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THE BEHAVIOR OF JUVENILE *ALLIGATOR MISSISSIPPIENSIS* AND *CAIMAN CROCODILUS* EXPOSED TO LOW TEMPERATURE.—Most studies of crocodilian thermal biology have concentrated on thermal preferences (Colbert et al., 1946; Diefenbach, 1975; Johnson et al., 1978), upper thermal tolerances (Colbert et al., 1946), and the physiology (Smith, 1979) and behavior of thermoregulation (Fish and Cosgrove, 1987; Lang, 1979; Spotila, 1974). Many of these have been concerned with the responses of animals to heating trials (Smith, 1976; Smith and Adams, 1978; Smith et al., 1984) or in gradients where only the upper range of body temperatures selected in the wild are represented (Lang, 1987). Few studies have concentrated on the responses to low temperatures, and these have focused on the American alligator, *Alligator mississippiensis*. Winter behavior and activity patterns of adult alligators have been examined in South Carolina (Brisbin et al., 1982), North Carolina (Hagan et al., 1983) and Louisiana (Chabreck, 1965). Adult alligators (> 1.8 m) bask on warmer winter days and, in response to freezing weather exhibit a submerged breathing posture (Smith, 1979) in which the tip of their snout is kept out of the water while the rest of the body is extended into deeper/warmer water (Hagan et al., 1983). Hence, adult alligators survive freezing conditions by maintaining air holes in the ice of frozen ponds, rather than by staying submerged under the ice.

Few observations have been made on the winter activity of juvenile alligators, particularly those < 1 m, due to the difficulty in locating them. It has been suggested that juvenile alligators overwinter in dens with adults (Kellogg, 1929; McIlhenny, 1935); however, appropriate den sites are not always available (Murphy, 1981). Because small alligators are likely to be frozen in or under the ice, they may not be able to exhibit the same behavior as adults (i.e., submerged breathing) under freezing conditions. The ability of small alligators to behaviorally adjust to periods of low temperature may be an important factor contributing to the alligator's survival in the northern portion of the range.

In addition to the effect of body size on thermal behavior of crocodilians, there may be behavioral and physiological differences between species with temperate and tropical ranges (Lang, 1979, 1981). Lang (1979, 1987) has suggested that crocodilians living in thermally equitable environments (i.e., the tropics) are thermoconformers while those which occur in variable environments (temperate areas) are thermoregulators. If these differences are species specific (rather than simply related to the animal's current thermal environment), then a species with a natural tropical distribution (such as *Caiman crocodilus*) should show different responses to low temperatures than a species like the American alligator that has a temperate distribution.

Since at least the 1950s, *C. crocodilus* have been released in canals in parts of south Florida (Wilson and Porras, 1983). The largest known breeding population of caimans is at the Homestead Air Force Base (HAFB), Homestead, Dade County, Florida (Ellis, 1980; pers. obs.). In addition, there are probably breeding populations in western Dade County (J. Wasilewski, pers. comm.), and both juvenile and adult caimans have been captured in Ft. Lauderdale, Broward County (pers. obs.). Because caimans are an exotic species, there is some interest in determining the potential for caimans to colonize more northern counties in Florida. The natural tropical/subtropical distribution of *C. crocodilus* suggests that low temperatures (< 15 C) may be a factor that will limit how far north in Florida breeding populations of caimans can occur. The purpose of this study was to: 1) determine the ability of small alligators to survive freezing conditions; and 2) compare the responses of small alligators (warm-temperate) and caimans (tropical) to cold weather.

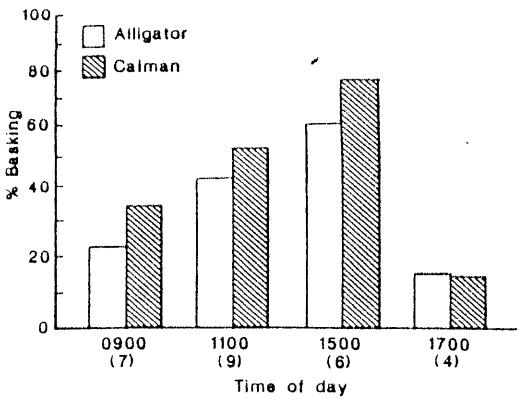

Fig. 1. The percentage of alligators and caimans basking at different times, pooled over all observation periods between 15 Nov. 1985 and 2 Dec. 1985 (number of days observations were made).

Materials and methods.—Five *Caiman crocodilus* (90–2035 g; ±SD = 535.1 ± 839.0 g, 37–80 cm TL; ±SD = 46.7 ± 18.7 cm) were collected from the HAFB in Dec. 1984. They were maintained in a 130 cm × 80 cm cattle tank at 25–30 C until Oct. 1985 when they were moved to a tank in an unheated building at the Savannah River Ecology Laboratory (SREL) in Aiken, South Carolina, where air temperatures fluctuated between 15–30 C and water temperatures between 18–25 C. Nine *A. mississippiensis* (58–552 g, ±SD = 290.8 ± 156.9, 28–56 cm TL, ±SD = 47.7 ± 11.4 cm) were obtained either from Par Pond, Savannah River Plant, Aiken County, South Carolina (five), or from Kiawah Island, Charleston County, South Carolina in mid-Oct. 1985 and housed in tanks in the unheated building until 14 Nov. 1985. All animals were fed chicken and beef heart twice a week and had access to land, water and a heat lamp.

On 14 Nov. 1985, all animals were placed in a 10 × 15 m clay-lined outdoor pond at SREL. Maximum pond depth was 150 cm. Ample shoreline was available for basking. A 1 × 0.75 m basking platform was placed in the middle of the pond to act as a supplemental basking site.

Air, water and substrate temperatures were recorded at the pond's edge every other day at 0900, 1100, 1500, 1700 h during Nov.–Dec., and every third day at 0900, 1100, 1500 h in Jan.–Feb. Maximum and minimum air and water temperatures were recorded daily at 0900 h (Weksler max-min thermometer, ±0.5 C). Air temperatures ranged from −7–33 C and water temperatures from 0–25 C. December and Jan. were the coldest months (mean temperature for each month 7.4 C) and Nov. the warmest (mean temperature 18.6 C). Animals were recorded as basking (on shore or in shallow water with part of the body out of water) or not basking (all other positions). Cloacal temperatures were taken on two occasions using a quick reading cloacal thermometer (Miller and Webber, Inc.).

Results.—During mid–late Nov., alligators and caimans were often observed basking from mid-morning through the afternoon (Fig. 1). A greater percentage of caimans were observed basking than alligators at 0900, 1100, 1500, but this difference was significant only at 1500 h (one tailed Wilcoxon signed rank test, $P < 0.05$, Fig. 1). Both species basked more often during the mid-afternoon (i.e., 1500 h). No negative interactions (i.e., fighting or chasing) were observed within or between species; in fact, caimans and alligators were often observed basking on top of one another.

In early Dec. air temperatures dropped rapidly. At 2030 h on 2 Dec., air temperature was 6 C and water temperature 15.6 C. All animals were submerged at this time. A minimum air temperature of 2.2 C was recorded at 0900 h the next morning. Minimum water temperatures ranged from 12.2 C (shallow water) to 12.9 C (deep water).

Three of the five caimans died as a result of exposure. One caiman was found dead on the bank at 0900 h on 3 Dec. Three were found in shallow water and were lethargic but exhibited strong gape response. The fourth was found in 8 cm of water in a hole 5 m from the pond. This animal's cloacal temperature was 8.8 C, it had no righting response, and died 4 d later of pneumonia (E. Howerth, pers. comm.). Another caiman died of the same cause 7 d later. The two surviving caimans were removed from the pond. One exhibited signs of pneumonia but recovered within a week. The other did not exhibit signs of infection. Neither animal was returned to the pond. In contrast, all of the alligators were in the deepest portion of the pond, and none died. Location (deep vs shallow water) of the two species on 3 Dec. was significantly different (Fisher's exact test, $P < 0.01$) as was the proportion of each species surviving the first cold front (one tailed Fisher's exact test, $P < 0.05$).

On the night of 28 Jan., air temperature reached a low of −7 C, causing the formation

of 2.5 cm of surface ice on the pond. Water temperatures ranged from 0–4.5 C at 0800 h. Three alligators were frozen to a fence which ran through the center of the pond; their bodies were perpendicular to the surface with their nostrils above the ice. Two exhibited a submerged breathing posture (Smith, 1979) with their nostrils exposed and four, including the two smallest animals, both less than 40 cm (hatchlings) were frozen under the ice. Cloacal temperatures (Tc) recorded from seven animals ranged from 0–4.4 C (±SD = 1.0 C ± 1.6). The two smallest animals were observed pushing on the ice, apparently trying to break through to breathe. Both animals subsequently died (both had Tc of 0.0 C); apparently they drowned. The other animals were lethargic and appeared bloated. However, none of the larger (>50 cm) animals died, even though three of them were trapped underneath the ice for at least 12 h.

A layer of ice remained on the pond until the morning of 30 Jan. As the ice melted the surviving seven alligators began to move to shore to bask. All but one animal were basking by 1300 h that day (air temperature 12.4 C), and continued to bask until 1700 h when the air temperature dropped to 7.0 C. The next day they again basked for most of the day. By the third day after the ice melted they returned to a more normal basking behavior, basking mainly in the afternoon on bright sunny days.

Discussion.—Hatchling alligators in this study did not maintain air holes, and were therefore trapped under the ice and drowned. However, when the larger (>50 cm) alligators maintained air holes, they survived temperatures as low as 0.4 C. Hagan et al. (1983) reported the survival of an adult radio-collared alligator in 2.0 C water in North Carolina. There is also a report of a 0.5 m alligator surviving (and growing to 1.25 m) six winters in Pennsylvania (Barton, 1955) where the mean temperature for the coldest months varied from −5.5–1.3 C. Clarke (1953). reported a 0.5 m alligator surviving three winters in Virginia where an average winter has 40 d of minimum temperature at or below freezing. Hence, it may not only be the physiological tolerance to low temperature per se that limits the alligator's distribution northward, but also an inability of hatchlings and yearlings to survive even short periods of ice formation. Winter freezes lasting several days or more may also act as a means of population regulation by killing an entire cohort of young. However in some situations juvenile alligators remain in close association with adults at least through the first winter (Dietz, 1979) and in some cases for up to 18 mo (Chabreck, 1965). Hence, it may be possible that, in some areas, the juveniles survive severe cold fronts by overwintering in dens with adults, or by using air holes maintained by adults.

There were noticeable differences in both the basking patterns and the behavior of caimans and alligators when exposed to low temperatures. These differences support the suggestion by Lang (1979, 1981, 1987) that there may be differences in thermal behavior between species that have temperate and tropical ranges.

In this study, the caimans were observed basking more often than the alligators in the afternoon, possibly as a result of differences in heating rates, i.e., the caimans might heat slower and therefore require longer basking to reach the same temperature. It is also possible that even by basking throughout the afternoon, the caimans were not able to reach a suitable temperature to resist infection. The immune response is often reduced in reptiles at lower temperatures (Cooper et al., 1985). *Crocodylus acutus* and *C. niloticus* also die when exposed to low temperatures (Barbour, 1923; Coulson and Hernandez, 1964), and the historical distribution of *C. acutus* in Florida reflects this intolerance to low temperature, following very closely the isocline for the mean low temperature (18 C) in Jan. (Kushlan and Mazzotti, 1989). Caimans in the United States may also be limited in distribution by an intolerance to low temperatures.

The ability to withstand low temperature has both physiological and behavioral components. We do not know if the caimans would have survived the first cold snap if they had remained in the deepest portion of the pond as the alligators did. All crocodilians use water as a means of thermoregulating, but the patterns of movement differ between species. Although *A. mississippiensis* move onto land to bask during the day, *C. porosus* under similar conditions remain submerged during the day to avoid rapid heating and move onto land at night (Lang, 1987). Alligators are observed basking in the winter only on warm (air temperature >10 C) sunny days, while tropical species may continue to bask during cool weather (air temperature <10 C). Neill (1971) observed a captive *C. acutus* in Palm Beach County, Florida attempting unsuccessfully to raise its body temperature by basking

during cool winter weather: "On a cold day in winter, the reptile would move into a patch of sunlight that struck the pool. It would even move out of the water to follow the patch of sunlight, rapidly becoming chilled and numbed by the cold substratum and air." Neill pointed out that this behavior may be appropriate in the tropics where morning temperatures rapidly increase, but can be lethal in temperate areas. The caimans in this study may have moved into the shallow water and onto shore early in the morning to bask, and were unable to raise their body temperature. They may also have been searching for subterranean dens or sites for burrowing to escape from the low temperatures. *Crocodylus niloticus* and *C. sinensis* are known to burrow in response to low temperatures. If unable to burrow *C. niloticus* will die when exposed to freezing temperatures (Pooley, 1969). *Caiman crocodilus* are also known to burrow in litter or mud as refuge from drought and extreme temperatures (Staton and Dixon, 1975; Gorzula, 1978; Lang, 1987), so it is not unreasonable to assume that this behavior could also be exhibited in response to low temperatures, and that if allowed to burrow, caimans could survive even lower temperatures than reported in this study.

That the caimans in this study could not withstand low temperatures, and that two of five caimans collected from the HAFB in 1988 also died after 6 h exposure to 10 C (pers. obs.) suggest that: 1) the caimans currently established in south Florida will probably not move north into areas that experience routine freezes; however, the possibility of the introduction of more cold tolerant populations exists; and 2) there may be differences in thermal tolerances and thermal strategies of alligators and caimans. However, because of the unknown origin of the caimans from HAFB and the wide distribution of caimans in South America, further study is needed to determine whether the difference observed between the alligators and caimans in this study (i.e., caimans basking more, moving into shallow water instead of staying in the deeper/warmer portion of the pond, and having a low tolerance to temperatures <10 C) are species-specific or whether responses vary between populations exposed to different environmental regimes.

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