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## **Australian Freshwater Crocodiles (*Crocodylus johnstoni*) Transport Their Hatchlings to the Water**

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## Australian Freshwater Crocodiles (*Crocodylus johnstoni*) Transport Their Hatchlings to the Water

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**ABSTRACT.**—Remote video cameras recorded eight instances of nest excavation and parental transport of offspring to the water by Australian freshwater crocodiles (*Crocodylus johnstoni*) inhabiting Lake Argyle in northwestern Australia. Parental assistance during hatching appears to be vital for successful emergence of hatchlings from nests in this area.

In most, if not all, crocodylian species, adults provide some level of parental care to their offspring (Lang, 1987; Shine, 1988). One consistent feature involves adults opening nests and transporting newly hatched individuals (presumably their own progeny) to the water (e.g., *Alligator mississippiensis*, Kushlan, 1973; Watanabe, 1980; Huang and Watanabe, 1986; *Caiman crocodilus*, Alvarez del Toro, 1969; Staton and Dixon, 1977; *Caiman latirostris*, C. Piña pers. comm.; *Crocodylus acutus*, Ogden and Singletary, 1973; *Crocodylus cataphractus*, J. Brueggen pers. comm.; *Crocodylus moreletii*, Hunt, 1975; *Crocodylus novaeguineae*, Lang, 1980; *Crocodylus niloticus*, Pooley and Gans, 1976; Pooley, 1977; *Crocodylus palustris*, Whitaker and Whitaker, 1976; Subba Rao, 1977; *Crocodylus siamensis*, J. Brueggen pers. comm.; *Osteolaemus tetraspis*, Tryon, 1980; *Paleosuchus trigonatus*, Magnusson et al., 1985). Lang (1987) mentioned that transport of eggs and young to the water appears universal among crocodylians, with the exception of one or two species with very long, slender snouts. The absence of records for this behavior in some crocodylian species may reflect a genuine lack of this behavior or simply a lack of reports.

Despite considerable research on the Australian freshwater crocodile (*Crocodylus johnstoni*) over the last three decades (e.g., Johnston, 1973; Webb, 1980; Webb et al., 1983a; Smith, 1987; Cooper-Preston, 1992; Tucker, 1997; Chibeba, 2003), hatchling transport of this slender-snouted species has not been documented in-detail in the wild. The species is a hole-nester that oviposits during the dry season (mostly around August; Webb et al., 1983a), and eggs hatch at the beginning of the wet season (November/December). Wild adult *C. johnstoni* do not defend their nests during the incubation period (Webb et al., 1983a) but will do so in captivity. Both captive and wild adults have been reported to open their nests in response to calls from the hatchlings (Compton, 1981; Smith, 1987; Cooper-Preston, 1991). In the McKinlay River (Northern Territory), indirect evidence suggests that nest opening may occur over several days (Webb et al., 1983a). Although several previous authors suggested that *C. johnstoni* also carry the young to water, this behavior has not been documented in-detail. Here, we describe aspects of this parental behavior for wild *C. johnstoni*.

### MATERIALS AND METHODS

Lake Argyle (16°29'S, 128°75'E in East Kimberley, tropical Western Australia) contains the largest population of *C. johnstoni* in Australia (>30,000 nonhatchlings; G. Webb Pty.

Ltd. 1989; WMI 2005, 2009). The large area of available habitat (about 1,000 km<sup>2</sup>) provides abundant aquatic food resources for adult crocodiles, but a lack of suitable nest-sites concentrates nesting in small areas (Somaweera and Shine, 2012; Somaweera et al., 2011). In 2010, we monitored the nesting of *C. johnstoni* in five study sites in the northern part of the lake— four of them (Bamboo Cove, Croc Bay, Gundarim Bay, and BBQ Island Bay) on the mainland and the other at the Bay of Islands (BOI) separated from the mainland by >2 km of deep water. Extensive searches and camera trappings failed to record any land predators (mammalian or reptilian) on islands at BOI. Banks of these northern sites are mainly gravel substrate made from Proterozoic sandstone and glacial sedimentary rocks (DME, 1996). Riparian vegetation and floating vegetation mats are frequent along the banks in all sites and are used as nursery grounds by hatchlings.

In August 2010, 67 *C. johnstoni* nests were located based on fresh disturbance to the soil surface at the five study sites. The nests were a mean distance of 7.71 m (range 2.1–20.5 m; SE 1.12 m) from the shoreline. Motion-sensitive infrared triggered digital still/video cameras (Bushnell Trophy Cam) were deployed ~50 cm aboveground to cover all or most nests at each study site (Fig 1a). The memory cards of the cameras were changed every third day, and cameras were left on-site until 1 December 2010. Visits to sites were brief and total time spent at each camera was <2 min.

### RESULTS

Crocodiles were seen basking on the nesting banks, but none visited the nests during the incubation period until mid-November. By 1 December 2010, we had obtained footage of eight nests being excavated by crocodiles, the first on 18 November 2010. We heard hatchling vocalizations 1–5 days prior to the nests being opened (in response to vibrations or sounds made while we were walking nearby). This prehatching vocalization induces and synchronizes hatching in siblings and stimulates the adults to open the nest (Vergne and Mathevon, 2008; see also review by Britton, 2001). We could not ascertain whether the same female that laid the nest excavated it at hatching time. Based on the estimated size of the crocodiles involved (approximately 180–240 cm in total length), they were all mature adults but of unknown sexes.

Adults mainly used their forelegs to rake and dig and their hind legs to remove the gravel piled up from digging (Fig 1b). In approximately 70% of cases, only the two limbs of either the right or the left side were used at a given time. The head and body lay on the ground throughout most of the digging, with

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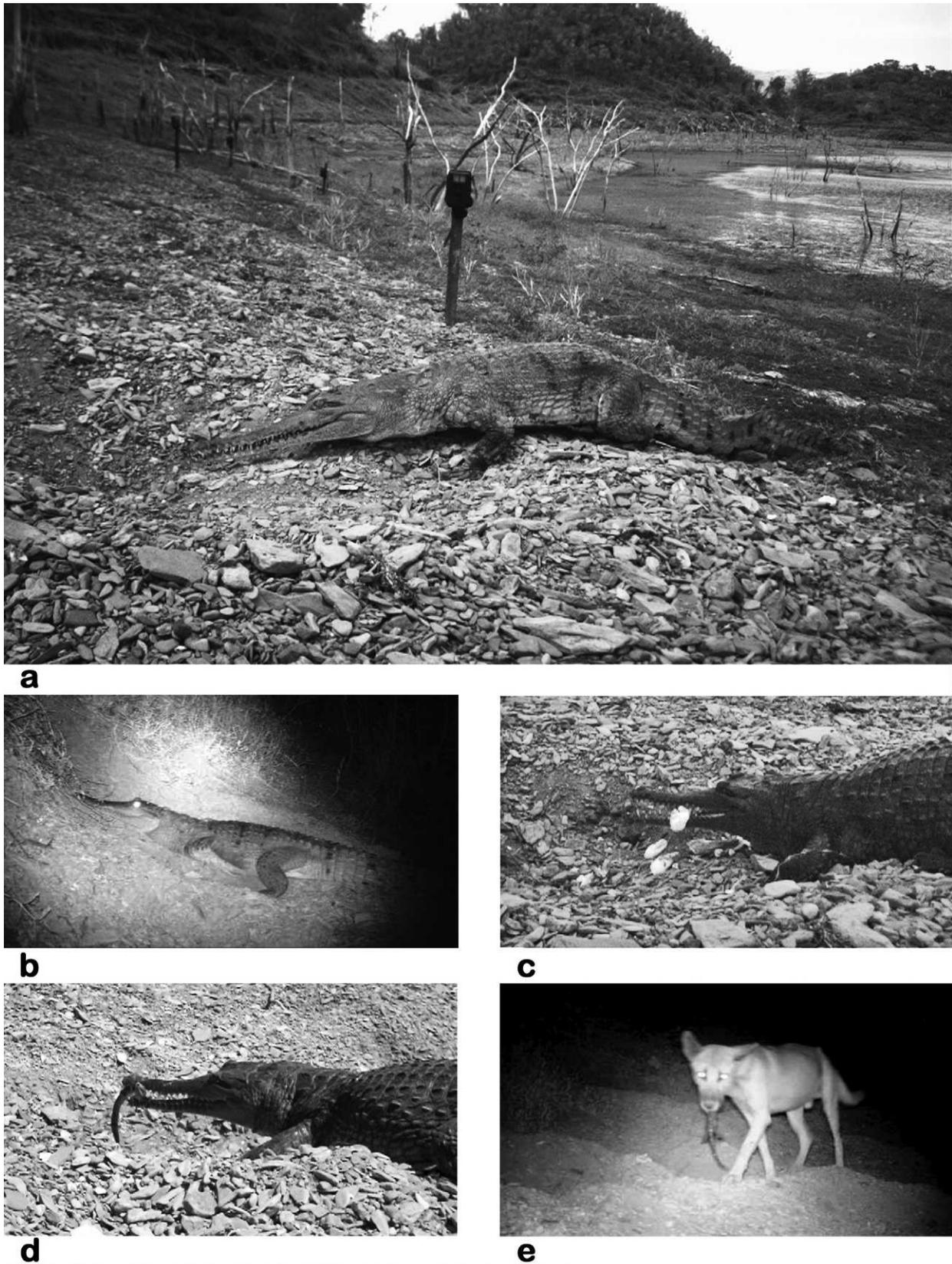


FIG. 1. At Lake Argyle in Western Australia, the nesting sites of Freshwater Crocodiles (*Crocodylus johnstoni*) mainly comprise a gravel substrate (a). During the hatching period, the adults open the nests (b), assist hatching by chewing unhatched eggs in their mouths (c) and transport hatchlings to water (d). However, predation of hatchlings remaining at the nest sometimes occurs before the adult returns from such a trip (e).

the body repositioning to different directions during regular stops (lasting from ~30 sec to >45 min) in digging.

Seven of the eight excavations commenced during daylight hours (two between 0800–1000 h; one between 1300–1400 h; four between 1600–1800 h), and only one commenced at night (0200–0300 h). Excavation of nests took an average of 1.4 h (range 0.4–2.2 h), and transportation of neonates took an average of 2.0 h (range 1.1–6.2 h). Three adults returned once each to their nests after 12.5, 17, and 26 h, respectively, to dig again even though no eggs remained.

As hatchlings emerged from the nests, they maintained a head erect posture until the adult picked them up with the tip of the snout (Fig 1d). In one nest, a hatchling was held in the adult's mouth for 1.4 min before the adult began to position it inside the mouth. Some hatchlings hung across the mouth during transportation, but most were not visible in the video footage of adults heading toward water; the hatchlings likely were within the gular pouch in these cases. The footage suggests that only one hatchling was transported at a time.

We found no evidence of hatchlings walking to water by themselves. Three hatchlings from one site remained in the "pit" for ~17 min until the adult's return, during which time one of them was predated by a Dingo *Canis lupus dingo* (Fig 1e). Torresian crows (*Corvus orru*) visited three nests 0.5–14 h after excavation and scavenged the remaining eggs and hatchlings. Ants were observed in one nest with damaged eggs.

On two occasions, adults assisted hatchlings to emerge by chewing and manipulating the eggs in their mouths (Fig 1c). Four of the eight nests opened by adults had infertile eggs remaining in the nests. In three nests (including two nests containing infertile eggs), six partially opened eggs with fully developed but dead young were found in shallow water, suggesting that the adults may differentiate between infertile eggs and those containing hatchlings and may have carried the eggs with dead offspring to water. Maternal assistance in hatching by chewing/manipulating eggs has been documented for some crocodylians (e.g., *Alligator mississippiensis*, Garrick and Lang, 1977; Hunt, 1987; *Alligator sinensis*, Huang and Watanabe, 1986; *C. crocodilus*, Alvarez del Toro 1969; *Caiman yacare*, Cintra, 1988; *C. novaeguineae*, Lang, 1987; *C. siamensis*, J. Brueggen pers. comm.) as has the carrying of unhatched eggs to water and aiding of hatching by females (e.g., *C. acutus*, Ogden and Singletary, 1973; *C. niloticus*, Pooley, 1977). No instances of adult *C. johnstoni* swallowing the eggs at nests were recorded (as has been reported for *A. mississippiensis* by Hunt, 1987).

Debris associated with hatching was sometimes observed at the water's edge or in shallow water. Three hatchlings collected 1–2 days after hatching (based on the width of the yolk scar: Webb and Smith, 1984) still had remnants of the allantoic membrane attached to the yolk scar. Captive adult *C. moreletii* manipulated hatchlings in their mouths to remove embryonic debris (Hunt, 1980).

We excavated three nests that were not attended by adults after 95 days since laying, although the nests had vocalizing young. Of the 43 hatchlings, 11 were dead, and all had kinked tails, a symptom of high incubation temperatures (see review by Ferguson, 1985). Twenty-one of the 32 live hatchlings also had swollen abdomens ("yolk bellies"), also indicative of high temperature incubation (Webb et al., 1983b). The eggs of seven additional nests that were excavated 100 days postlaying contained 73 dead and decomposing embryos (all >38 days old in development stage based on morphology: Webb et al., 1983a) and 21 dead, fully developed hatchlings. Crocodile nest

temperatures at Lake Argyle in 2010 varied considerably, with several days exceeding 35°C and then dropping to ~28°C resulting from heavy rains in early and mid-October. Those thermal fluctuations may have killed some embryos (R. Somaweera, unpubl. data).

We do not know why some nests were not excavated. Our visits to the sites were brief, but it is possible that adult crocodiles were disturbed. The unopened nests were adjacent to the nests that were opened and did not differ significantly from opened nests with regard to nest depth ( $F_{1,17} = 0.001$ ,  $P = 0.97$ ), compactness of surface substrate ( $F_{1,17} = 0.018$ ,  $P = 0.89$ ), distance from shoreline ( $F_{1,17} = 0.046$ ,  $P = 0.83$ ), or density of nests ( $F_{1,17} = 2.57$ ,  $P = 0.13$ ). Possibly, hatchlings in some nests may not have vocalized. Adult crocodylians typically open the nest in response to hearing prehatching calls (Britton, 2001). Female *Crocodylus porosus* did not open nests that contained only dead embryos (Magnusson, 1980), presumably because of lack of vocalization.

#### DISCUSSION

Adult *C. johnstoni* carried only one hatchling at a time to the water, consistent with observations on *C. acutus* (Ogden and Singletary, 1973) and *C. siamensis* (Brueggen, 2002). However, simultaneous transport of multiple hatchlings occurs in other crocodylian taxa (e.g., *C. moreletii*, <12 hatchlings [Hunt, 1977]; *C. niloticus*, <19 [Pooley, 1977]). Parental transport of hatchlings from the nest to water could protect the newborn from predators, especially when drought increases the distance between nest and water (Hunt, 1987). Thus, the ability to transport many neonates at one time would enable hatchlings to be protected from opportunistic predators; and if the crèche/pod is quickly formed, the mother can focus on its defense (Hunt, 1987). Although parents sometimes transport the young on the snout, on the head, or on the back (Pooley, 1974) or merely lead them to water (Whitaker and Whitaker, 1984), buccal transport is the most common form of neonate transport.

The number of neonates carried by a parent may be affected by the size of the adult relative to the hatchling (larger adults with smaller neonates may fit more hatchlings in the mouth) and clutch size (species with larger number of offspring may carry more hatchlings at once to reduce the number of visits to and from the nest). Relative jaw size (gular pouch capacity) could also be important. The species known to carry multiple neonates (e.g., *C. moreletii*, *C. niloticus*) are all large species and have broad snouts and, thus, may have more space in the gular pouch compared to narrow-snouted species. However, Hunt (1987) stated that *A. mississippiensis*, a broad-snouted species, rarely transported more than one neonate at a time.

The significance of adult intervention in the hatching process of crocodylians is not well understood. The level of parental care shown by individual animals can vary considerably, even within a species. Our limited observations over three nesting seasons (2008–2010) did not reveal any unassisted hatching events, and nests not opened by adult *C. johnstoni* appeared to fail. Similarly, Joanan (1969) reported that >50% of the young in nests that were not opened by adult *A. mississippiensis* died inside the nest, and examination of 150 *C. niloticus* nests indicated that no hatchlings managed to crawl out of the nest without maternal help (Modha, 1967). In *Melanosuchus niger*, suffocation of hatchlings that had pipped (broken through the shell), but in the absence of a female to release them so that they could not emerge from the nest, was a significant cause of

mortality (Villamarin-Jurado and Suarez, 2007). Only 5.3% of *C. acutus* hatchlings from abandoned nests managed to emerge (Tabet et al., 2006), and despite some *C. moreletii* hatchlings exiting the nest unassisted, most from unopened nests were killed by ants and rice rats (Platt et al., 2008). However, unassisted hatching of crocodilians is known (e.g., Joanen, 1969; Wilkinson, 1983; Allsteadt, 1994; Platt et al., 2008) including in *C. johnstoni* (Webb et al., 1983a).

Webb et al. (1983a) reported *C. johnstoni* hatchlings emerging unassisted from a nest in the McKinlay River. Nesting substrates in that area are mainly soft friable sand, whereas Lake Argyle crocodiles are forced to nest in gravel (compactness of the nesting substrate in northern Lake Argyle is  $1.8 \pm 0.08$  kg/cm<sup>2</sup> and average particle size on top is 3.43 cm [R. Somaweera, unpubl. data; Fig 1a,c,d]), which may restrict the ability of hatchlings to emerge unassisted. However, some reptile hatchlings manage to emerge even through very compact substrates (e.g., jacky dragon *Amphibolurus muricatus* hatchlings emerge unassisted from nests of  $1.5 \pm 1.1$  kg/cm<sup>2</sup> compactness; Warner and Shine, 2008).

Of the 67 nests located in the 2010 season, 38 (56.7%) were predated by 1 December 2010, leaving 29. Of these, eight were excavated successfully by adult crocodiles. Ten additional nests contained some fully formed embryos, which had either died in the nest or probably would have died without assistance. Eggs in the remaining 11 nests either hatched or were predated after 1 December, when the cameras were no longer active. If the 11 nests whose fate is not known are excluded, then all hatchlings that successfully entered the population did so because of assistance provided by adults. For Lake Argyle, nest excavation and hatchling transport to the water by adults may be vital for successful recruitment of hatchlings into the population.

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#### LITERATURE CITED

- ALLSTEADT, J. 1994. Nesting ecology of *Caiman crocodilus* in Cano-Negro, Costa-Rica. *Journal of Herpetology* 28:12–19.
- ALVAREZ DEL TORO, M. 1969. Breeding the spectacled caiman, *Caiman crocodilus*, at Tuxtla Gutierrez Zoo. *International Zoo Yearbook* 9:35–36.
- BRITTON, A. 2001. Review and classification of call types of juvenile crocodilians, and factors affecting distress calls. In G. Grigg, F. Seebacher, and C. Franklin (eds.), *Crocodilian Biology and Evolution*, pp. 364–377. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- BRUEGGEN, J. 2002. Crocodilians: Fact vs. Fiction. In Proceedings of the 16th Working Meeting of the Crocodile Specialist Group, pp. 204–210. IUCN, Gland.
- CHIBEBA, A. M. 2003. Nesting Ecology of the Australian Freshwater Crocodile, *Crocodylus johnstoni*, on the McKinlay River: Setting a Baseline for Assessing the Potential Impact of the Exotic Cane Toad, *Bufo marinus*. Unpubl. master's thesis, Charles Darwin University, Darwin, Northern Territory, Australia.
- CINTRA, R. 1988. Nesting ecology of the Paraguayan caiman (*Caiman yacare*) in the Brazilian pantanal. *Journal of Herpetology* 22:219–222.
- COMPTON, A. W. 1981. Courtship and nesting behaviour of the Freshwater Crocodile, *Crocodylus johnstoni*, under controlled conditions. *Australian Wildlife Research* 8:443–450.
- COOPER-PRESTON, H. 1992. Geographic Variation in the Population Dynamics of *Crocodylus johnstoni* (Kreffth) in Three Rivers in the Northern Territory, Australia. Ph.D. diss., University of New England, Armidale, New South Wales, Australia.
- FERGUSON, M. W. J. 1985. Reproductive biology and embryology of the crocodilians. In C. Gans, F. Billet, P. Maderson (eds.), *Biology of the Reptilia*. Vol. 14, pp. 329–491. John Wiley and Sons, New York.
- G. WEBB PTY. LTD. 1989. The results of crocodile surveys in Lake Kununurra and Lake Argyle (Western Australia), February–March 1989. Report to CALM, 1989.
- GARRICK, L. D., AND J. W. LANG. 1977. Social signals and behaviors of adult alligators and crocodiles. *American Zoologist* 17:225–239.
- HUANG, Z., AND M. E. WATANABE. 1986. Nest excavation and hatching behaviors of Chinese alligator and American alligator. *Acta Herpetologica Sinica* 5:5–9.
- HUNT, R. H. 1975. Maternal behaviour in the Morelet's crocodile, *Crocodylus moreletii*. *Copeia* 1975:763–764.
- . 1977. Aggressive behaviour by adult Morelet's crocodiles *Crocodylus moreletii* towards young. *Herpetologica* 33:195–201.
- . 1980. Propagation of Morelet's crocodile. In J. B. Murphy, and J. T. Collins (eds.), *Reproductive Biology and Diseases of Captive Reptiles*. pp. 161–165. SSAR Contribution to Herpetology 1. SSAR, Oxford, Ohio.
- . 1987. Nest excavation and neonate transport in wild *Alligator mississippiensis*. *Journal of Herpetology* 21:348–350.
- JOANEN, T. 1969. Nesting ecology of alligators in Louisiana. In Proceedings of the 23rd Annual Conference of the Southeastern Association of the Game Fish Commission, pp. 141–151.
- JONSON, C. R. 1973. Behaviour of the Australian crocodiles, *Crocodylus johnstoni* and *C. porosus*. *Zoological Journal of the Linnean Society* 52:315–336.
- KUSHLAN, J. A. 1973. Observations on maternal behaviour in the American alligator, *Alligator mississippiensis*. *Herpetologica* 29:256–257.
- LANG, J. 1980. Reproductive behaviours of New Guinea and saltwater crocodiles. In Proceedings of the SSAR Symposium on Reproductive Biology and Conservation of Crocodiles, Milwaukee, WI, USA, August 1980. Abstract.
- . 1987. Crocodilian behaviour: implications for management. In G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), *Wildlife Management: Crocodiles and Alligators*. pp. 273–294. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- MAGNUSSON, W. E. 1980. Hatching and creche formation by *Crocodylus porosus*. *Copeia* 1980:359–362.
- MAGNUSSON, W. E., A. P. LIMA, AND R. M. SAMPAIO. 1985. Sources of heat for nests of *Paleosuchus trigonatus* and a review of crocodilian nest temperatures. *Journal of Herpetology* 19:199–207.
- MODHA, M. L. 1967. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *African Journal of Ecology* 5:74–95.
- OGDEN, J. C., AND C. SINGLETARY. 1973. Night of the crocodile. *Audubon* 75:32–37.
- PLATT, S. G., T. R. RAINWATER, J. B. THORBJARNARSON, AND S. T. McMURRY. 2008. Reproductive dynamics of a tropical freshwater crocodilian: Morelet's crocodile in northern Belize. *Journal of Zoology* 275:177–189.
- POOLEY, A. C. 1974. Parental care in the Nile crocodile. *Lammergeyer* 21: 43–45.
- . 1977. Nest opening response of the Nile crocodile *Crocodylus niloticus*. *Journal of Zoology* 182:17–26.
- POOLEY, A. C., AND C. GANS. 1976. The Nile crocodile. *Scientific American* 234:114–124.
- SHINE, R. 1988. Parental care in reptiles. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*. Volume 16: pp. 275–329.
- SMITH, A. M. A. 1987. The Sex and Survivorship of Embryos and Hatchlings of the Australian Freshwater Crocodiles, *Crocodylus johnstoni*. Unpubl. Ph.D. diss., Australian National University, Canberra, Australia Capital Territory.
- SOMAWEERA, R., J. WEBB, AND R. SHINE. 2011. It's a dog-eat-croc world: dingo predation on the nests of freshwater crocodiles in tropical Australia. *Ecological Research*. 26:957–967.
- STATON, M. A., AND J. R. DIXON. 1977. Breeding Biology of the Spectacled Caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos. *Fish*

- and Wildlife Service, Wildlife Research Report 5. United States Department of the Interior, Washington, DC.
- SUBBA RAO, M. V. 1977. On breeding crocodiles. *Science Today* October: 29–33.
- TABET, M. A., R. R. SOBERÓN, J. B. THORBJARNARSON, AND R. R. TARGARONA. 2006. American crocodile (*Crocodylus acutus*) egg losses related to nesting females behaviour, at the Delta del Cauto Wildlife Refuge, Cuba. *In* Proceedings of the 18th Working Meeting of the IUCN-SSC Crocodile Specialist Group, pp. 332–341. IUCN, Gland, Switzerland. Available from: [http://www.iucnscg.org/365\\_docs/attachments/protarea/18th-6b8e5b33.pdf](http://www.iucnscg.org/365_docs/attachments/protarea/18th-6b8e5b33.pdf)
- TRYON, B. W. 1980. Observations on reproduction in the West African dwarf crocodile with a description of parental behaviour. *In* J. B. Murphy and J. T. Collins (eds.), *Reproductive Biology and Diseases of Captive Reptiles*. pp. 167–185. SSAR Contribution to Herpetology 1. SSAR, Oxford, Ohio.
- TUCKER, A. D. 1997. Ecology and Demography of Freshwater Crocodiles (*Crocodylus johnstoni*) in the Lynd River of North Queensland. Unpubl. Ph.D. diss., University of Queensland, St. Lucia, Queensland, Australia.
- VERGNE, A. L., AND N. MATHEVON. 2008. Crocodile egg sounds signal hatching time. *Current Biology* 18:R513–R514.
- VILLAMARIN-JURADO, F., AND E. SUAREZ. 2007. Nesting of the Black Caiman (*Melanosuchus niger*) in northeastern Ecuador. *Journal of Herpetology* 41:164–167.
- WARNER, D. A., AND R. SHINE. 2008. Maternal nest-site choice in a lizard with temperature-dependent sex determination. *Animal Behaviour* 75:861–870.
- WATANABE, M. E. 1980. The Ethology of the American Alligator (*Alligator mississippiensis*) with Emphasis on Vocalizations and Responses to Vocalizations. Unpubl. Ph.D. diss., New York University, New York.
- WEBB, G. J. W. 1980. Nesting Biology of *Crocodylus johnstoni* in the Northern Territory. *In* C. B. Banks and A. A. Martin (eds.), *Proceedings of the Melbourne Herpetological Symposium*. pp. 19–21. Melbourne Zoological Gardens. May 1980.
- WEBB, G. J. W., AND A. M. A. SMITH. 1984. Sex ratio and survivorship in the Australian Freshwater Crocodile *Crocodylus johnstoni*. *Symposia of the Zoological Society of London* 52:319–355.
- WEBB, G. J. W., R. BUCKWORTH, AND S. C. MANOLIS. 1983a. *Crocodylus johnstoni* in the McKinlay River, N.T. VI. Nesting biology. *Australian Wildlife Research* 10:607–637.
- WEBB, G. J. W., G. C. SACK, R. BUCKWORTH, AND S. C. MANOLIS. 1983b. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Australian Wildlife Research* 10:571–605.
- WHITAKER, R., AND Z. WHITAKER. 1976. Collection and hatching of marsh crocodile (*C. palustris*) eggs. *Journal of the Bombay Natural History Society* 73:403–407.
- . 1984. Reproductive biology of Mugger. *Journal of the Bombay Natural History Society* 81(2):119–127.
- WILKINSON, P. 1983. Nesting ecology of the American Alligator in coastal South Carolina. South Carolina Wildlife and Marine Resources Department.
- WMI. (Wildlife Management International) 2005. Results of Spotlight Surveys of Crocodiles in Lake Argyle and Lake Kununurra, 2005. Report to CALM, 2005.
- WMI. (Wildlife Management International) 2009. Results of Spotlight Surveys of Crocodiles in Lake Argyle, 2009. Report to DEC, 2009.

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