

Body Temperatures and Behavior of American Alligators during Cold Winter Weather

I. LEHR BRISBIN, JR., EDWARD A. STANDORA
and MICHAEL J. VARGO

Savannah River Ecology Laboratory, P. O. Drawer E, Aiken, South Carolina 29801

ABSTRACT: Data from two large (188 and 135 kg) male alligators (*Alligator mississippiensis*) indicated that 4-5 C seemed to be the lowest body temperatures that they could endure with subsequent recovery. Although one animal in shallow water managed to keep a breathing hole open for several days, in ice that was 1.5 cm thick, it later died following a decrease of its body temperature to 4.0 C. The second alligator which was located in a deeper portion of the reservoir used both terrestrial and aquatic basking behavior to raise its body temperature and level of activity. Except in the case of basking events, there was no clear evidence of significant elevations of the body temperatures of either the live or dead alligators above those of their adjacent water. When located side-by-side, diurnal cycles of deep body temperatures of both the live animal and the dead animal's carcass were similar, with deep body temperatures exceeding adjacent water temperatures to a maximum extent near dawn and usually falling below water temperatures during the afternoon and early evening hours. The physical properties and thermal inertia of the bodies of such large alligators, when placed in appropriate microclimates, may be sufficient in themselves to explain the general patterns and levels of body temperature changes observed at these low temperatures.

INTRODUCTION

Studies of the body temperatures and thermoregulation of crocodilians suggest that these reptiles are capable of using their large body sizes and resultant thermal inertia to buffer their body temperatures against extreme climatic conditions (Spotila *et al.*, 1972; Smith, 1976, 1979; Terpin, 1976). The Crocodylia, however, are strictly tropical in their distribution, with the exception of the genus *Alligator* (Kellogg, 1929). Field studies of alligators in the northernmost portion of their range therefore provide an opportunity to compare the natural thermoregulatory responses of these reptiles to those of the more common smaller temperate ectotherms. Such information should help to determine the role of low temperatures in limiting the northward distribution of the Crocodylia and the importance of climatic cooling in bringing about the late Cretaceous extinction of many other large-bodied archosaurs. Recent proposals that many dinosaurs may have been homeothermic (Desmond, 1976) might also be supported if it could be demonstrated that present-day crocodilians possess thermoregulatory abilities which promote survival during periods of cold weather.

This paper reports the body temperatures and behavior of two large, free-living, adult male American alligators (*Alligator mississippiensis*) during extremely cold winter weather, including periods of subfreezing temperatures and heavy ice formation. Following the death of one of the animals, an opportunity arose to compare the body temperatures of the dead animal with those of the remaining live one, under similar microclimatic conditions. Such comparisons should help to determine the extent to which physiological or behavioral mechanisms, as opposed to the physical properties of the alligator's body itself, may be responsible for the body temperature patterns observed.

METHODS

Study area. — This study took place in the "Pond B" reservoir of the Par Pond reservoir complex on the U.S. Department of Energy's Savannah River Plant located in Barnwell Co., South Carolina (32° 18' N, 81° 33' W). This region represents the northwesternmost extension of this species' range into this part of the southeast. Average monthly temperatures in this region over the past 10 years have been 4.9, 4.6 and 4.9 C for December, January and February, respectively. Extreme lows for these same months during the same period were -8.9, -15.6 and -10.0 C, respectively. A minimum air temperature of -8.4 C was recorded during the course of the study reported here.

Although the Par Pond reservoir system was constructed to receive heated effluents from nuclear production reactors, the "Pond B" reservoir has been under ambient temperature conditions since 1964. Detailed descriptions of the Par Pond and "Pond B" habitats have been provided elsewhere (Parker *et al.*, 1973; Gibbons and Sharitz, 1974; Domy *et al.*, 1977). Briefly, the "Pond B" reservoir comprises some 110 ha of open water with a maximum depth of approximately 10 m. The northern portion of the reservoir includes several shallow coves with stands of rooted emergent vegetation. In the deeper parts of the lake, the bottom slopes more abruptly from shore and the shoreline is more open, being cleanly edged with old-field vegetation dominated by *Andropogon* sp. Studies of the alligator population occupying the Par Pond reservoir system (Murphy and Brisbin, 1974; Murphy, 1977; Murphy, 1981) have indicated that a breeding population, now heavily weighted towards large adults, has apparently been resident in the area for a considerable time.

Procedures. — On 4 January 1977, a large adult male alligator was discovered lying in shallow water (approximately 90-100 cm) in one of the northern coves of the reservoir. This alligator, which appeared lethargic in the cold water, was captured and outfitted with a radio transmitter collar similar to that described by Standora (1977). This collar contained only a locational transmitter and no temperature-sensing leads were implanted in the animal. Following release, this animal (325 cm total length, 188 kg body weight) moved approximately 200 m to the W and was again found in water of similar depth the following day. This alligator remained in this location with no evidence of movement or other activity until 17 January, when it was again removed from the water for 45 min and a calibrated thermistor probe inserted into the cloaca and/or colon, to a depth of approximately 30 cm, and sutured in place. Because of the alligator's torpid state during this period, the free end of the probe could easily be retrieved and plugged into a YSI model 401 telethermometer, while the investigator was standing on ice that had formed above the alligator. Air, water and deep body (cloacal/colonic) temperatures of this alligator were read periodically (± 0.1 C), until on 20 January it was concluded that the animal had died, since the breathing hole that had earlier been kept open in the ice just above the animal's snout, had frozen over.

On 23 January, a second large adult male alligator was found approximately 1.8 km SE of the first, lying about 2 m offshore in the deeper portion of the lake. This alligator was perpendicular to the shoreline with its head pointed inshore and was lying on top of sloping bottom sediments in water which was approximately 80 cm deep at the head, 150 cm deep at the cloaca and 200 cm deep at the tip of the tail. The steeply sloping bottom on which this alligator was laying led directly to the deepest portion of the reservoir, which was less than 0.5 km from where the alligator was positioned.

This second alligator (277 cm total length, 135 kg body weight) also appeared to be lethargic when it was removed from the water for about 30 min to be outfitted with a radio transmitter collar and a telethermometer probe, as described previously. For the second alligator, the free end of the body temperature probe was attached to a small buoy which floated on the water surface above the alligator. Since no ice formed above this animal, body temperatures were read by retrieving the free end of the probe from a boat and then connecting it to the telethermometer and reading them directly from the

animal below. At the same time, a second probe was lowered and positioned visually using a glass-bottomed viewing box, so as to read the temperature of: (1) the water at the dorsal part of the alligator's thorax; (2) on the dorsal surface of the midpoint of its tail, and (3) in the surface water. The temperatures of the air (at a height of ca. 1 m) and of the shallow water at the nearest point on shore were also recorded.

On 1 February, the carcass of the dead alligator was towed to the location where the second alligator had remained in essentially the same position since it was first fitted with the cloacal temperature probe. The carcass of the dead animal was placed in a position identical to that of the live animal approximately 15 m from the latter. From 1-7 February, the cloacal temperatures of both the live and dead alligators and the air and water temperatures proximate to each, were read from a boat at 4-hr intervals (0400, 0800, 1200, 1600 and 2000 hr), using procedures described above. On 7 February, a warming trend caused the live alligator to emerge from the water to bask and move about the reservoir, and the study was terminated at that time. Body, air and water temperatures for the first and second alligators, while both were located at the deeper water site, were compared using analyses of variance. Statistical computations were performed using the Statistical Analysis System (Barr *et al.*, 1976).

RESULTS

A body temperature of 5.1 C was recorded for the first alligator when it was first discovered lying in shallow water. At that time, the air temperature was 9.0 C and a water temperature of 5.9 C was recorded next to the alligator's body. Over the next 29 days, 18 determinations of air and water temperatures, taken in the mid to late afternoon at the site where the alligator remained lying in shallow water, indicated average air and water temperatures of 5.2 C and 6.1 C, respectively, with minimum values of -3.1 C and 4.8 C, respectively. It is possible, however, that even lower temperatures were reached late at night during this period. By 17 January, a cover of ice, approximately 0.5 cm thick, had formed in the part of the cove where the alligator was located. Three days later, this ice cover had increased to a thickness of about 1.5 cm and easily supported the weight of the investigator above the alligator, while a small hole was broken in the ice near the base of the alligator's tail to retrieve the free leads from the cloacal probe. During this period, a small rounded opening, about 10 cm in diam, remained open in the ice directly above the tip of the alligator's snout, apparently as a result of the occasional efforts of the alligator to raise its snout to the surface to breathe. It appeared that such breathing movements could be undertaken without the necessity of the alligator's raising itself from its resting position on the bottom of the shallow water. With the exception of such presumed breathing movements, there was no evidence of any other movements or activity during this period. On 20 January, the breathing hole above the alligator's snout had frozen over and this suggested that the alligator had died some time during the previous night. Body temperatures were monitored from this individual over the following 11 days until, as explained above, its body was moved and repositioned near that of the second live alligator which had been found in deeper water.

Unlike the first alligator in the shallow water cove, the second alligator in the deep water made minor changes in the position of its body on several occasions between 1-7 February. These movements consisted of either moving towards the shoreline, until at one point the snout was within 1 m of the land, or alternatively, of sliding backwards down the slope of the bottom into deeper water, while still maintaining its body axis perpendicular to and pointed towards shore. These movements of the live alligator could, in the extreme, vary the depth of water in which it was located by more than 1.5 m. Whenever such shifts in the position of the live alligator were observed, the dead alligator was also moved to a corresponding position in deeper or shallower water, respectively.

At 1400 hr on 7 February, with an air temperature of 8.5 C, the live alligator was

observed on shore basking in direct sun, where it remained until 1530 hr, at which time it returned to the water following an inadvertent disturbance by the observers. A reading of deep body temperatures, immediately following this animal's return to the water, indicated that the basking event had raised its temperature to 11.0 C, which was 3.8 C warmer than the water temperature and 3.6 C warmer than that of the dead alligator (Fig. 1). That evening and the following day, the live animal seemed to be more active and swam to several different locations in the general vicinity of the deep water site. Late the following afternoon, this alligator was observed with its head out of the water, suggesting a position of aquatic basking just under the water surface, as described by Smith (1979). Immediately after this head-emergent basking event, the deep body temperature of the live alligator was 7.6 C while that of the dead animal was 6.9 C and the water and air temperatures were 6.9 and 7.2, respectively (Fig. 1, Table 1).

Comparisons of the air, water and deep body temperatures of the live and dead alligators at the deep water site are presented in Table 1. Because of the possibility that some bacterial decay may have occurred in the carcass of the dead alligator, resulting in some increase in its temperature after it was moved to the deeper water site, a two-way analysis of variance was conducted upon the differences between the body temperatures of each animal and the corresponding average temperatures of its adjacent water. The results of these analyses indicated that both the live and dead alligators' body temperatures differed from the temperatures of their adjacent water in the same way ($F = 0.19$; $df = 1,58$; $P = 0.67$) and that both showed only a slight tendency to change the ways in which their body temperatures differed from those of their adjacent water over time, throughout the period of observation ($F = 3.49$; $df = 1,58$; $P = 0.07$). However, the failure of the interaction term to show statistical significance ($F = 0.01$; $df = 1,58$; $P = 0.93$) confirmed that any tendencies of the live and dead alligators to change the relationships between their body temperatures and those of their adjacent water over time were similar for the two animals. Thus, any progressive effect of bacterial decay in the carcass of the dead animal throughout the period of study apparently did not influence the results observed.

A correlation analysis revealed that the deep body temperatures of both the live and dead alligators were more closely correlated with the temperature of the water immediately adjacent to their respective bodies than with the temperatures of either the air, surface water or shallow water ($r = 0.66$ and 0.34 for adjacent water temperatures vs. $r = 0.49$ and 0.30 for surface water temperatures, $r = 0.36$ and 0.27 for shallow water temperatures and $r = -0.11$ and -0.14 for air temperatures, for the live and dead alligators, respectively). Neither of the preceding correlations involving air temperature was statistically significant and only the live alligator's body temperature was significantly correlated with the surface and shallow water temperatures ($P \leq 0.05$ being the criterion for significance of correlation).

Linear regression analyses revealed that the body temperatures of the dead animal were much less closely coupled to the temperature of the adjacent water than were those of the live alligator (Table 2; Fig. 1). In cyclic downswings of body temperatures, those of the live animal were nearly always the first to turn back toward adjacent water temperatures, frequently preceding the same responses by the dead animal by as much as 8 hr (Fig. 1). The general cycle of changes in the body temperatures of both animals suggested a lag of 12-16 hr in the peaking of differences between body and water temperatures, relative to the times of peaking air temperatures which generally occurred in the midafternoon. This produced a pattern of minimal body-water temperature differences near midday and maximal differences at or shortly after midnight, with deep body temperatures themselves also tending to be higher during the night than during the day, except in the case of basking events (Fig. 1).

From 1-7 February, the deep body temperatures of the live alligator averaged 0.21 ± 0.59 (SD) C warmer than its adjacent water, while those of the dead animal averaged

0.29 \pm 0.70 (sd) C warmer. A t-test for paired comparisons indicated that these average difference values did not themselves differ ($t = 0.91$, $df = 30$, $P > 0.05$). The 95% confidence limits about both of these values included zero difference between body and water temperatures.

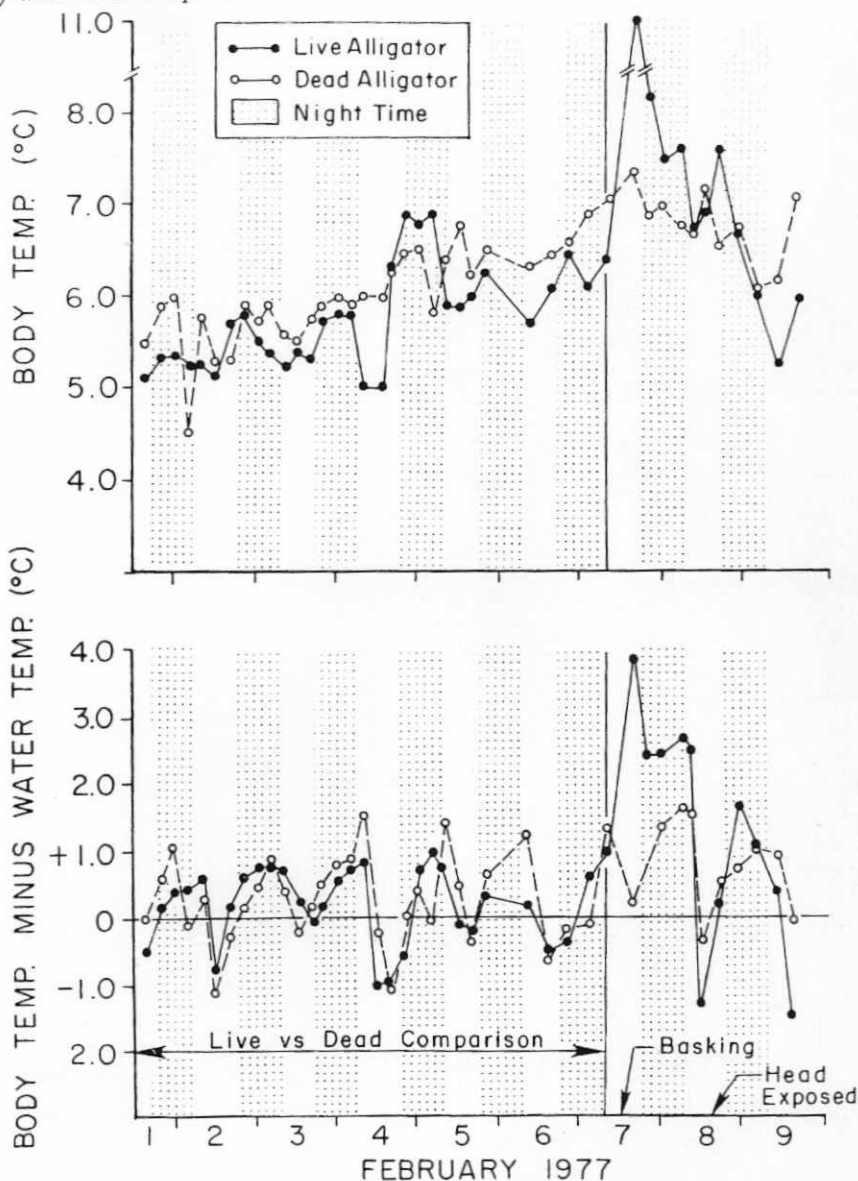


Fig. 1.—Temporal changes in deep body temperatures and in the differences between deep body temperatures and adjacent water temperatures for both a live adult male alligator and the carcass of a recently deceased adult male alligator of comparable size, while located approximately 15 m apart on the bottom of a deep water site of the "Pond B" reservoir of the Savannah River Plant. The double-headed arrow indicates the period over which statistical comparisons of the live vs. dead animal were made as reported in the text and in Tables 1 and 2

TABLE 1.—Comparisons of the deep body, air and water temperatures recorded for a live adult male alligator and the carcass of a recently deceased adult male alligator of comparable size, located approximately 15 m apart on the bottom in a deep water site of the "Pond B" reservoir of the Savannah River Plant, between 1-7 February, 1977

	Air temperature ^a	Surface water temperature ^a	Shallow water temperature ^a	Live alligator		Dead alligator	
				Water temperature ^b	Deep body temperature ^c	Water temperature ^b	Deep body temperature ^c
Mean	4.4 ^d	5.4	5.7	5.6	5.8	5.7	6.0
Coefficient of variation	66.6	15.2	18.9	14.1	9.7	12.4	8.9
Maximum	9.9	7.2	8.2	7.4	6.9	7.4	7.0
Minimum	0.3	4.0	4.0	4.2	5.0	4.4	4.5
Sample size	30	31	31	31	31	31	31

^aMeasured at a point midway between the two animals, 1 m above the water surface. Shallow water temperature was measured at the shoreline where water depth was approximately 5-10 cm

^bMeasured as the average of the water temperatures at the dorsal surface of the thorax and on the dorsal surface of the midpoint of the tail

^cMeasured at a depth of approximately 30 cm inside the cloaca

^dAll values are in C

DISCUSSION

The usually accepted lower limit of body temperature for the alligator generally has been considered to be 3 C, as attributed to Colbert *et al.* (1946). Data presented by these authors, however, do not clearly support the conclusion that 3 C is the critical lower limit of body temperature for this species, and such a claim is indeed not made by those authors. To the best of our knowledge, the minimum body temperature of 5.0 C attained by the second (live) alligator in the present study is the lowest body temperature ever reported for this species under natural conditions with subsequent recovery to normal health and activity. Although the first alligator attained a minimum body temperature of 4.0 C while still alive (as evidenced by the animal's breathing hole in the ice being kept open), the death of this animal approximately 3 days later does not permit this temperature to be recorded as a minimum limit from which recovery is possible. Based on the information presented in this study, the critical lower limit of body temperature for these alligators would appear to be somewhere between 4.0 and 5.0 C.

General accounts of the natural history of the alligator in the Southeast (*e.g.*, Kellogg, 1929; McIlhenny, 1935) indicate that during winter, alligators make frequent use of subterranean dens into which they retreat during periods of cold weather. Extensive searches of both the "Pond B" and Par Pond reservoir shorelines, however, have failed to reveal any such alligator dens and no radio-collared alligators in the Par Pond area have ever been known to use dens in winter (Murphy, 1977; *in press*).

Deep-water reservoirs such as those occupied by the alligators in this study, represent atypical and possibly marginal habitat for this species, as compared to the more typically used shallow marshes (Joanen and McNease, 1972; Murphy, 1977). However such deep-water areas may also serve as heat sources and/or sinks which could serve the same function as subterranean dens for alligators in shallow-water marshes. The behavior and fates of the two alligators observed in this study tend to support this hypothesis. The alligator which remained in direct proximity to the deeper portions of the lake and occasionally shifted the position of its body downwards into deeper water survived the winter cold spell, enduring air temperatures as low as -8.4 C at night, while the alligator which remained immobile in the shallower cove died. The use of deep-water pools by overwintering alligators has also been reported by Kellogg (1929), and Spotila (1974) has discussed the use of water in conjunction with behavioral thermoregulation in this species.

Torpid and lethargic states have been reported in overwintering alligators by earlier studies (*e.g.*, Kellogg, 1929; McIlhenny, 1935). Almandariz (1975) reports the induction of torpor in tropical crocodylians at temperatures ranging from 8-11 C. Even though the alligators observed in the present study appeared to be quite lethargic and would, on some occasions, respond only with slow limb movements to prodding with a

TABLE 2.—Results of linear regression analyses in the form: $y = a + bx$, relating deep body temperatures^a (y) to adjacent water temperatures^b (x) for both a live adult male alligator and the carcass of a recently deceased adult male alligator of comparable size, while located approximately 15 m apart on the bottom in a deep water site of the "Pond B" reservoir of the Savannah River Plant^c

	Degrees of freedom	y-intercept (a)	Slope (b)	Coefficients of correlation (r)	F	Probability of a greater F
Live alligator	30	3.1	0.48	0.66	22.63	0.0001
Dead alligator	30	4.5	0.26	0.34	3.85	0.0595

^aMeasured at a depth of approximately 30 cm inside the cloaca

^bMeasured as the average of the water temperatures at the dorsal surface of the thorax and on the dorsal surface of the midpoint of the tail

^cAll temperatures are measured in C

boat paddle, these animals still remained capable of performing routine body movements such as raising the snout to the surface to breathe and moving into deeper water on a regular basis. It cannot be determined, however, whether the death of the first alligator in the shallow cove resulted from the icing over of its breathing hole when torpor became so deep that breathing movements became too widely spaced to prevent ice formation, or whether the alligator first died and then the breathing hole iced over secondarily. It is possible that stress associated with removing this alligator from the water twice may have contributed to its eventual death, although the second alligator which survived was also treated similarly. No autopsy could be performed on the dead alligator because of the use of its carcass in the second part of this study, and its state of health at the beginning of the study is unknown.

Data presented by Frair *et al.* (1972) and Neill and Stevens (1974) have led these latter authors to conclude that thermoregulation by large sea turtles must be largely a physical process based on the thermal inertia of their large body sizes, as seems to also have been the case with the alligators in the present study. The thermal inertia of large varanid lizards (McNab and Auffenberg, 1976), like that of the alligators in the present study, prevented them from reaching thermal equilibrium over night, and the body temperatures of these lizards, like those of the alligators, generally exceeded that of their substrate during most of the nighttime hours. A detailed analysis of thermoregulation through the thermal inertia of large ectotherm body size is provided by Spotila *et al.* (1973).

The major difference between the body temperature patterns of the live and dead alligators was in the greater degree to which the temperatures of the live animal matched the temperatures of its adjacent water (Table 2; Fig. 1). This difference may have been due, at least in part, to the larger body size (188 vs. 135 kg body weight) of the dead animal. The effect of differences in body size (and hence in surface/volume ratio) upon heating and cooling time constants of alligators is discussed in detail by Robertson and Smith (1979). The closer coupling of the body temperatures of the live alligator to its adjacent water temperature could also have resulted from changes of blood flow or other physiological mechanisms, which have been found to enable crocodylians to significantly increase body temperatures while basking in cool shallow water (Robertson and Smith, 1979; Smith, 1976; Smith, 1979). Such shallow-water basking appears to have been employed by the live alligator while under study at the deep water site. There was no clear evidence of a significant overall elevation of the average body temperatures of either the live or dead animal above that of their adjacent water, as was also reported for alligators by Smith (1975, 1979) and for sea turtles by Heath and McGinnis (1980). The temperature relations of the live alligator, and to some extent those of the dead one as well, corresponded closely to the description of prebasking thermoregulatory relationships described by Smith (1975) for this species. There was, however, little evidence of endogenous production of metabolic heat by the live animal in this study as has been suggested elsewhere for large alligators (Smith, 1976, 1979). Such a situation is to be expected in light of the very low body temperatures experienced by the alligators in the present study.

The pattern of increase in body temperature following the terrestrial basking of the live alligator on 7 February (Fig. 1) was generally similar to other reports of body temperature increases in this species following basking (Spotila, 1974; Smith, 1975, 1979). The magnitude of the increase in body temperature produced by the basking event reported here (4.6 C, Fig. 1) was similar in magnitude to those reported by Smith (1979), who reported postbasking increases in alligator body temperatures from 4.0-4.5 C above water temperature.

The results of this study emphasize the importance of behavioral mechanisms as a means of regulating the body temperatures of the alligator, even during periods of cold winter weather. Physical properties inherent in the thermal inertia of large body size and physiological mechanisms involving cutaneous blood flow patterns might also con-

tribute to alligator roles at this time behavioral thermoregulation by alligators may be this need not be homeothermic re large alligator, appropriate micro general pattern

Acknowledgments

United States Dep
Smith and James
Lynn Standora for

- ALMANDARZ, E. 1975. *Am. Midl. Nat.* 15:171-172
- BARR, A. J., J. H. 1975. *SAS Institut*
- COLBERT, E. H., 1975. *American dinosaurs.*
- DESMOND, A. J. 1975. *Am. Midl. Nat.* 15:171-172
- DOMBY, A. H., D. 1975. *Am. Midl. Nat.* 15:171-172
- FRAIR, W., R. G. 1972. *Am. Midl. Nat.* 15:171-172
- GIBBONS, J. W. 1975. *Am. Midl. Nat.* 62:660-670
- HEATH, M. E. 1980. *Am. Midl. Nat.* 103:1-10
- JOANEN, T. AND L. 1975. *Am. Midl. Nat.* 15:171-172
- KELLOGG, R. 1925. *Bull. No. 1*
- MCILHENNY, E. A. 1975. *Am. Midl. Nat.* 15:171-172
- MENNING, B. K. 1975. *Am. Midl. Nat.* 15:171-172
- MURPHY, T. M., 1975. *Am. Midl. Nat.* 15:171-172
- _____. 1977. *Dis. thermally*
- _____. 1981. *Th. South Car (SRO-NE*
- NEILL, W. H. 1974. *Am. Midl. Nat.* 15:171-172
- PARKER, E. D., 1975. *Am. Midl. Nat.* 15:171-172
- ROBERTSON, S. L. 1979. *American*
- SMITH, E. N. 1975. *Zool.*, 48:

ermoregulatory abilities during cold winter weather although their ould seem to be secondary to the more primary importance of egulatory mechanisms. While the body temperatures of large dically be higher than that of the water in which they are located, egarded as presumptive evidence for a physiologically based ation of body temperature. The physical properties of the body of a 1 the use of appropriate behavioral positioning under the apatic conditions, may be sufficient in themselves, to explain the levels of body temperature changes observed.

This study was supported by a contract (EY-76-C-09-0819) between the ent of Energy and the University of Georgia. We thank Drs. E. Norbert Spotila for critical readings of the manuscript, and Pamela Brisbin and ir help with fieldwork.

LITERATURE CITED

- The use of chilled water to transfer adult crocodilians. *Int. Zoo Yearb.*,
- ODNIGHT, J. P. SALL AND J. T. HELWIG. 1976. A user's guide to SAS 76. Inc., Raleigh, North Carolina. 329 p.
- B. COWLES AND C. M. BOGERT. 1946. Temperature tolerances in the gator and their bearing on the habits, evolution, and extinction of the *l. Am. Mus. Nat. Hist.*, **86**:329-373.
- The hot-blooded dinosaurs. Dial Press, New York. 238 p.
- INE AND R. W. McFARLANE. 1977. Radiocesium dynamics in herons in- taminated reservoir system. *Health Phys.*, **33**:523-532.
- CMAN AND N. MROSOVSKY. 1972. Body temperature of *Dermochelys coriacea*: om cold water. *Science*, **177**:791-793.
- l. R. SHARITZ. 1974. Thermal alteration of aquatic ecosystems. *Am. Sci.*,
- M. MCGINNIS. 1980. Body temperature and heat transfer in the green sea *mydas*. *Copeia*, **1980**:767-773.
- CNEASE. 1972. A telemetric study of adult male alligators on Rockefeller iana. *Proc. Southeast Assoc. Game Fish Comm.*, **1972**:252-275.
- The habits and economic importance of alligators. *U.S. Dep. Agric. Tech.* 36 p.
35. The alligator's life history. Christopher Publ. House., Boston. 117 p.
- V. AUFFENBERG. 1976. The effect of large body size on the temperature the Komodo dragon, *Varanus komodoensis*. *Comp. Biochem. Physiol.*,
- I. L. BRISBIN, JR. 1974. Distribution of alligators in response to thermal reactor cooling reservoir, p. 313-321. In: J. W. Gibbons and R. R. Sharitz al ecology. U. S. Atomic Energy Comm. Symp. Series (CONF-730505). nical Information Service. Springfield, Virginia.
- ution, movement, and population dynamics of the American alligator in a red reservoir. M. S. Thesis, Univ. Georgia, Athens. 58 p.
- opulation status of the American alligator on the Savannah River Plant, ia. Publ. of the Savannah River National Environmental Research Park 4), Aiken, South Carolina.
- . D. STEVENS. 1974. Thermal inertia versus thermoregulation in "warm" nas. *Science*, **184**:1008-1010.
- F. HIRSCHFIELD AND J. W. GIBBONS. 1973. Ecological comparisons of cted aquatic environments. *J. Water Pollut. Control Fed.*, **45**:726-733.
- o E. N. SMITH. 1979. Thermal indications of cutaneous blood flow in the gator. *Comp. Biochem. Physiol.*, **62A**:569-572.
- ermoregulation of the American alligator, *Alligator mississippiensis*. *Physiol.*, 194.

- . 1976. Cutaneous heat flow during heating and cooling in *Alligator mississippiensis*. *Am. J. Physiol.*, **230**:1205-1210.
- . 1979. Behavioral and physiological thermoregulation of crocodylians. *Am. Zool.*, **19**: 239-247.
- SPOTILA, J. R., O. H. SOULE AND D. M. GATES. 1972. The biophysical ecology of the alligator: heat energy budgets and climate spaces. *Ecology*, **53**:1094-1102.
- , P. W. LOMMEN, G. S. BAKKEN AND D. M. GATES. 1973. A mathematical model for body temperatures of large reptiles: implications for dinosaur ecology. *Am. Nat.*, **107**:391-404.
- . 1974. Behavioral thermoregulation of the alligator, p. 322-324. *In*: J. W. Gibbons and R. R. Sharitz (EDS.). Thermal ecology. U.S. Atomic Energy Commission Symp. Series (CONF-730505). National Technical Information Service. Springfield, Virginia.
- STANDORA, E. A. 1977. An eight-channel radio telemetry system to monitor alligator body temperatures in a heated reservoir, p. 70-79. *In*: F. M. Long (ED.). Proc. First Int. Conf. Wildl. Biotelemetry. Publ. Univ. of Wyoming, Laramie.
- TERPIN, K. M. 1976. Thermoregulatory adaptations and heat energy budget analyses of the American alligator, *Alligator mississippiensis*. M. A. Thesis, State Univ. Coll. at Buffalo, Buffalo, New York. 56 p.

SUBMITTED 26 FEBRUARY 1981

ACCEPTED 28 JULY 1981