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Reproductive Ecology of the Chinese Alligator (*Alligator sinensis*) and Implications for Conservation

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ABSTRACT.—The Chinese alligator is one of the world's most critically endangered reptiles. Although there is a relatively large captive population, in the wild small groups of alligators are limited to a few small ponds in an agricultural landscape in southeastern Anhui Province. As part of an effort to develop plans for the conservation of Chinese alligators in the wild, we investigated aspects of the reproductive ecology of wild alligators during a survey of the last remaining groups. We also compiled published and unpublished information on the reproduction of alligators in captivity and in the wild. Nesting was only reported from four sites in 1999, and we describe two of these areas. Because of the intense human use of the landscape, alligators seek small patches of relatively undisturbed vegetation for nesting, and these fall into two main categories: vegetated hillsides, usually covered with pine trees, and small islands in agricultural ponds. Our observations of one nest on a pine hillside suggest that pine needles may make a poor nest substrate leading to lethally low temperatures for developing embryos. The selection of sites for the reintroduction of alligators should take the nature of potential nesting habitat into consideration.

The Chinese alligator (*Alligator sinensis*) is one of the world's most critically endangered reptiles. Current estimates suggest that no more than 130 individuals remain in the wild in a human-dominated landscape in the lower Changjiang (Yangtze River) valley (JT and XW, pers. obs.). In this area, alligators are restricted to a small number of agricultural ponds within a five-county region in southern Anhui Province (Wan et al., 1998; Thorbjarnarson and Wang, 1999). Because a relatively large captive population is found in breeding centers and zoos in China and North America (Behler, 1995; Wan et al., 1998), efforts to retain a viable population in the wild can focus on the restoration of wetlands or identification of existing areas of suitable habitat where captive-reared alligators can be released (Wan et al., 1998; Thorbjamarson and Wang, 1999). Nevertheless, the long-term survival of small groups of wild alligators will require intensive management and a thorough understanding of the ecology and behavior of the Chinese alligator. However, although a great deal of information is available on the biology of the American alligator, very little is known about its Asian congener, and most of this is from captive animals.

Here, we present information on Chinese alligator nesting in the wild collected during a population survey conducted in 1997 and 1999. We also summarize other published and unpublished information on the reproduction of wild Chinese alligators that has been collected by the Anhui Province Forestry Bureau, as well as the reproduction of captive alligators, including the Anhui Research Center for Chinese Alligator Reproduction (ARCCAR), a captive breeding center managed by the Anhui Forestry Bureau.

MATERIALS AND METHODS

Field surveys were conducted in August 1997 and July to October 1999 at 26 sites within the five county region of the National Chinese Alligator Reserve (NCAR), including all 13 sites officially designated by the Chinese government for the protection of the alligator (here referred to as "designated sites"; Thorbjarnarson and Wang, 1999). At most of the designated sites the Anhui Forestry Bureau (AFB) employed a local farmer as a caretaker to oversee the protection of the alligators. At most sites, the caretaker and other local farmers were good sources of information regarding the number of alligators, the location of nests, and the history of nesting in the region. Information on recent alligator nests was also provided by the Jinxiang County offices of the AFB.

In 1999, we used temperature data-loggers (HOBO-Temp) to measure egg cavity temperature in wild nests. Nests were measured, and the general area surrounding nests was characterized and data recorded on standardized data sheets. Egg mass was measured using a 100-g Pesola scale.

RESULTS AND DISCUSSION

Size and Age.—The Chinese alligator is one of the world's smallest crocodilians, with a maxi-

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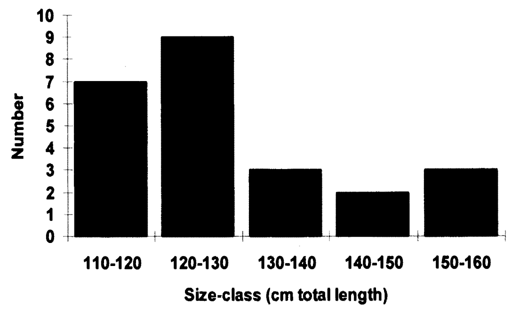

FIG. 1. Size-class distribution of 24 adult females (> 110 cm TL) in a sample captured by Chu (1957).

mum reported total length of around 200 cm TL. In May 1995, a 1.98-m male (38 kg) was captured near the city of Ma'anshan (Anhui Province) by farmers. A 1.99-m male was kept in the Bronx Zoo for several years, and a captive specimen in Russia measured 2.03 m and weighed 42 kgs (J. Behler, pers. comm). A male kept in the National Zoo measured 2.01 m TL when it died in 1976. The mean length of seven wild adult males collected in Zhejiang Province was 158.2 cm (128–203 cm TL; SD = 26.0 cm; Huang et. al, 1987).

Huang (in Groombridge, 1982) gave a maximum length of females of 175 cm TL. Hsaio (1934) recorded an 18-yr-old female that was 175 cm long. From a sample of seven adult females in Zhejiang Province, mean total length was 131.4 cm (116–150 cm; SD = 12.8 cm; Huang et al., 1987). Chen (1991) reported the mean total length of 19 adult females was 135.0 cm (range 117.5–144.0 cm). Mean sizes of a sample of 24 wild adult (> 110 cm TL) females captured by Chu (1957) was 129.8 cm (range 114.5–159.5; SD = 13.4 cm; Fig. 1).

The minimum size of reproduction in females was reported by Huang (in Groombridge, 1982) to be 92 cm TL. However, this appears to be an erroneous figure from Chu (1957) based either on a female missing part of its tail or mismeasured (using the accompanying head length value the female would have measured 116.6 cm TL). Chen (1985) gave a minimum length of female reproduction of 110 cm TL. Chen (1985) estimated that females mature in 6–7 yr. Maximum age reports come principally from captive animals in U.S. zoos and indicate that the oldest individuals in captivity are 60–70 yr old and that healthy animals have continued to reproduce into their fifth decade of life (J. Behler, pers. comm.).

Annual Reproductive Cycle.—The Chinese alligator inhabits the climatic transition between subtropical and temperate regions of eastern China. Like the American alligator, activity is reduced for much of the year because of low temperatures. From late October through mid-April, Chinese alligators are dormant in subterranean dens dug into the edges of ponds or marshes. At Hongxin, Zhu (1997) reported seeing basking alligators in mid-May. After their spring emergence, alligators are principally diurnal, avoiding activity during the cold nights. In June, as temperatures warm, alligators become increasingly nocturnal (Huang, 1982). Courtship, bellowing, and mating starts in early June and appears to peak in mid-June (Zhu, 1997). During this time, males may move from pond to pond searching for females (Chen and Li, 1979). Chen (1985) reported that females begin building the nest 10–25 days after mating. Females nest in late June and early July, and nests hatch in September. Females open the nest and assist the neonates to emerge from the eggs and transport them in their mouth to nearby water (Huang and Watanabe, 1986).

Courtship and Mating.—Bellowing behavior is similar to that of American alligators (Garrick and Lang, 1977; Vliet, 1989). ARCCAR staff report that both sexes bellow, and bellowing can be heard during most of the year while alligators are active, with a peak in mid-June during courtship (Chen and Li, 1979). Huang (1982) indicated copulation and courtship behaviors are typical for crocodilians. Wang and Huang (1997) found that, over a 12-yr period at the Yingjibian breeding center in Zhejiang Province, the mating season ranged from 23 May to 27 June.

Timing of Nesting.—In captivity, nesting takes place during a short period (usually three weeks) in late June and early-mid July (W. Xie, pers. comm.; Chen and Wang, 1984; Webb and Vernon, 1992). Unusual weather conditions may alter nesting schedules. Zhang (1995) reported that heavy rains and low summer temperatures in 1995 delayed nesting by approximately 20 days (to 13 July). The mean date of egg laying for 11 wild nests in Jinxiang County was 28 June, and hatching was 18 September. The two wild nests located in 1999 were both estimated to have been laid on 15 July.

Incubation is variously reported to last 70 days (Huang, 1982), 68 days (Huang and Watanabe, 1986) and 60–70 days (Chen, 1985; range 57–88 days). Huang (1983) noted that at the Shanghai Zoo artificially incubated eggs hatched in 67–83 days, whereas "naturally" incubated eggs hatched in less than 65 days. Information from wild nests in Jinxiang County indicate a mean incubation time of 81.5 days for 11 nests (Jinxiang AFB Office, pers. comm.).

Like all crocodilians the sex of hatchling Chinese alligators is determined by the temperature of incubation (Lang and Andrews, 1994), but the exact relationship has not yet been well worked out. Staff at ARCCAR indicated that the critical temperature (producing an even mixture of males and females) is 31° C (C. Wang, pers. corom.). Chen (1990) reported that mostly males were produced at incubation temperatures above 33°C and females below 28°C.

Nests and Nesting.—As with all members of the Alligatoridae, Chinese alligators make mound nests of leaf litter and vegetation. Two wild nests we measured in 1999 averaged 95 × 82 cm and 42 cm in height. Chen (1985) reported the height of nests ranged from 43 cm to 72 cm. Zhu (1997) found nest dimensions at Hongxin (a wild nest) were 45 cm high and 90 cm in diameter.

At the Shanghai Zoo, Huang (1983) noted that some females nested every year, whereas others nested biennially. Oviposition lasted 30–40 min and took place at dawn. A female responds to the vocalizations of the young in the nest by digging the nest open using her forelimbs. A female will assist neonates in hatching by gently breaking open the egg in her jaws and will carry neonates in her mouth (Huang and Watanabe, 1986).

The nest sites used by female Chinese alligators today reflect the highly altered environments in which they live; small artificial ponds set within agricultural landscapes. Within these areas, female alligators seek small patches of relatively undisturbed vegetation for nesting, and the presence of sites suitable for nesting may explain why alligators have survived in certain areas and not in others. During our surveys in Anhui Province in 1997 and 1999, we visited sites where wild nests had been reported in recent years, as well as two active nests. In these areas, the combination of artificial ponds set in relict wetlands adjacent to vegetated hillsides has provided a mix of habitats that has allowed some reproduction and recruitment to occur. Active nests at two sites (Shaung Ken and Zhuangtou) were located at the bases of pine trees on hillsides 20–40 m from small artificial ponds used for water storage for rice cultivation. In one case, the nest mound was between three pine tree trunks and measured 90 × 80 × 40 cm high and was composed of grass stems, leaves, pine needles, twigs, and fern fronds. Inside the nest were a total of 17 eggs (12 banded) at a depth of 14 cm. Eggs from this nest were collected by ARCCAR staff for artificial incubation and 12 of 17 eggs hatched on 10 September.

The other nest measured 100 × 83 × 43 cm high and was 1 m from the base of a 4.5-m high pine tree. The main nest material was pine needles but also included grass stems and leaves from bamboo and herbaceous vegetation. Two nests were observed at this same site in 1997 from which eggs had previously been collected by ARCCAR. One nest was at the same location as the 1999 nest, and the other was on a nearby low pine ridge and was qualitatively similar in terms of nest size and position. Eggs from the 1999 nest were left to incubate naturally, but none of the 19 eggs hatched (all eggs were banded), presumably as a result of low incubation temperature.

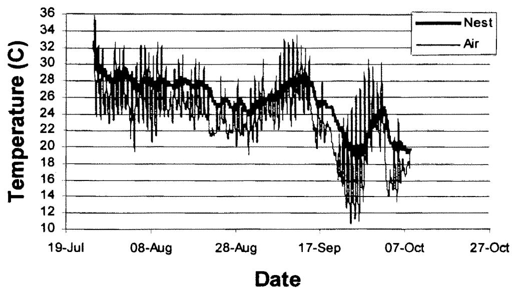

FIG. 2. Nest egg cavity and air temperature measured at the Zhuangtou nest in 1999.

Aside from vegetated hillsides, local farmers reported that alligators use small islands for nesting. Like the vegetated hillsides, small islands set in agricultural ponds receive relatively little human use and offer terrestrial refuges where females can build nests.

Nest cavity temperature was measured at the Zhuangtou nest from 25 July through early-October using a datalogger (Fig. 2). Temperature recordings indicate that incubation temperatures were low, but in the viable range, for the first month. After mid-August, egg temperatures started to dip down into the lethal range for embryos (< 26°C) in association with a period of rain. During the second half of September, after the nest should have hatched under normal circumstances, air and nest temperatures plummeted (Fig. 2). Low temperatures may be the result of the slow decomposition rates of the primary nest material (pine needles; Gholz et al., 1985).

Clutch and Egg Size.—The two 1999 nests we observed had 17 and 19 eggs. Chen (1985) reported a range of clutch sizes of 7–52, and Huang (1983) gave a range 8–41 for the Shanghai Zoo. Mean clutch size in captivity (ARCCAR 1983–1997) was 26.4 for alligators collected from the wild (F_1) and 25.8 for F_2 alligators that were born in captivity (Table 1) and ranged from 15–49 (Wan et al., 1998). Mean clutch size at the Yinjian breeding center from 1984–1991 was 23.1 (Webb and Vernon, 1992), and one female (1.38 m TL, 9.8 kg) produced an average of 24 eggs during each of four years (Lu et al., 1988). The mean clutch size of 10 nests from this same breeding center was reported to be 23.6 by Wang and Huang (1997).

TABLE 1. Production of eggs and mean clutch size for F_1 and F_2 alligators at ARCCAR from 1983–1997 (from Wan et al., 1998).

Year	F_1 nests	F_1 eggs	F_1 mean clutch	F_2 nests	F_2 eggs	F_2 mean clutch
1983	12	264	22.0			
1984	20	501	25.1			
1985	30	809	27.0			
1986	29	801	27.6			
1987	37	1045	28.2			
1988	41	1194	29.1	1	25	25.0
1989	29	812	28.0	5	143	28.6
1990	30	833	27.8	4	109	27.3
1991	26	682	26.2	9	219	24.3
1992	32	881	27.5	10	264	26.4
1993	30	853	28.4	12	353	29.4
1994	39	950	24.4	30	709	23.6
1995	23	447	19.4	22	540	24.5
1996	23	521	22.7	40	919	23.0
1997	28	921	32.9	62	1610	26.0
Mean			26.4			25.8

TABLE 2. Number of nests and eggs collected from the wild alligator population in the NCAR (from Wan et al, 1998; and ARCCAR pers. comm.

Year	# nests	# eggs collected	Mean/nest
1982	10	224	22.4
1983			
1984	16	154	9.6
1985	4	80	20.0
1986	7	104	14.9
1987	5	99	19.8
1988	5	64	12.8
1989	1	19	19.0
1990	1	22	22.0
1991			
1992	1	23	23.0
1993			
1994	4	84	21.0
1995	2	41	20.5
1996	1	22	22.0
1997	3	60	20.0
1998	0	0	
1999	4	69	17.3
Mean			16.6

The mean clutch size from collected wild nests ($N = 64$) in the NCAR reserve was 16.6 (Table 2); however if the 1984 data are excluded (because of unusually low clutch size reported that may represent just viable eggs), mean clutch size increases to 19.0. The average clutch size of 11 wild nests (left in situ) found in Jinxiang County between 1984 and 1989 was 22.9. Combining these data, the overall mean of wild nests in the NCAR was 19.7.

For the two wild nests in 1999, mean egg mass was 42.8 g, and mean egg dimensions were 6.08 × 3.36 cm. From a sample of seven inviable eggs measured by us at ARCCAR in August 1997 (including a range of large and small eggs), mean dimensions were 5.80 × 3.58 cm, and mean mass was 43.9 g (range 32–65 g). Mean egg mass has been reported at 44.6 g (Huang, 1982), 45 g (Zhu, 1997; mean dimensions 3.5 × 6 cm), and 42.1 g (Chen, 1985; mean dimensions 3.50 × 5.97 cm, $N = 178$). Huang (1983) gave a range of values for egg measurements from the Shanghai Zoo (length: 56–61 mm; width: 34–38 mm; mass: 33–48.7 g).

The total mass of the two wild clutches we measured in Anhui in 1999 was 808 and 734 g. Based on an average clutch size of 19.7 and 45.0 g mean egg mass, the estimated mean clutch mass for wild females is 887 g. Assuming an average adult female size of 130 cm TL and 6.9 kg, the mean reproductive investment (clutch mass/female mass × 100) is 12.8%.

Hatchlings average 20–21 cm TL and weigh 30 g (Huang, 1982; Chen, 1991). Zhu (1997) reported mean length and weight of neonates are 22.5 cm and 28.9 g.

Nesting Levels.—The number of annual nests has declined sharply, even during the last 10 yr. This is reflected in both the number of eggs collected by ARCCAR from wild nests (Table 2) as well as the total number of nests reported in the wild (Thorbjarnarson and Wang, 1999). In 1998, there were no nests reported in the wild, but in 1999 there were four, all but one of which was collected for incubation at ARCCAR.

Conservation Implications.—The numbers of American alligators were reduced by the 1960s because of commercial hunting, but large areas of their habitat remained intact and following protection populations quickly rebounded (Joanen et al., 1997). Chinese alligators have reproduced well in captivity , and now there is a large captive population, primarily in China (Wan et al., 1998) but also at a number of zoos around the world (Behler, 1995). However, the lack of habitat and enormous human use pressures on the areas where alligators are now found has limited any recovery of the wild population (Thorbjarnarson and Wang, 1999).

Alligators are now found largely in two kinds of areas; valley bottoms that are intensely cultivated, primarily with rice, or in ponds in low hills at the ecotone between rice cultivation and pine plantations (Thorbjarnarson and Wang, 1999). Nesting is limited to small patches of vegetation where there is relatively little human disturbance, principally on vegetated hillsides or small islands. The vegetated hillsides are typically poor soil areas where food crops cannot be grown and where trees, mostly pines, have been planted. Ponds in these areas are biologically unproductive and provide poor habitat for adults alligators. Because of the unsuitability of the soil for burrowing, adult alligators in these areas may have to travel overland to reach their winter burrows.

None of the existing designated sites for alligator conservation offer the potential for the long-term maintenance of viable alligator populations (JT and XW, pers. obs). The last hope for retaining viable groups of Chinese alligators in the wild is to locate areas of suitable wetland habitat where captive-reared individuals from the breeding centers can be released. To be successful, the reintroduction program must be a multidisciplinary effort, involving social and economic considerations for the local communities as well as biological criteria for habitat quantity and quality , genetic and demographic features of the newly established populations. Although alligators are very adaptable in terms of their nesting requirements, the evaluation of sites for their potential to establish alligator populations needs to address the question of suitable nesting habitat as one of the primary considerations. Our study suggests that hillside ponds in pine plantations, aside from offering a poor aquatic habitat for the alligators, may also be unsuitable for alligator nesting and should not be considered for alligator reintroduction programs.

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Dietary Habits and Reproductive Biology of Typhlopid Snakes from Southern Africa

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ABSTRACT.—**We studied diets, sexual dimorphism, and reproductive biology of six taxa of poorly known African blindsnakes (*Rhinotyphlops lalandei, Rana mucruso, Rana schlegelii petersii, Rana schlegelii schlegelii, Typhlops bibronii,* and *Typhlops fornasinii*) by dissection of 649 preserved museum specimens. Females matured at larger sizes than conspecific males, and the degree of sexual size dimorphism was most extreme in the large heavy-bodied *R. s. schlegelii*. Reproduction was highly seasonal in temperate-zone *T. bibronii* and *R. lalandei*, with vitellogenesis in spring, oviposition in late summer, and hatching in autumn. All species were oviparous, with mean clutch sizes of four to 25 eggs. Clutch sizes were strongly correlated with maternal body size in *T. bibronii* and *R. lalandei*. African *Rhinotyphlops* and *Typhlops* fed mainly on larvae and pupae of ants (88–97% of prey items for five of the six species), but adult termites were also eaten. Only *R. mucruso* fed on termites to a significant degree (38% of prey items). All species fed infrequently on large numbers of small prey (mean number of prey per stomach = 80.4, range 1–927 items). Remarkably, although they attain almost 1 m in length, the world's largest blindsnakes, *R. schlegelii* and *R. mucruso*, fed on relatively small termites and ant brood. Collectively, our data show that typhlopid snakes have remarkably conservative diets, supporting the idea that the peculiar skull morphology of the Typhlopidae is an adaptation to feeding on small, clumped, immobile prey. Our findings support the hypothesis that the binge-feeding strategy of typhlopid snakes (rapid ingestion of prey, low feeding frequency, and large meal size) evolved to minimize the time spent inside ant nests and, thus, to reduce the risk of prey-inflicted injuries.**

Modern snakes (clade Macrostomata) are characterized by their ability to subdue and swallow large prey (Rieppel, 1988). Not surprisingly, dietary demands are believed to have been crucial in the evolutionary origin and radiation of snakes (Gans, 1961; Rieppel, 1980; Greene, 1983; Lee et al., 1999). Evolutionary changes that increased lower jaw mobility allowed the first snakes to ingest larger prey than their lizard ancestors, which in turn facilitated a fundamental shift in foraging mode from frequent feeding on relatively small prey, to infrequent feeding on relatively large prey (Greene, 1983). Although many recently evolved ophidian clades display the latter "snake-like" foraging mode, members of one basal snake clade—the Scolecophidia (wormlike burrowing snakes from three families)—display a very different feeding strategy: infrequent ingestion of huge numbers of tiny prey (Thomas, 1985; Webb and Shine, 1993a; Webb et al., 2000a).

What factors have favored the evolution of microphagy within the Scolecophidia? Greene

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