

BEHAVIORAL THERMOREGULATION OF SMALL AMERICAN ALLIGATORS IN WATER: POSTURAL CHANGES IN RELATION TO THE THERMAL ENVIRONMENT.—Crocodylians can thermoregulate by alternating between terrestrial and aquatic environments. Water with its high thermal conductance and heat capacity can be used as an effective heat sink or thermally stable environment by crocodylians (Spotila et al., 1972; Spotila, 1974; Diefenbach, 1975; Johnson et al., 1976; Lang, 1976; Smith, 1979). Once immersed in water, crocodylians can behaviorally thermoregulate by varying the position of the body with respect to the water surface (Johnson, 1973; Smith, 1975, 1979).

The purpose of this study was to examine the behavioral mechanisms of thermoregulation of small alligators when floating in water. We hypothesized that the floating posture and body temperature of the alligators would be influenced by the water temperature and radiant heat exposure.

Methods.—Five juvenile alligators (*Alligator mississippiensis*) were obtained from the Rockefeller Wildlife Refuge in Grand Chenier, Louisiana. They ranged in mass from 315–990 g (mean: 611 g) and snout–vent length from 26.9–36.1 cm (mean: 31.2 cm). During the 2 mo experimental period, the alligators were maintained indoors in a 1.22 × 0.88 m enclosure, which included an artificial pond (0.86 × 0.7 × 0.2 m). A black slate basking platform was illuminated with a 100 W lightbulb. Two weeks prior to experimentation, the 100 W light was removed and a 250 W IR heat lamp was placed over the artificial pond. The IR lamp was on for 2 h each day. The ambient air temperature was maintained at 22–25 C and the light regime was constant. The alligators were fed weekly on a diet of tuna and chicken.

Experiments were conducted in a thermally insulated, 120 liter aquarium of the dimensions 39.7 × 75.5 × 40.0 cm. One 75.5 × 40.0 cm glass wall of the aquarium was left uninsulated for observations of the experimental animal. Water height was adjusted in the aquarium so

that the animal could float with its head above the water without its feet touching the bottom. Water temperature (T_w) was monitored with a thermistor probe located in a corner of the aquarium 20 cm above the floor and connected to a Yellow Springs Instruments Tele-Thermometer Model-42SC. T_a was maintained within ± 1 C by circulating the aquarium water through a copper coil emersed in a water bath. Water was drawn from the aquarium with a Beckett N-100 submersible pump, which circulated the water at a rate of 38 liter/h. A 250 W IR heat lamp was situated 33 cm above the surface of the water.

We viewed the animal through the glass wall of the aquarium with a video camera connected to a monitor situated in an adjoining room. Illumination was provided from two 93 W incandescent lights located in front of the aquarium.

The posture of each alligator floating at the surface of the water was examined at water temperatures of 15, 25, and 35 C with or without exposure to IR. Animals were placed individually in the aquarium for 2 h. The alligator was allowed to equilibrate to the environmental conditions for 1 h. During the second hour, the postural angle of the trunk of the alligator's body to the water surface was measured with a protractor in degrees from the video monitor. Measurements were within $\pm 0.5^\circ$. Data were collected at 10 min intervals. At the end of the experimental period, the alligator was removed from the aquarium and the cloacal temperature (T_b) was recorded within 1 min with a Schulteis Quick Reading Thermometer.

Each alligator was tested only once a day and never on the same day as feeding. Additionally, individuals were randomly assigned to the various combinations of T_a and IR to avoid experimental effects.

Data were analyzed using 2-Way Analysis of Variance (ANOVA). Individual contrasts were made using Student-Newman-Keuls test (SNK) and differences from zero were made using t-test. Variation about means was expressed as \pm one standard error (SE).

Results.—Upon introduction into the aquarium, the alligators were observed to float with their head at the surface. The trunk and tail were inclined at various angles to the water sur-

TABLE 1. MEANS (\pm SE) OF ORIENTATION ANGLES (DEG) AND $T_b - T_a$ (C) FOR DIFFERING IR CONDITIONS

	IR	Temperature (C)		
		15	25	35
Angle	On	3.9 (2.1)	9.0 (1.4)	11.4 (7.0)
	Off	44.3 (3.0)	27.7 (2.7)	15.9 (2.8)
$T_b - T_a$	On	0.4 (0.2)	0.4 (0.1)	0.1 (0.1)
	off	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

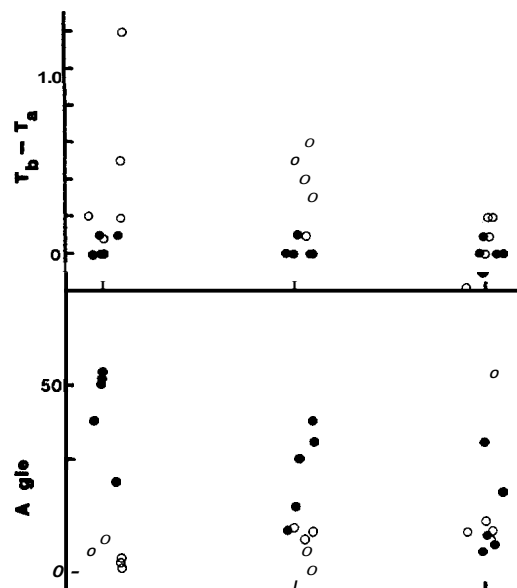
face depending on the environmental conditions. The alligators were capable of changing the inclination of the body without movement of legs or the tail. It was assumed that the degree of buoyancy was controlled by changes in the lung volume, since *Caiman* can change inclination while floating by active ventilation (Gans and Clark, 1976).

Using ANOVA, we found that the interaction of T_a and IR as factors affecting the postural angle was statistically significant ($P < 0.001$), but this interaction did not significantly affect the temperature differential (Table 1). IR was statistically significant in its effect on postural angle ($P < 0.001$) and temperature differential ($P < 0.002$). No significant effects were noted for T_a (Fig. 1).

Without exposure to IR, T_b approximated T_a over the range of T_a (Fig. 1), so that $T_b - T_a$ was not significantly different from zero (t-test). The mean postural angle in degrees assumed by the alligators decreased steadily from 44.3 ± 3.0 – 15.9 ± 2.8 as T_a increased from 15–35 C without IR. At $T_a = 35$ C, the alligators spent 28.6% of the time with their dorsum oriented horizontal to the water surface.

Supplemental exposure to IR had a pronounced effect on the orientation of alligators to the surface of the water, particularly at low T_a (Fig. 1). At 15 C, the alligators spent 80% of the time oriented horizontally with their dorsum either at or above the water surface, resulting in a mean postural angle of 3.9 ± 2.1 degrees. T_b was found to increase by 0.4 C above T_a .

Alligators exposed to IR at 25 and 35 C demonstrated a slight but non-significant decrease for both postural angle and temperature differential compared to 15 C (SNK) (Fig. 1). The mean postural angle increased to 9.0 ± 1.4 and 11.4 ± 7.0 at 25 and 35 C, respectively. The temperature differential remained high at 25 C with a mean value of 0.4 ± 0.1 , but was not



significantly different from zero at 35 C (t-test). This appeared to be associated with a decrease in the amount of time at the surface for alligators at 35 C with IR.

Alligators floating in water at T_a 's of 15 and 25 C demonstrated a significant postural orientation toward the surface when exposed to radiant heat. This resulted in a significant increase in body temperature above ambient water temperature ($P < 0.05$; SNK). The alligators were thus able to bask at the water surface by regulating the inclination of the body. The orientation of the alligator during aquatic basking was similar to the high float previously described by Smith (1975, 1979). At the two lower temperatures without IR radiation, the postural angle was large, so that only the top of the head was exposed. Without the additional heat input, T_b 's were essentially equal to T_a .

Discussion.—Johnson (1973) and Smith (1975, 1979) reported that crocodylians floated in water at different postural orientations as a behavioral mechanism for thermoregulation. Spotila (1974) found that alligators in water regulated the

amount of heat gain from solar radiation by changing the amount of dorsal surface exposed to the sun. An alligator was thus able to maintain body temperature near preferred levels over an extended period (Spotila, 1974). Small *Caiman* can maintain a body temperature 4 C above ambient water temperature when the dorsum was exposed to a heat source (Diefenbach, 1975). Such a response is considered to be facilitated by the differential distribution of blood flow through the body (Griggs and Alchin, 1976; Drane et al., 1977; Turner and Tracy, 1983; Smith et al., 1984).

At 35 C, the alligators in the present study displayed a reversal from the general trend of postural orientation exhibited at 15 and 25 C. The alligators moved away from the surface when exposed to supplemental IR, but moved toward the surface without IR. The observed behavior of the alligators at 35 C was assumed to be a response of the animals to possible overheating. Basking at such a high temperature would result in the incurrence of a high endogenous heat load which would be detrimental. The lethal temperature for alligators has been reported as 38–39 C, while the preferred temperature was 32–35 C (Colbert et al., 1946). Thus it appears that the alligators would avoid exposure to supplemental IR by controlling postural orientation to take advantage of the thermal stability and thermal gradient of the water and maintain their preferred temperature. Without supplemental IR, the alligators floating at the surface could utilize the cooler air and surface water to maintain T_b within the range of the preferred temperature.

A considerable amount of time is spent in the water by these amphibious reptiles so that the ability to control aquatic thermoregulation by behavioral mechanisms has adaptive benefits. Young crocodilians have been reported to remain in the water and not bask ashore (Diefenbach, 1975). Additionally, crocodilians must remain motionless at the surface for extended periods when waiting for prey (Johnson, 1973; Pooley and Gans, 1976; Schaller and Crawshaw, 1982) and therefore are unable to utilize shuttling as a means of thermoregulating. Postural changes when floating could be important in the thermoregulation of these ambush predators. Since the aquatic environment is an integral part of the ecology of crocodilians, the control of aquatic basking by postural orientation can act as an important behavioral mechanism for thermal balance.

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LITERATURE CITED

- COLBERT, E. H., R. B. COWLES AND C. M. BOGERT. 1946. Temperature tolerances in the American alligator and their bearing on the habits, evolution, and extinction of the dinosaurs. *Bull. Amer. Mus. Nat. Hist.* 86:327–374.
- DIEFENBACH, C. O. DA C. 1975. Thermal preferences and thermoregulation in *Caiman crocodilus*. *Copeia* 1975:530–540.
- DRANE, C. R., G. J. WEBB AND P. HEUER. 1977. Patterns of heating in the body trunk and tail of *Crocodylus porosus*. *J. Thermal Biol.* 2:127–130.
- GANS, C., AND B. CLARK. 1976. Studies on ventilation of *Caiman crocodilus* (Crocodilia: Reptilia). *Resp. Physiol.* 26:285–301.
- GRIGGS, G. C., AND J. ALCHIN. 1976. The role of the cardiovascular system in thermoregulation of *Crocodylus johnstoni*. *Physiol. Zool.* 49:24–36.
- JOHNSON, C. R. 1973. Behavior of the Australian crocodiles, *Crocodylus johnstoni* and *C. porosus*. *Zool. J. Linn. Soc.* 52:315–336.
- , G. J. W. WEBB AND C. TANNER. 1976. Thermoregulation in crocodilians. 11. A telemetric study of body temperature in the Australian crocodiles, *Crocodylus johnstoni* and *Crocodylus porosus*. *Comp. Biochem. Physiol.* 53:143–146.
- LANG, J. W. 1976. Amphibious behavior of *Alligator mississippiensis*: roles of a circadian rhythm and light. *Science* 191:575–577.
- POOLEY, A., AND C. GANS. 1976. The Nile crocodile. *Sci. Amer.* 234:114–124.
- SCHALLER, G. B., AND P. G. CRAWSHAW, JR. 1982. Fishing behavior of Paraguayan caiman (*Caiman crocodilus*). *Copeia* 1982:66–72.
- SMITH, E. N. 1975. Thermoregulation of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* 48:177–194.
- . 1979. Behavioral and physiological thermoregulation of crocodilians. *Amer. Zool.* 19:239–247.
- , E. A. STANDORA AND S. L. ROBERTSON. 1984. Physiological thermoregulation of mature alligators. *Comp. Biochem. Physiol.* 77:189–193.
- SPOTILA, J. R. 1974. Behavioral thermoregulation of the American alligator, p. 322–324. *In: Thermal ecology*. J. W. Gibbon and R. R. Sharitz (eds.). U.S. Atomic Energy Commission Symposium Series CONF-730505, Oak Ridge, Tennessee.
- , O. H. SOULE AND D. M. GATES. 1972. The

biophysical ecology of the alligator: heat energy budget and climate space. *Ecology* 53:1094-1102.
TURNER, J. S., AND C. R. TRACY. 1983. Blood flow to appendages and the control of heat exchange in American alligators. *Physiol. Zool.* 56:195-200.

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