 1981
<i>C. johnstoni</i> Johnston's Crocodile	<i>C. johnstoni</i>	H, J	Australia	mentioned	Webb et al., 1983a
<i>C. porosus</i> Saltwater Crocodile	<i>C. porosus</i>	H	Australia	assumed	Webb and Manolis, 1998
	<i>C. johnstoni</i>	J, A	Australia	mentioned, observed in wild	Webb and Manolis, 1998; A. Bowman , personal observation
	<i>C. palustris</i>	A	Bundala NP, Sri Lanka	observed in wild	R. Whitaker , personal

<i>C. porosus</i>	H, J, SA	Wildman River, Australia; Northern Australia	observed in wild; stomach contents	Webb and Messel, 1977; Messel and Vorlicek, 1987; Webb and Manolis, 1998
<i>Caiman crocodilus crocodilus</i> Common Caiman	H	Venezuela	observed in wild	Seijas, 1988
<i>Caiman latirostris</i> Broad-snouted Caiman	J, SA	Llanos, Venezuela; Paraguay	mentioned; observed in wild	Staton and Dixon, 1975; Medem, 1981; Schaller and Crawshaw, 1982
<i>Caiman latirostris</i> Broad-snouted Caiman	J	South America	mentioned	Webb and Manolis, 1998
<i>Caiman yacare</i> Yacare Caiman	E	Florida, USA	observed in captivity	Walkowich, 2009
<i>Crocodylus niloticus</i> Nile Crocodile	E, H, J, SA	Uganda and Northern Rhodesia; Lake Rudolf, Africa	mentioned; observed in wild; stomach contents mentioned	Cott, 1961; Modha, 1967; R.A. Ferguson, personal observation
<i>Melanosuchus niger</i> Black Caiman	H, A	South America	mentioned	Medem, 1981
<i>Paleosuchus palpebrosus</i> Cuvier's Dwarf Caiman		Colombia	mentioned	Medem, 1981
<i>Paleosuchus trigonatus</i> Schneider's Smooth-fronted Caiman		Colombia	mentioned	
<b>Lizards</b>				
<i>Ctenosaura similis</i> Black Spiny-tailed Iguana	E, H	Costa Rica	observed in wild	J.B. Montero, personal observation
<i>Heloderma suspectum</i> Gila Monster	E, H	Costa Rica	observed in wild	J.B. Montero, personal observation
<i>Iguana iguana</i> Green Iguana	E	North America	mentioned	Pooley and Ross, 1989
<i>Tupanambis teguixin</i> Tegu Lizard	E	Gatun Lake, Panama	observed in wild	Dugan et al., 1981
	E	Mamiraua' Sustainable Development Reserve, Brazil	observed in wild	Da Silveira et al., 2010

<i>Melanosuchus niger</i>	E	Rupununi Savannah Region, Guyana; Mamiraua ' Sustainable Development Reserve, Brazil	observed in wild	Taylor, 2006; Da Silveira et al., 2010
<i>Tupinambis nigropunctatus</i> Golden Tegú	E	Llanos, Venezuela	observed in wild	Rivero-Blanco, 1974; Staton and Dixon, 1977; Ayarzagüena, 1980
<i>Tupinambis</i> sp. Tegú	E	South America	mentioned	Webb and Manolis, 1998
<i>Caiman crocodilus</i>	E	Brazilian Pantanal	assumed	Cintra, 1988
<i>Caiman yacare</i>	E	Central Amazon basin	observed	Villamarin-Jurado and Suarez., 2007
<i>Melanosuchus niger</i>	E			Vyas, 2010
<i>Varanus bengalensis</i> Bengal Monitor	E	Vishwamitri River, India	observed in wild	
<i>Gavialis gangeticus</i>	E	India	mentioned/ assumed	Bustard and Choudhury, 1981; Vyas, 2010; Chowfin and Leslie, 2013
<i>Gavialis gangeticus</i>	E, J	India	mentioned	Whitaker and Basu, 1983
<i>Varanus flavescens</i> Yellow Monitor	E	McKinlay River, Australia	mentioned	Webb, et al. 1982; 1983a
<i>Varanus gouldii</i> Sand Goanna	E	India	mentioned	Whitaker and Basu, 1983
<i>Varanus griseus</i> Desert Monitor	E, J	Lake Murray District, Papua New Guinea	mentioned	Hall and Johnson, 1987
<i>Varanus indicus</i> Mangrove Monitor	E	Liverpool River, Australia	stomach contents	Magnusson, 1982
<i>C. porosus</i>	E	Kimberley, Australia	observed in wild	Somaweera et al., 2011a; R. Somaweera , personal observation
<i>Varanus mertensi</i> Merten's Water monitor	E, H			Waitkuwait, 1986, 1989
<i>Varanus niloticus</i> Nile Monitor	E, H	Ivory coast	mentioned	Corbet, 1960; Cott, 1961; Mohda, 1967; Hutton and Child, 1989
<i>C. niloticus</i>	E, H	Zimbabwe; Africa	observed in wild; mentioned	Chibebe, 2003; Somaweera et al., 2011a
<i>Varanus panoptes</i> Yellow-Spotted Goanna	E	McKinlay River, Australia; Lake Argyle, Australia	mentioned	
<i>C. johnstoni</i>	E			

<i>Varanus salvator</i> Asian Water Monitor	<i>C. palustris</i>	E	Sri Lanka	mentioned	Deraniyagala, 1939; Whitaker and Whitaker, 1979
<i>Varanus</i> sp. Varanid	<i>C. porosus</i>	E, H, J	Sri Lanka; India	observed in wild	Deraniyagala, 1939; Whitaker and Whitaker, 1977; Gramentz, 2008
	<i>C. cataphractus</i>	E	Africa	mentioned	Webb and Manolis, 1998
	<i>C. johnstoni</i>	E	Katherine River, Australia	mentioned	Cooper-Preston, 1991
	<i>C. palustris</i>	E, H	Iran	mentioned	Mobaraki, 2002
	<i>C. porosus</i>	E	Australia	mentioned	Messel and Vorlicsek, 1987
	<i>Tomistoma schlegelii</i>	E	East Asia	mentioned	Webb and Manolis, 1998
<b>Snakes</b>					
<i>Boa constrictor</i> Boa Constrictor	<i>C. acutus</i>	H, J	Turneffe Atoll, Belize; Costa Rica	assumed; observed in wild	Platt et al., 2004; J.B. Montero, personal observation
	<i>C. moreletii</i>	SA	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
	<i>Caiman crocodilus fuscus</i>	H, J	Costa Rica	observed in wild	J.B. Montero, personal observation
<i>Drymarchon melanurus</i> Indigo Snake	<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
	<i>Caiman crocodilus chiapasius</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
	<i>Caiman crocodilus crocodilus</i>	H	Mexico	mentioned	Alvarez del Toro, 1974
<i>Eunectes murinus</i> Green Anaconda	<i>Caiman crocodilus crocodilus</i>		Llanos, Venezuela; South America	mentioned	Staton and Dixon, 1975; Ayarzagueno, 1980; Medem, 1981; Medem, 1983; Lopez-Corcuera, 1984; Rivas et al., 1999; Rivas, 2000
<i>Eunectes notaeus</i> Yellow Anaconda	<i>Paleosuchus</i> spp. Caiman	SA	South America South America	mentioned mentioned	Magnusson, 1989 Strussmann, 1997

	<i>Caiman yacare</i>	H	Pantanal of Pocone, Brazil	observed in wild	Cintra, 1989
<i>Liasis olivaceus</i> Olive Python	<i>C. johnstoni</i>	H	Kimberley, Australia	observed in wild	D. Woods, personal observation
<i>Python bivittatus</i> Burmese Python	<i>A. mississippiensis</i>	SA, A	Florida, USA	observed in wild; stomach contents	Ditmars, 1931; Snow et al., 2007b
<i>Python sebae</i> African Rock Python	<i>C. acutus</i>		North America	assumed	Reed and Rodda, 2009
	<i>C. niloticus</i>		Africa	mentioned	Spawls and Branch, 1995; Reed and Rodda, 2009
	<i>Osteolaemus tetraspis</i>		Southern Nigeria	stomach contents	Luiselli et al., 2001
<b>Turtles</b>					
<i>Apalone</i> spp. Soft-shelled Turtle	<i>A. mississippiensis</i>	H	North America	mentioned	Levy, 1991
<i>Chelonea rugosa</i> Northern Long-necked Turtle	<i>C. johnstoni</i>	H	McKinlay River, Australia	mentioned	Webb et al., 1983a; Chibebe, 2003
	<i>C. porosus</i>	H	Australia	observed in captivity	Webb and Manolis, 1998
<i>Chelus fimbriatus</i> Matamatas	<i>Caiman</i>	H	South America	mentioned	Medem, 1981
<i>Chelydra serpentina</i> Common Snapping Turtle	<i>C. moreletii</i>	J	Mexico	stomach contents	Alvarez del Toro and Sigler, 2001
<i>Chelydra</i> spp. Snapping Turtle	<i>A. mississippiensis</i>	H	North America	mentioned	Levy, 1991
<i>Nilssonia gangeticus</i> Soft-shelled Turtle	<i>C. palustris</i>	H, J	India	observed in captivity	R. Whitaker, personal observation
	<i>Gavialis gangeticus</i>	H, J	India	observed in captivity	R. Whitaker, personal observation
<i>Pelusios simuatus</i> Hinged Terrapin	<i>C. niloticus</i>	H	Africa	mentioned	Guggisberg, 1972
<i>Phrynops Geoffroanus</i> Side-necked Turtle	<i>Caiman</i>	H	South America	mentioned	Anderson 1898
<i>Trionyx</i> and <i>Chitra</i> spp. Freshwater Turtles	<i>Gavialis gangeticus</i>	H, J	India	observed in wild, mentioned	Whitaker and Basu, 1983
<i>Trionyx triunguis</i> Nile Soft-shelled Turtle	<i>C. cataphractus</i>	H	Ivory coast	assumed	Waitkuwait, 1986, 1989
	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Guggisberg, 1972 Anderson 1898

**BIRDS****Corvids**

<i>Corvus albus</i> Pied Crow	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Cott, 1971; Pooley, 1969; Guggisberg, 1972
<i>Corvus orru</i> Torresian Crow	<i>C. johnstoni</i>	E	Lake Argyle, Australia	observed in wild	Somaweera et al., 2011a
Crows	<i>C. palustris</i>	E, H	Sri Lanka	observed in wild	Jayewardene, 2004
<i>Rhinocorax rhipidurus</i> Fan-tailed Raven	<i>C. niloticus</i>	E	Lake Rudolf, Africa	observed in wild	Modha, 1967

**Diving birds**

<i>Pelecanus onocrotalus</i> Great White Pelicans	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Cott, 1971; Guggisberg, 1972; Pooley, 1974
<i>Phalacrocorax brasilianus</i> Neotropic Cormorant	<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001

**Raptors**

<i>Bubo africanus</i> Spotted Eagle Owl	<i>C. niloticus</i>	H	Zululand, Africa	mentioned	Pooley, 1969
<i>Buteo magnirostris</i> Roadside Hawk	<i>C. acutus</i>	H	Mexico	observed in wild	Alvarez del Toro and Sigler, 2001
<i>Buteogallus urubitinga</i> Great Black Hawk	<i>C. moreletii</i>	H, J	Mexico; Central America	mentioned	Alvarez del Toro and Sigler, 2001; Navarro-Serment, 2004
<i>Buteogallus urubitinga</i> Great Black Hawk	<i>Caiman crocodilus</i>	H, J	Llanos, Venezuela	mentioned	Ayarzaguena, 1980
<i>Cathartes aura</i> Turkey Vulture	<i>Caiman yacare</i>	H	Pantanal of Pocone, Brazil	observed in wild	Cintra, 1985, 1989
<i>Coragyps atratus</i> Black Vulture	<i>C. acutus</i>	E	Florida, USA	observed in wild	M. Brien, personal observation
<i>Cuncuma vocifer</i> Fish Eagle	<i>C. intermedius</i>	E	Gatun Lake, Panama	observed in wild	Dugan et al., 1981
	<i>C. niloticus</i>	E	South America	mentioned	Steel, 1989
	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Pooley, 1969; Cott, 1971; Guggisberg, 1972

<i>Gypohierax angolensis</i> Palm-nut Vulture	<i>C. niloticus</i>	E	Africa	mentioned	Steel, 1989
<i>Haliaeetus leucogaster</i> White-bellied Sea Eagle	<i>C. johnstoni</i>	H	Australia	mentioned	Webb and Manolis, 1998
<i>Haliaeetus vocifer</i> African Fish Eagle	<i>C. niloticus</i>	H	Africa	reported	R.A. Fergusson , personal observation
<i>Haliastur sphenurus</i> Whistling Kite	<i>C. johnstoni</i>	H	Australia	observed in wild	Webb and Manolis, 1998; R. Somaweera , personal observation
<i>Herpetotheres cachinnans</i> Laughing Falcon	<i>C. acutus</i>	H	Mexico	observed in wild	Alvarez del Toro and Sigler, 2001
<i>Milvus migrans</i> Black Kite	<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<i>Milvus migrans govinda</i> Pariah Kite	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Cott, 1971; Pooley, 1969; Guggisberg, 1972
<i>Milvus</i> sp. Kites	<i>C. palustris</i>	H	Andhra Pradesh, India	observed in wild	B.C. Choudhury, personal observation
<i>Pandion haliaetus</i> Osprey	<i>C. porosus</i>	H	Orissa, India	observed in wild	S. Kar, personal observation
<i>Polyborus plancus</i> Crested Caracara	<i>C. johnstoni</i>	H	Australia	mentioned	Webb and Manolis, 1998
	<i>A. mississippiensis</i>	H	North America	mentioned	Levy, 1991
	<i>Caiman crocodilus</i>	E	Llanos, Venezuela	mentioned	Rivero-Blanco, 1974; Ayarzagüena, 1980
	<i>Caiman latirostris</i>	E	Santa Fe, Argentina	observed in wild	Larriera and Pina, 2000
	<i>Caiman yacare</i>	E, H	Pantanal of Pocone, Brazil	observed in wild	Cintra, 1985, 1989
<b>Waders</b>					
<i>Ardea alba</i> Great White Egret	<i>C. acutus</i>	H	Costa Rica	observed in wild	J.B. Montero, personal observation
	<i>Caiman crocodilus fuscus</i>	H	Costa Rica	observed in wild	J.B. Montero, personal observation
<i>Ardea cinerea</i> Grey Herons	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Cott, 1971; Guggisberg, 1972; Pooley, 1974
<i>Ardea cocoi</i> White-necked Stork	<i>Caiman crocodilus crocodilus</i>	H, J	Venezuelan Guayana	mentioned	Goetzula, 1978

	<i>C. niloticus</i>	H	Africa	observed in wild	R.A. Fergusson, personal observation
<i>Ardea goliath</i> Goliath Heron	<i>C. niloticus</i>	H	Africa	observed in wild	R.A. Fergusson, personal observation
<i>Ardea herodias</i> Great Blue Heron	<i>A. mississippiensis</i>	J	North America	mentioned	Neill, 1971
<i>Ardea purpurea</i> Purple Heron	<i>C. moreletii</i>	H	Central America	mentioned	Navarro-Serment, 2004
Egrets	<i>C. cataphractus</i>	H	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Egretta alba</i> Great Egret	<i>C. palustris</i>	E, H	Sri Lanka	mentioned	Jayewardene, 2004
<i>Egretta garzetta</i> Little Egret	<i>C. cataphractus</i>	H	Ivory coast	mentioned	Waitkuwait, 1986, 1989
	<i>C. niloticus</i>	H	Africa	mentioned	Modha, 1967; Pooley, 1969; Cott, 1971; Guggisberg, 1972
<i>Ephippiorhynchus asiaticus</i> Black-necked Stork	<i>C. palustris</i>	H	Andhra Pradesh, India	observed in wild	B.C. Choudhury, personal observation
<i>Ephippiorhynchus senegalensis</i> Saddle-billed Stork	<i>C. niloticus</i>	H	Africa	mentioned	Pooley and Ross, 1989
<i>Euxenura maguari</i> Maguari Stork	<i>Caiman crocodilus</i>	J	Llanos, Venezuela	mentioned	Staton and Dixon, 1977
<i>Grus canadensis</i> Sandhill Crane	<i>A. mississippiensis</i>	H	North America	mentioned	Audubon, 1827
<i>Guara alba</i> American Ibis	<i>A. mississippiensis</i>	H	North America	mentioned	Audubon, 1827
Herons and storks	<i>C. palustris</i>	J	Asia	mentioned	Webb and Manolis, 1998
<i>Heterocnus mexicanus</i> Tiger Bittern	Caiman	H, J	Mexico	mentioned	Alvarez del Toro, 1974
<i>Jabiru mycteria</i> Jabiru Stork	<i>C. moreletii</i>	H	Central America	mentioned	Navarro-Serment, 2004
	<i>Caiman crocodilus</i>	H, J	Venezuelan Guayana	mentioned	Gorzula, 1978; Romero, 1983
	<i>Caiman crocodilus crocodilus</i>	H	Venezuelen Llanos	observed in wild	Romero, 1983
	<i>Caiman yacare</i>	H	Pantanal of Pocone, Brazil	observed in wild	Cintra, 1989
<i>Leptoptilos crumeniferus</i> Marabou Stork	<i>C. niloticus</i>	E, H	Africa	mentioned	Pooley and Ross, 1989; Alderton, 1998
<i>Mycteria americana</i> American Wood Stork	<i>C. moreletii</i>	H	Central America	mentioned	Navarro-Serment, 2004
<i>Mycteria leucocephala</i> Painted Stork	<i>Caiman crocodilus</i>	H, J	Venezuelan Guayana	mentioned	Gorzula, 1978
	<i>C. palustris</i>	H	Yala NP, Sri Lanka	observed in wild	G. Rajapakse, personal observation
<i>Nycticorax caledonicus</i>	<i>C. johnstoni</i>	H	Lake Argyle, Australia	observed in wild	R. Somaweera, personal observation



Nankeen Night Heron						observation
<i>Nycticorax nycticorax</i> Black-crowned Night Heron			Llanos, Venezuela	H, J	mentioned	Ayarzaguena, 1980
<i>Threskiornis aethiopicus</i> Sacred Ibis			Africa	H	mentioned	Modha, 1967; Pooley, 1969; Cott, 1971; Guggisberg, 1972
<i>Tigrisoma lineatum</i> Rufescent Tiger-heron			Tambopata NP, Peru	H	observed in wild	D. Johnston, personal observation
<i>Tigrisoma mexicanum</i> Bare-throated Tiger Heron			Central America	H	mentioned	Alvarez del Toro and Sigler, 2001; J.B. Montero, personal observation
			Mexico	J	mentioned	Alvarez del Toro and Sigler, 2001
			Mexico	H	mentioned	Alvarez del Toro and Sigler, 2001
			Costa Rica	H	observed in wild	J.B. Montero, personal observation
<b>MAMMALS</b>						
<b>Canines</b>						
<i>Canis aureus</i> Golden Jackal			Vishwamitri River, India; India; Sri Lanka	E	mentioned; observed in wild	Webb and Manolis, 1998; Vyas, 2010; S. Karunaratne, personal observation
			National Chambal Sanctuary, India	E	observed in wild	Choudhury, 1981; Hussain, 1999
<i>Canis latrans</i> Coyote			Mexico	E	mentioned	Alvarez del Toro and Sigler, 2001
			Costa Rica	E	observed in wild	J.B. Montero, personal observation
<i>Canis lupus dingo</i> Dingo			Lake Argyle, Australia	E, H	remote camera traps	Somaweera et al., 2011a
<i>Canis lupus familiaris</i> Feral Dog			Mexico	E	mentioned	Alvarez del Toro and Sigler, 2001
			Vishwamitri River, India; Iran	E, H	observed in wild	Vyas, 2010; A. Mobaraki, personal observation

<i>Cerdocyon thous</i> Fox	Crab-eating	<i>Caiman crocodilus crocodilus</i>	H	Llanos, Venezuela; Venezuelan Guayana; Brazil	mentioned	Alvarez del Toro, 1974; Gorzula, 1978; Ayarzagüena, 1980; Crawshaw and Schaller, 1980
		<i>Caiman yacare</i>	E	Brazilian Pantanal	assumed;	Cintra, 1988; Campos, 1993
<i>Crocuta crocuta</i> Spotted Hyaena		<i>C. niloticus</i>	E	Throughout S and E Africa	observed in wild	R.A. Fergusson, personal observation
<i>Hyaena hyaena</i> Striped Hyaena		<i>C. niloticus</i>	J, A	Lothagam, Kenya	skeletal remains from dens	Leakey et al., 1999
<b>Felids</b>						
<i>Felis aurata</i> Golden cat		<i>C. cataphractus</i>	H	Ivory coast	assumed	Waitkuwait, 1986, 1989
<i>Felis catus</i> Domestic Cat		Crocodiles?	H	India	mentioned	Rao, 1992
<i>Leopardus pardalis</i> Ocelot		<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
		Caiman	H, J	Madre De Dios, Peru; South America	Mentioned; scat analysis	Alvarez del Toro, 1974; Emmons, 1987, 1989; Gorzula, 1978
		<i>Caiman crocodilus</i>	J	Mexico	mentioned	Alvarez del Toro, 1974
		<i>Caiman crocodilus chiapasius</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<i>Leptailurus serval</i> Serval		<i>C. niloticus</i>	E	Africa	mentioned	Steel, 1989
<i>Nandinia binotata</i> Tree Civet		<i>C. cataphractus</i>	E, J	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Panthera leo</i> African Lion		<i>C. niloticus</i>	A	Africa	mentioned	Cott, 1961; Pienaar, 1969
<i>Panthera leo persica</i> Asiatic Lion		<i>C. palustris</i>	A	Gujarat, India	observed in wild	B. Pandya, personal observation (Sanctuary magazine)
<i>Panthera onca</i> Jaguar		<i>C. acutus</i>	SA	Chiapas, Mexico	observed in wild	Alvarez del Toro, 1974; Alvarez del Toro and Sigler, 2001
		<i>C. moreletii</i> Caiman	A A, SA	Central America Venezuelan llanos; Madre De Dios, Peru	mentioned mentioned; scat analysis	Navarro-Serment, 2004 Emmons, 1987; Cavalcanti and Gese, 2009
		<i>Caiman crocodilus</i>	A, SA	Venezuelan llanos	mentioned	Emmons, 1989;

					Scognamillo et al., 2003
	<i>Caiman crocodilus crocodilus</i>	E, A	Mamiraua´ Sustainable Development Reserve, Brazil; South America	mentioned; observed in wild	Medem, 1983; Da Silveira et al., 2010
	<i>Caiman crocodilus fuscus</i>	SA	Chiapas State, Mexico	scat analysis	Dominguez-Laso and Mendoza, 2008
	<i>Caiman yacare</i>	SA, A	Mamiraua´ Sustainable Development Reserve, Brazil; Southern Pantanal, Brazil	observed in wild	Polisar et al., 2003; Da Silveira et al., 2010; Azevedo and Verdade, 2012
	<i>Melanosuchus niger</i>	E, A	Mamiraua´ Sustainable Development Reserve, Brazil; Central Amazon basin	observed in wild	Villamarin-Jurado et al., 2008 ; Da Silveira et al., 2010
	<i>Paleosuchus trigonatus</i>	A	Central Amazon	assumed	Magnusson and Lima, 1991
<i>Panthera pardus</i> Leopard	<i>C. cataphractus</i>	H, J	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Panthera tigris</i> Bengal Tiger	<i>Osteolaemus tetraspis</i>		Congo	mentioned	Blake, 1993
<i>Puma concolor</i> Puma	<i>C. palustris</i>	A	Rajasthan, India	observed in wild	M.D. Parashar , personal observation
	<i>A. mississippiensis</i>		Florida, USA	mentioned	Dalrymple and Bass, 1996
	<i>Caiman crocodilus</i>		Venezuelan llanos	mentioned	Scognamillo et al., 2003
<b>Herpestids</b>					
<i>Atilax paludinosus</i> Water Mongoose	<i>C. cataphractus</i>	E, H	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Herpestes auropunctatus</i> Small Indian Mongoose	<i>C. niloticus</i>	E	Africa	assumed	R.A. Fergusson , personal observation
<i>Herpestes edwardsi</i> Grey Mongoose	<i>C. porosus</i>	H	Orissa, India	observed in wild	S. Kar , personal observation
	<i>C. porosus</i>	H	Orissa, India	observed in wild	S. Kar , personal observation
	<i>Gavialis gangeticus</i>		India	assumed	Choudhury, 1981; Hussain, 1999
<i>Herpestes ichneumon</i> Egyptian Mongoose	<i>C. niloticus</i>	J	Africa	mentioned	Anderson 1898

<i>Herpestes</i> spp. Mongoose	<i>C. palustris</i>	E, H	India; Iran; Sri Lanka	mentioned	Webb and Manolis, 1998; Mobaraki, 2002
<i>Herpestes vitticollis</i> Striped-necked Mongoose	<i>C. palustris</i>	E	Sri Lanka	observed in wild	S. Karunaratne, personal observation
<i>Ichneumia albicauda</i> White-tailed Mongoose	<i>C. niloticus</i>	E	Africa	mentioned	Steel, 1989
<b>Mustelids</b>					
<i>Aonyx capensis</i> African Clawless Otter	<i>C. cataphractus</i>	E, H	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Conepatus chinga</i> Molina's Hog-nosed Skunk	<i>Caiman latirostris</i>	E	Santa Fe, Argentina	observed in wild	Larriera and Pina, 2000
<i>Eira barbara</i> Tayra	<i>C. moreletii</i> <i>Caiman yacare</i>	A E	Central America Brazilian Pantanal	mentioned assumed	Navarro-Serment, 2004 Cintra, 1988; Larriera and Pina, 2000
<i>Galictis vittata</i> Greater Grison	<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<i>Lontra canadensis</i> River Otter	<i>A. mississippiensis</i>	H	North America	mentioned	Ogden, 1978; Deitz and Hines, 1980; McIlhenny, 1987
<i>Lontra longicaudis</i> Neotropical Otter	<i>C. moreletii</i>	J	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<i>Lutra maculicollis</i> Spotted neck Otter	<i>C. cataphractus</i>	E, H	Ivory coast	mentioned	Waitkuwait, 1986, 1989
<i>Mellivora capensis</i> Ratel	<i>C. niloticus</i> <i>Gavialis gangeticus</i>	E E	Africa National Chambal Sanctuary, India	mentioned assumed	Pooley and Ross, 1989 Choudhury, 1981; Hussain, 1999
<i>Neovison vison</i> American Mink	<i>A. mississippiensis</i>	H	North America	mentioned	Allen and Neill, 1952
<i>Pteronura brasiliensis</i> Giant Otter	<i>Caiman yacare</i>	SA	South America	observed in wild	Ribas et al., 2012
Skunks ( <i>Conepatus</i> , <i>Mephitis</i> and <i>Spilogale</i> spp.)	<i>C. acutus</i>	E	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
	<i>C. moreletii</i>	E	Mexico	mentioned	Alvarez del Toro and Sigler, 2001
<b>Primates</b>					
<i>Cebus apella</i> Tufted Capuchin	<i>Caiman crocodilus</i>	E	Mamiraua' Sustainable	observed in wild	Da Silveira et al., 2010

			Development Reserve, Brazil			
	<i>Caiman yacare</i>	E	Brazilian Pantanal	assumed		Crawshaw and Schaller, 1980; Cintra, 1988
	<i>Melanosuchus niger</i>	E	Central Amazon basin	assumed		Villamarin-Jurado et al., 2008
<i>Papio anubis</i> Olive Baboon	<i>C. niloticus</i>	E	Africa	mentioned		Pooley and Ross, 1989
<i>Papio ursinus</i> Chacma Baboon	<i>C. niloticus</i>	E	Africa	observed in wild; mentioned		Parker and Watson, 1970
Procyonids						
<i>Nasua narica</i> White-nosed Coati	<i>C. acutus</i>	H	Costa Rica	observed in wild		J.B. Montero , personal observation
	<i>Caiman crocodilus fuscus</i>	E	Costa Rica	observed in wild		J.B. Montero , personal observation
<i>Nasua nasua</i> Ring-tailed Coati	<i>Caiman yacare</i>	E	Brazilian Pantanal	tracks and faeces		Crawshaw and Schaller, 1980; Cintra, 1988; Campos, 1993
<i>Procyon cancrivorus</i> Crab-eating Raccoon	<i>C. acutus</i>	E	Bahia Portete, Colombia	observed in wild		Abadia, 1996
<i>Procyon lotor</i> North American Raccoon	<i>Caiman yacare</i>	E	Brazilian Pantanal	assumed		Cintra, 1988
	<i>A. mississippiensis</i>	H	Louisiana, USA; Par Pond, USA; Okefonokee Swamp, USA	mentioned; observed in wild; remote camera traps		Joanen, 1969; Ogden, 1978; Ogden, 1978; McIlhenny, 1987; Hall and Johnson, 1987; McIlhenny, 1987; Brandt, 1989; Hunt, 1987
	<i>C. acutus</i>	E	Florida, USA; Mexico; Costa Rica; Turneffe Atoll, Belize; Blackbird Cay, Belize	observed in wild		Ogden, 1978; Kushlan and Mazzotti, 1989; Platt, 1996; Platt and Thorbjarnarson, 1996; Alvarez del Toro and Sigler, 2001
	<i>C. moreletii</i>	E	Mexico	mentioned		Alvarez del Toro and Sigler, 2001
	<i>Caiman crocodilus</i>	E	Mexico; South America	mentioned		Alvarez del Toro, 1974; Medem, 1983

	<i>Caiman crocodilus fuscus</i>	E	Costa Rica	observed in wild	Allsteadt, 1994
<b>Rodents</b>					
<i>Bandicota indica</i> Greater Bandicoot Rat	<i>C. porosus</i>	H	Orissa, India	observed in wild	S. Kar , personal observation Gorzula, 1978
<i>Dasyprocta</i> sp. Agouti	<i>Caiman crocodilus crocodilus</i>	H	Venezuelan Guayana	observed in captivity	
<i>Oryzomys palustris</i> Rice Rat	<i>A. mississippiensis</i>	E	Florida, USA; Okfenokee Swamp, USA	remote camera traps; observed in wild	Hunt, 1987; Hunt and Odgen, 1991
<i>Oryzomys</i> sp. Rice Rat	<i>C. moreletii</i>	E	Belize	observed in wild	Platt et al., 2008
Rats	<i>C. porosus</i>	E	Australia	mentioned	Messel and Vorlicsek, 1987
<i>Rattus collettii</i> Dusky Rat	<i>Gavialis gangeticus</i>	E	Chambal River, India	observed in wild	Whitaker and Basu, 1983
<i>Thricomys</i> sp. Rats	<i>C. porosus</i>	E	Australia	mentioned	Steel, 1989
Unidentified mouse	<i>Caiman yacare</i>	E	Brazil	assumed	Larriera and Pina, 2000
	<i>Melanosuchus niger</i>	E	Ecuador	remote camera traps	Villamarin-Jurado and Suarez, 2007
<b>Suids</b>					
<i>Phacochoerus africanus</i> Common Warthog	<i>C. niloticus</i>	E	Africa	mentioned	Cott, 1961, 1975
<i>Potamochoerus porcus</i> Bush Pig	<i>C. niloticus</i>	E	Africa	mentioned	Cott, 1961, 1975
<i>Sus scrofa</i> Wild/ Feral Pig	<i>A. mississippiensis</i>	E	North America	observed in wild	Fogarty, 1974; Ruckel and Steele, 1984; Woodward et al., 1992; Elsey et al., 2012 Webb et al., 1983a Hollands, 1984; Hall and Johnson, 1987 R. Somaweera, personal observation
	<i>C. johnstoni</i>	E	Australia	mentioned	
	<i>C. novaeguineae</i>	E	Papua New Guinea	mentioned	
	<i>C. palustris</i>	E	Tissa, Sri Lanka	observed in wild	
	<i>C. porosus</i>	E	Orissa, India; Australia	observed in wild	Messel and Vorlicsek, 1987 Thorbjarnarson, 1991 Gorzula, 1978
	<i>Caiman crocodilus</i>	E	Brazil	mentioned	
	<i>Caiman crocodilus</i>	H	Venezuelan Guayana	mentioned	

<i>crocodilus</i>						
	<i>Caiman latirostris</i>	E	Santa Fe, Argentina	observed in wild	Larriera and Pina, 2000	
	<i>Caiman yacare</i>	E	Pantanal	tracks and faeces	Campos, 1993	
	<i>Tomistoma schlegelii</i>	E	Sumatra	mentioned	Bezuijzen et al., 1998	
<i>Tayassu tajacu</i>	<i>C. moreletii</i>	E	Belize	assumed	Platt et al., 2008	
Collared Peccary						
<b>Viverrids</b>						
<i>Genetta maculata</i>	<i>Rusty-spotted Genet</i>	H, J	Africa	mentioned	Pooley and Ross, 1989	
<i>Viverra civetta</i>	<i>African Civet</i>	J	Africa	mentioned	Cott, 1961	
<b>Ursids</b>						
<i>Ursus americanus</i>	<i>Black Bear</i>	E	Florida, USA; North America; Okefenokee Swamp, USA	mentioned; remote camera traps	Metzen, 1977; Hunt, 1987; Hunt and Odgen, 1991	
	<i>C. acutus</i>	E	Everglades National Park, USA	mentioned	Moore, 1953 cited in Mazzotti, 1989	
<i>Ursus ursinus</i>	<i>Sloth Bear</i>	?	South Asia	mentioned	Pooley and Ross, 1989	
<b>Other mammals</b>						
<i>Conepatus leuconotus</i>	<i>Hog-nosed Skunk</i>	H	Americas	mentioned	Ogden, 1978; McIlhenny, 1987	
<i>Dasyopus novemcinctus</i>	<i>Nine-band Armadillos</i>	E	Brazilian Pantanal	assumed	Cintra, 1988	
<i>Didelphis albiventris</i>	<i>Opossum</i>	E	Brazilian Pantanal	assumed	Cintra, 1989	

\* Stage of crocodile: (E): egg; (H): hatchling; (J): juvenile; (SA): sub-adult; (A): adult.

\* 'Caimans' could refer to any of the subspecies of *Caiman crocodilus*. The relevant subspecies is mentioned whenever known.

\* Whenever the situation is not given 'observations' were listed as 'observed in wild', including all records that are based on secondary evidences. (egg and nest damage signs, foot prints, bite marks in carcasses).

\* The native range of the species is listed under 'region', even for records obtained elsewhere under captivity.

\* Records of 'young' animals are listed as 'juveniles'.