

## Thermophilic Response of the American Alligator and the American Crocodile to Feeding

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The body temperatures ( $T_b$ ) and thermal behavior of juvenile *Alligator mississippiensis* and *Crocodylus acutus* were monitored in an outdoor enclosure equipped with aquatic and terrestrial thermal gradients. Both species selected significantly higher and less variable  $T_b$ s when fed than when fasted. Within each species, there were considerable individual differences in  $T_b$ , particularly after feeding. This variation may have been related to differences in appetite or to social factors. Fed alligators had significantly higher and less variable  $T_b$ s than fed crocodiles, a difference that may reflect environmentally-related differences in their thermal strategies. In crocodilians, digestion is promoted by an increase in  $T_b$ , but appetite may depend on heat availability rather than on proximate temperatures. Thermophily following feeding probably is common among reptiles, especially in aquatic and nocturnal species that are active over a wide range of  $T_b$ s. The notion of a single preferred  $T_b$  is inconsistent with the demonstrated effects of ingestion and other factors on the thermal preferences of some reptiles, and an adjustable thermostat model is more appropriate.

THE widely-held tenet that reptiles regulate their body temperatures at fixed, inherent levels (Bogert, 1949; Licht et al., 1966) has produced an abundance of studies designed to measure the mean or median body temperature of a particular species (Brattstrom, 1965; Templeton, 1970). This parameter, referred to as the preferred body temperature or thermal preferendum, has been used extensively in interspecific comparisons aimed at elucidating the physiological and ecological significance of reptilian temperature regulation (Bogert, 1949; Brattstrom, 1965; Licht et al., 1966; Dawson, 1967, 1975; DeWitt, 1967a; Templeton, 1970). However, within the last decade, the validity of the notion of regulation at unalterable, species-specific thermal levels has been seriously questioned. Investigators have found that a reptile's thermal behavior and its body temperature are influenced by internal and external factors, e.g., reproductive state (Garrick, 1974) and light (Veron and Heatwole, 1970).

One important factor is ingestion. Certain lizards and snakes (Regal, 1966) and turtles (Moll and Legler, 1971) have been observed to initiate or prolong thermophilic behavior, e.g., basking, in response to feeding. Body temper-

atures that were elevated above fasting levels have been reported for recently-fed snakes (Benedict, 1932; Regal, 1966; Kitchell, 1969; McGinnis and Moore, 1969; Goodman, 1971; Saint Girons, 1975; Van Mierop and Barnard, 1976), a lizard (Witten and Heatwole, 1978), turtles (Gatten, 1974) and crocodilians (Lang, 1975a). In addition, lowered body temperatures during fasting have been noted in some lizards (Wilhoft, 1958; Hardy, 1962; Cogger, 1974). In contrast to all of these studies, which indicate a thermal response to changes in nutritional status, no such response was detected in an iguanid lizard (*Sauromalus obesus*; Case, 1976), aquatic turtles (various species; Boyer, 1965) and a crocodilian (*Caiman crocodilus*; Dieffenbach, 1975c).

In the present study, I investigated the effect of feeding on the body temperature preference and thermal behavior of juvenile American alligators (*Alligator mississippiensis*) and American crocodiles (*Crocodylus acutus*). The study was designed to detect individual and interspecific differences as well as temporal differences in thermal preference related to ingestion.

The discussion includes a review of recent reports of thermophily following feeding in

other reptiles with reference to significance of these studies to models of reptilian thermoregulation.

### MATERIALS AND METHODS

Ten juveniles (13-14 months old) of each species were borrowed from a commercial crocodilian exhibition known as "Gatorama" in south-central Florida, U.S.A. All were the progeny of captive breeding populations maintained in a natural setting at the facility (Garrick and Lang, 1977). Prior to the study, they were held with others of the same age in outdoor pens and were fed a varied diet of ground meat (usually chicken necks), fishes, crustaceans and insects several times a week. The alligators ( $N = 10$ ) had a mean weight of 353 grams (range = 260-430) and a mean total length of 52.7 cm (range = 45.7-59.0). The crocodiles ( $N = 10$ ) were nearly equivalent in weight ( $\bar{x} = 376$  grams; range = 240-498) and in length ( $\bar{x} = 49.5$  cm; range = 43.0-53.5).

The study was conducted for a six-week period (Oct., Nov., 1973) at the Archbold Biological Station, Lake Placid, Florida (30 km north of Gatorama). For the first four weeks the animals were not fed; during the last half of this period, the animals were considered to be postabsorptive (=fasted condition). Then, for the final two weeks, ground chicken necks were provided daily in an amount (225 grams total) sufficient to enable all individuals to feed ad libitum (=fed condition). All animals fed during this period, and many fed daily.

The animals were housed in a screened enclosure (2 m x 5 m x 3 m high) that was exposed to ambient light and temperature. The natural light cycle was approximately LD 11:13. Air temperatures ( $T_a$ ) in the enclosure were monitored continuously on a recording thermograph.

Within the enclosure, separate aquatic and terrestrial thermal gradients were operated 24 hr each day for the duration of the experiment. An aquatic thermal gradient was created by heating one end of a water-filled metal trough (1 m x 2 m x 100 mm deep) with a submerged, thermostatically controlled heating element. The aquatic gradient decreased gradually from 40 C at the heated end to 20 ± 3 C at the cool end. Baffles restricted mixing of the water but allowed the animals to move freely. The pool was flush with the sand substrate, and permitted animals to move freely between land and

water. The heating element was reversed midway through the experiment to control for any position preference. Adjacent to the pool, three 250-watt red-glass heat lamps were suspended .5 m apart and .25 m above the substrate. The terrestrial gradient ranged from 45 C directly below the lamps to ambient temperatures elsewhere in the enclosure. In addition, sunlight and shade were available within the enclosure throughout the day.

Ambient temperatures during the fasting and feeding periods were nearly equal. The mean  $T_a$  for each day was computed by integrating the 24-hour record using a compensating polar planimeter. The distribution of the daily mean  $T_a$  for the fasting period ( $N = 14$  days;  $\bar{x} = 20.7$  C; range = 14.6-26.1 C) did not differ significantly (Mann-Whitney U-test;  $P > 0.05$ ) from that for the feeding period ( $N = 14$  days;  $\bar{x} = 20.6$  C; range = 17.8-26.5). During the fasting period,  $T_a$  ranged from 9-29 C; and during the feeding period, the range was 11-30 C. Throughout the study most days were sunny and clear.

Individual alligators and crocodiles were marked initially. A quick-registering mercury thermometer was used to measure body temperature ( $T_b$ ) to the nearest 0.1 C, 5 cm within the cloaca. The  $T_b$ s and positions of the 20 subjects were recorded during each sampling. No more than 1-3 samples were taken on any given day at intervals of at least 4 hours. Care was taken to minimize disturbance to the animals during sampling, and individuals were repositioned where caught within the enclosure. Sampling times varied each day and were matched for the fasting and feeding periods. The distribution of sampling times was as follows: 0800-1200 = 5; 1200-1600 = 6; 1600-2000 = 8; 2000-2400 = 5; 2400-0400 = 0; 0400-0800 = 3 ( $N = 27$  per individual per condition). For analysis,  $T_b$ s recorded during the day (0800-2000), when natural sources of heat were available are distinguished from  $T_b$ s monitored at night (2000-0800) when these sources were absent.

The  $T_b$ s of individuals and the pooled  $T_b$ s of each species were analyzed for differences in distribution (Mann-Whitney U-test; Siegel, 1956) and variability (F-test; Sokal and Rohlf, 1969) during the fasting vs. feeding treatments, using a criterion for significance of  $P < 0.05$  (one-tailed test). The pooled  $T_b$ s of each species were compared in the various treatments using a criterion for significance of  $P < 0.05$  (two-

TABLE 1. BODY TEMPERATURES SELECTED BY FASTED VS. FED JUVENILE ALLIGATORS IN AN OUTDOOR THERMAL GRADIENT. Mean body temperature ( $T_b \pm 1$  standard deviation (std) and range (parentheses) for each individual (a through j) is shown for daytime (0800-2000) and nighttime (2000-0800). Fed minus fasted differences in  $T_b$  and std are shown at night. Pooled values (a-j combined) at bottom of table. N = 27 per animal per treatment (day = 19; night = 8); pooled N = 190 (day), 80 (night).

	Fasted-Daytime		Fasted-Nighttime		Fed-Daytime		Fed-Nighttime		Daytime		Nighttime	
	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$\Delta T_b$	$\Delta T_b$	$\Delta T_b$	$\Delta T_b$
a	28.5 $\pm$ 2.0	(25.2-32.5)	30.2 $\pm$ 2.8	(26.4-34.5)	32.6 $\pm$ 3.0	(25.5-36.6)	32.1 $\pm$ 2.8	(28.0-35.7)	4.1 <sup>a</sup>	1.0	1.9	0.0
b	28.9 $\pm$ 3.3	(24.0-34.5)	26.7 $\pm$ 3.6	(20.3-30.8)	32.2 $\pm$ 2.7	(27.0-34.0)	33.3 $\pm$ 2.6	(29.0-36.2)	3.3 <sup>c</sup>	-0.6	6.6 <sup>d</sup>	1.0
c	28.4 $\pm$ 2.2	(25.2-33.5)	28.7 $\pm$ 6.3	(12.5-29.8)	31.4 $\pm$ 3.0	(24.0-36.5)	30.5 $\pm$ 2.4	(27.5-34.8)	3.0 <sup>c</sup>	0.8	6.8 <sup>d</sup>	-3.9 <sup>e</sup>
d	28.2 $\pm$ 3.5	(24.0-34.2)	27.9 $\pm$ 5.0	(19.8-34.8)	31.8 $\pm$ 3.2	(25.5-35.5)	29.9 $\pm$ 2.0	(27.0-32.5)	3.6 <sup>d</sup>	-0.3	2.0	-2.9 <sup>d</sup>
e	27.8 $\pm$ 3.5	(21.9-34.5)	28.6 $\pm$ 4.1	(20.3-32.0)	30.9 $\pm$ 2.5	(27.2-36.0)	31.7 $\pm$ 1.5	(30.0-34.1)	3.1 <sup>e</sup>	-1.0	3.1 <sup>a</sup>	2.1 <sup>g</sup>
f	29.6 $\pm$ 3.2	(24.9-34.5)	28.7 $\pm$ 2.4	(25.7-32.5)	32.1 $\pm$ 2.0	(28.5-35.0)	31.9 $\pm$ 3.5	(24.5-35.0)	2.5 <sup>f</sup>	-1.2 <sup>b</sup>	3.0 <sup>a</sup>	1.6 <sup>h</sup>
g	29.1 $\pm$ 3.5	(25.2-34.5)	24.9 <sup>g</sup> $\pm$ 6.3	(13.0-31.0)	32.1 $\pm$ 2.3	(27.2-33.0)	30.6 $\pm$ 2.5	(27.2-34.0)	3.0 <sup>g</sup>	-1.2 <sup>a</sup>	6.1 <sup>b</sup>	-3.8 <sup>d</sup>
h	27.5 $\pm$ 3.4	(22.4-34.6)	22.6 <sup>h</sup> $\pm$ 6.3	(13.0-34.0)	28.9 $\pm$ 3.6	(21.2-33.0)	30.7 $\pm$ 2.5	(27.3-34.0)	1.4 <sup>h</sup>	0.2	8.1 <sup>a</sup>	4.1 <sup>a</sup>
i	29.3 $\pm$ 2.7	(24.5-34.0)	28.6 $\pm$ 3.2	(23.7-32.6)	30.7 $\pm$ 2.4	(27.3-35.0)	30.9 $\pm$ 2.9	(26.5-35.0)	1.4	-0.2	2.3	-0.3
j	29.6 $\pm$ 3.2	(22.0-35.6)	27.6 $\pm$ 2.9	(23.5-31.5)	31.2 $\pm$ 2.3	(28.0-35.0)	30.1 $\pm$ 2.9	(25.8-33.3)	1.6	-2.0 <sup>e</sup>	1.5	0.1
pooled (a-j)	28.7 $\pm$ 3.2	(21.9-35.6)	26.9 <sup>a</sup> $\pm$ 4.9 <sup>a</sup>	(12.5-34.8)	31.4 $\pm$ 2.8	(21.2-36.6)	31.0 $\pm$ 2.6	(24.5-36.2)	2.7 <sup>a</sup>	-0.4 <sup>a</sup>	4.1 <sup>a</sup>	-2.3 <sup>a</sup>

\*  $P < 0.05$ ; <sup>b</sup>  $P < 0.025$ ; <sup>c</sup>  $P < 0.01$ ; <sup>d</sup>  $P < 0.001$ .

TABLE 2. BODY TEMPERATURES SELECTED BY FASTED VS. FED JUVENILE CROCODILES IN AN OUTDOOR THERMAL GRADIENT. Mean body temperature ( $T_b \pm 1$  standard deviation (std) and range (parentheses) for each individual (a through j) is shown for daytime (0800-2000) and nighttime (2000-0800). Fed minus fasted differences in  $T_b$  and std are shown at night. Pooled values (a-j combined) at bottom of table. N = 27 per animal per treatment (day = 19; night = 8); pooled N = 190 (day), 80 (night).

	Fasted-Daytime		Fasted-Nighttime		Fed-Daytime		Fed-Nighttime		Daytime		Nighttime	
	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$T_b \pm 1$ std	(Range)	$\Delta T_b$	$\Delta T_b$	$\Delta T_b$	$\Delta T_b$
a	27.9 $\pm$ 3.5	(22.5-33.6)	30.1 $\pm$ 3.7	(23.0-34.0)	29.2 $\pm$ 2.4	(25.5-34.5)	28.8 $\pm$ 3.4	(25.0-34.0)	1.3 <sup>b</sup>	-1.1	-1.3	-0.5
b	29.4 $\pm$ 2.4	(25.8-34.0)	28.9 $\pm$ 3.7	(23.5-34.0)	29.8 $\pm$ 2.7	(25.0-36.2)	29.0 $\pm$ 2.1	(27.0-32.5)	0.4	0.3	0.1	-1.6 <sup>d</sup>
c	27.3 $\pm$ 2.2	(23.2-31.5)	26.4 $\pm$ 2.9	(22.4-30.0)	30.6 $\pm$ 3.1	(24.9-37.2)	29.4 $\pm$ 2.4	(25.0-32.0)	3.3 <sup>a</sup>	0.9	3.0 <sup>b</sup>	-0.5
d	28.1 $\pm$ 3.5	(23.0-33.7)	27.4 $\pm$ 3.6	(23.6-34.5)	30.4 $\pm$ 3.6	(21.5-35.5)	31.9 $\pm$ 5.0	(25.1-37.5)	2.3 <sup>b</sup>	0.1	4.5 <sup>b</sup>	1.4
e	27.4 $\pm$ 3.5	(20.4-34.2)	29.0 $\pm$ 3.2	(23.8-32.0)	28.6 $\pm$ 2.4	(25.0-36.0)	30.8 $\pm$ 2.9	(28.0-34.0)	0.8	-1.1	1.8	-0.3
f	27.4 $\pm$ 3.0	(23.3-34.0)	27.1 $\pm$ 3.7	(22.5-32.5)	30.4 $\pm$ 3.0	(22.5-34.1)	29.4 $\pm$ 2.9	(25.2-34.0)	3.0 <sup>c</sup>	0.0	2.3	-0.8
g	28.2 $\pm$ 4.3	(21.4-34.0)	29.8 $\pm$ 5.0	(18.2-34.0)	29.2 $\pm$ 3.7	(23.5-34.8)	29.2 $\pm$ 4.1	(19.0-35.0)	0.5	-0.6	-0.6	-0.9
h	27.7 $\pm$ 3.3	(20.7-35.7)	26.0 $\pm$ 5.7	(19.5-35.5)	28.1 $\pm$ 2.9	(21.5-36.7)	24.6 $\pm$ 4.9	(23.0-35.0)	0.8	-0.4	-1.4	-0.8
i	27.5 $\pm$ 2.6	(23.4-32.7)	27.3 $\pm$ 3.1	(22.7-30.8)	29.3 $\pm$ 2.9	(25.0-35.2)	29.5 $\pm$ 4.2	(23.0-35.5)	1.8 <sup>a</sup>	0.3	2.2	1.1
j	27.9 $\pm$ 3.0	(23.2-33.6)	27.9 $\pm$ 3.7	(23.0-32.5)	30.0 $\pm$ 2.8	(23.0-34.2)	30.4 $\pm$ 2.5	(27.0-34.0)	2.1 <sup>b</sup>	-0.2	2.5	-0.2
pooled (a-j)	27.9 $\pm$ 3.2	(20.4-35.7)	28.0 $\pm$ 3.9 <sup>a</sup>	(18.2-35.5)	29.5 $\pm$ 3.0	(19.5-37.2)	29.3 $\pm$ 2.8	(19.0-37.5)	1.6 <sup>a</sup>	-0.2	1.3 <sup>a</sup>	-0.4 <sup>a</sup>

\*  $P < 0.05$ ; <sup>b</sup>  $P < 0.025$ ; <sup>c</sup>  $P < 0.01$ ; <sup>d</sup>  $P < 0.001$ .

tailed test). The percentages of animals in the water during the feeding and fasting periods were compared by the test for equality of two percentages ( $P < 0.05$ , two-tailed test; Sokal and Rohlf, 1969).

#### BODY TEMPERATURES

Alligators.—Fed alligators selected higher and less variable  $T_b$ 's in comparison with fasted values (Table 1). The increase in  $T_b$  was greater at night ( $\Delta T_b = +4.1$  C; pooled for all individuals) than during the day ( $\Delta T_b = +2.7$  C). Variability in  $T_b$  was lower at night ( $\Delta \text{std} = -2.3$  C) than during the day ( $\Delta \text{std} = -0.4$  C). Fasted alligators maintained higher and less variable  $T_b$ 's in the daytime than at night, but these day-night differences were abolished when the alligators were fed (Table 1). Thus, the major effect of feeding was a definite elevation of  $T_b$  (day and night) relative to fasting levels and reduced variability in  $T_b$ , especially at night.

Among individual alligators, responses to feeding varied substantially. Some exhibited marked increases in  $T_b$  during the day and at night (Table 1: b, c, e, f, g) whereas the  $T_b$ 's of others increased during the day but not at night (Table 1: a, d). One showed an increase in nighttime  $T_b$  that was much greater than the daytime increase in  $T_b$  (Table 1: h). For two alligators, increases in  $T_b$ 's were insignificant (Table 2: i, j).

When fed, certain alligators showed little reduction in the variability of  $T_b$ 's (Table 1: a, b, i), while reductions were noticeable for others (Table 1: c, d, e, f, g, h, j), particularly at night. One showed a highly significant decrease in daytime  $T_b$  variation, but its  $T_b$  did not increase significantly with feeding (Table 1: j).

Crocodiles.—The crocodiles selected higher and less variable  $T_b$ 's when fed (Table 2), but these differences were not as pronounced as in the alligators. For crocodiles, the increase in  $T_b$  was greater during the day ( $\Delta T_b = +1.6$  C; pooled for all individuals) than at night ( $\Delta T_b = +1.3$  C). Variability in  $T_b$  was reduced at night ( $\Delta \text{std} = -0.4$  C), but not reduced significantly during the day ( $\Delta \text{std} = -0.2$  C). Fasted crocodiles maintained  $T_b$ 's at nearly equal levels during the day and night, but nighttime  $T_b$ 's were more variable than daytime ones. This day-night pattern was similar for the fed crocodiles (Table 2). Consequently, the major effect of feeding was a moderate increase in  $T_b$ 's (day

TABLE 3. PERCENTAGES OF ALLIGATORS AND CROCODILES IN THE WATER DURING THE DAY AND AT NIGHT IN FASTED VS. FED CONDITION. Significant differences between alligators and crocodiles in each condition are indicated by asterisks for values for crocodiles.

	Fasted	Fed	Fed-fasted
Alligators			
day	50	78	28****
night	76	84	8
Crocodiles			
day	35*	53****	18****
night	59**	80	21***

\*  $P < 0.05$ ; \*\*  $P < 0.025$ ; \*\*\*  $P < 0.01$ ; \*\*\*\*  $P < 0.001$ .

and night) and a reduction in  $T_b$  variability at night.

Individual crocodiles differed in their responses to feeding. Two animals had elevated  $T_b$ 's during the day and at night (Table 2: c, d) whereas four had higher  $T_b$ 's during the day only. In contrast, four others did not show significant increases in  $T_b$ 's when fed (Table 2: b, e, g, h). Only one individual showed a decrease in  $T_b$  variability when fed, but its  $T_b$  did not increase (Table 2: b).

#### BEHAVIOR

During the fasting period, equal numbers of alligators (50%) were observed in the water and on land throughout the day; but at night, more (76%) were observed in the water. During the feeding period, more alligators were seen in the water during the day, but the number in the water at night did not increase compared to the fasting period (Table 3). A small number of fasting alligators were observed beneath the heat lamps on land, 3% during the day and 10% at night. When fed, alligators were observed under the heat lamps twice as often during the day (7%), but little change was apparent at night.

Fasted crocodiles were seen more often on land (65%) than in the water during the day; but at night, more were in the water (59%). During the feeding period, the percentage in the water increased during the day and at night (Table 3). The number of crocodiles beneath the heat lamps (10% day and night) did not change in the fasted vs. fed conditions.

#### ALLIGATORS VS. CROCODILES

Fasted condition.—The fasting  $T_b$ 's of the alligators were higher than the crocodiles' during the

day ( $\Delta\bar{T}_b = +0.8$  C;  $P < 0.01$ ), but not significantly lower ( $\Delta\bar{T}_b = -1.1$  C;  $P > 0.05$ ) at night (Tables 1, 2). Variability in daytime  $T_{bS}$  was identical in both species. At night, however, alligator  $T_{bS}$  were more variable ( $\Delta\text{std} = +1.0$  C;  $P < 0.025$ ) than those of crocodiles (Tables 1, 2). The percentages of alligators in the water (day and night) were higher (about 15% more) than crocodiles (Table 3). Few alligators (about 1/2 the number of crocodiles) basked beneath the heat lamps during the day.

**Fed condition.**—More alligators than crocodiles had higher  $T_{bS}$  when fed, and the magnitude of these increases was greater than in the crocodiles. During the feeding period, the  $T_{bS}$  (pooled) of the alligators in comparison with the crocodiles were higher during the day ( $\Delta\bar{T}_b = +1.9$  C;  $P < 0.001$ ) and at night ( $\Delta\bar{T}_b = +1.7$  C;  $P < 0.001$ ) (Tables 1, 2). Alligators had less variable  $T_{bS}$  in comparison with crocodiles at night ( $\Delta\text{std} = -1.2$  C;  $P < 0.001$ ) but not during the day ( $\Delta\text{std} = -0.3$  C;  $P > 0.05$ ) (Tables 1, 2).

The number of alligators basking beneath the heat lamps increased threefold during the feeding period, but no change was apparent in the crocodiles. Although both species were in the water more often when fed, alligators utilized the aquatic gradient to a greater extent during the day; at night, the number of alligators and crocodiles in the water was nearly equal (Table 3).

#### EFFECT OF FEEDING ON THERMAL RESPONSE

**Body temperature.**—Despite distinct individual and interspecific differences (to be discussed below), both alligators and crocodiles selected significantly higher  $T_{bS}$  following feeding. Elevated  $T_{bS}$  in response to feeding have been reported previously in certain snakes, turtles and a lizard (references cited in introduction). Increased  $T_{bS}$  in these small crocodiles following feeding accord with my observations of adult alligators monitored in an outdoor enclosure exposed to natural environmental cycles. Individuals responded to feeding by behaviorally maintaining  $T_{bS}$  that were elevated 1–3 C above pre-feeding levels (Lang, 1975a). For Nile crocodiles (*Crocodylus niloticus*) in nature, a decrease in the number of animals on land in the sun was associated with reduced feeding activity (Modha, 1968). In contrast to these findings, Diefenbach (1975c) concluded tenta-

tively that the thermal preference of *Caiman crocodilus* was not affected by feeding.

Recent evidence suggests that the levels of  $T_b$  maintained by certain reptiles are dependent upon the amount of food ingested and the state of digestion. Saint Girons (1975) reported that vipers fed small prey (5–8% of body weight) maintained lower  $T_{bS}$  than snakes fed large prey (20–27% of body weight). In these snakes, the ingestion of small prey resulted in initial thermal levels similar to the levels at the end of the digestion of large prey. In addition, he noted a gradual decline in the  $T_{bS}$  of fed vipers from the first through fourth day following the ingestion of large prey and a return on the fifth day to fasting values. I observed similar relationships between the  $T_{bS}$  maintained by adult alligators and the amount of food eaten as well as the course of digestion (Lang, unpubl. obs.). These several lines of evidence, though preliminary, suggest that the thermal levels attained by some reptiles vary directly with the quantity of food initially ingested and inversely with the time since ingestion.

In the present study, variability in  $T_b$  was reduced during the feeding period. Reduced variability in  $T_b$  has been reported for recently fed turtles (Gatten, 1974) and snakes (Goodman, 1971; Saint-Girons, 1975). Less variation in a fed reptile's  $T_b$  might result from a reduction in mobility, particularly in a laboratory thermal gradient (Gatten, 1974). However, in the outdoor enclosure utilized by Saint Girons (1975), the snakes made frequent behavioral adjustments to maintain  $T_{bS}$  at high and relatively constant levels following feeding. The outdoor enclosure employed in this study would have resulted in varying  $T_{bS}$  for a relatively immobile animal due to the daily temporal changes in ambient temperatures. Consequently, the less variable  $T_{bS}$  of fed alligators and crocodiles probably reflect better regulation of  $T_{bS}$  during the feeding period.

Selection of lower  $T_{bS}$  at night was not particularly evident in alligators or crocodiles. A daily rhythm of thermal preference in response to a light-dark cycle has been detected in certain lizards (Regal, 1967; Myhr and Hammel, 1969; Spellerberg, 1974; Spellerberg and Smith, 1975) and snakes (Gehrmann, 1971a; Spellerberg and Phelps, 1975), but such a rhythm is apparently absent in other lizards (Wilhoft, 1958; Regal, 1978) and snakes (Goodman, 1971; Spellerberg, 1976). Several of the fasted alligators did have significantly lower  $T_{bS}$

at night relative to daytime values (Table 1: g, h). But, during feeding, the daytime and nighttime  $T_{bS}$  of these individuals were nearly equivalent and were higher than fasting values. This observation and the reduction in  $T_b$  variability noted above suggest that the net effect of feeding was an increase in the amount of time spent at relatively high  $T_{bS}$ .

Identifying factors that influence the time spent at a relatively high  $T_b$  level is important for understanding a reptile's thermal relations. For example, Regal (1966) reported that a boa, *Constrictor constrictor*, achieved  $T_{bS}$  of 31–36 C by basking continuously for 105 hr after it was fed. When the snake defecated at the end of this period, it ceased basking. Other workers have noted that, for individual snakes, thermophilic behavior accompanied by consistently high  $T_{bS}$  persisted until a meal was digested (Saint Girons, 1975; Van Mierop and Barnard, 1976). Thus, in some reptiles, the ingestion of food results not only in an increase in the level of  $T_b$  maintained during digestion but also in an increase in the amount of time spent at high  $T_{bS}$ .

To illustrate this point, the temporal aspect of a reptile's thermal response may be expressed as  $T_b$  multiplied by the length of time spent at that  $T_b$ . For example, if  $T_b$  is regulated at 28 C for 4 hours, the temporal-thermal relationship could be expressed as 112 degree-hours. In order to increase degree-hours,  $T_b$  could be raised (e.g., 31.5 C  $\times$  4 hours = 126 degree-hours) or the time increased (28 C  $\times$  4.5 hours = 126 degree-hours). Thus, either an increase in  $T_b$  or an increase in the time spent at a particular thermal level would result in an increase in degree-hours. An increase in the time spent at high  $T_{bS}$ , but not elevated relative to fasting levels, would allow a reptile to increase its degree-hours effectively after feeding. If environmental conditions permitted, such a response would be an alternative strategy for promoting digestion and would theoretically result in reduced variability in  $T_b$ .

An alligator (Table 1: j) and a crocodile (Table 2: b) both showed highly significant reductions in  $T_b$  variability without concomitant increases in  $T_{bS}$  during the feeding period. If less variable  $T_{bS}$  indicate better regulation of  $T_b$  (as suggested above), these individuals presumably were able to increase their degree-hours in response to feeding by spending more time at high, but not elevated, thermal levels. Gatten (1974) reported a significant reduction in the

$T_b$  variability of fed *Terrapene ornata*, but only a moderate rise in  $T_b$  relative to fasting values, and concluded that reduced variability in  $T_b$  reflected a change in the thermoregulatory pattern of this turtle following ingestion. These observations indicate that feeding has varied effects on a reptile's thermal preference, and that different species and/or individuals respond to feeding in different ways.

**Behavior.**—Changes in behavior were observed during the feeding period. Both species were more aquatic when fed. A position in the water presumably offered a more effective means of achieving high  $T_{bS}$  than positions on land and probably resulted in better control of  $T_b$  due to the thermal buffering effect of water.

Throughout the study, some of the alligators remained in the water during the day. In contrast, in another study in which an aquatic temperature gradient was not employed, juvenile alligators in outdoor pens remained on land throughout the day and spent the night in the water (Lang, 1976). Even though movements onto land were not cued directly by temperature but rather by light and a circadian rhythm, I interpreted a daytime position on land to be a thermally directed response to the natural thermal regime. When heat was available in the water, as it was in the present study, the alligators did not invariably move onto land during the day. This result supports my earlier suggestion that daytime movements onto land are ultimately heat-seeking responses to the daily cycle of temperature in nature.

#### EFFECT OF $T_b$ ON DIGESTION AND APPETITE

**Digestion.**—In ectothermic vertebrates, digestion is accelerated as temperature increases. Recent studies of *Caiman* indicate that the length of time a food item remains in the stomach decreases with increasing temperatures (Diefenbach, 1975a, b). The frequency and amplitude of gastric contractions increase with temperature, and proteolytic activity increases as well. In this crocodilian, food is digested three times faster at 30 C than at 15 C. Although information on the efficiency of digestion as a function of temperature is not available for crocodilians, the digestive efficiency of a snake (Goodman, 1971) and a lizard (Harlow et al., 1976) are known to vary with temperature. For example, the digestive efficiency of *Natrix taxiphiola* is maximized at 30 C and is

reduced at higher and lower  $T_b$ s (Goodman, 1971).

The optimum temperature for efficient digestion corresponded closely to the elevated  $T_b$ s (30 C) that were voluntarily selected by recently-fed snakes (Goodman, 1971). This result supports the suggestion made over three decades ago by Cowles and Bogert (1944) that digestion proceeds optimally at relatively high  $T_b$ s within the range of  $T_b$ s normally selected by a reptile. The functional significance of behavioral response that results in an increase in  $T_b$  during digestion is obvious. Increased digestive efficiency results in greater energy assimilation for expenditure on vital processes such as maintenance, growth and reproduction. In addition, the detrimental effects of low  $T_b$ s, principally a decrease in digestive efficiency and the increased potential for the putrefaction of undigested food, are minimized (Cowles and Bogert, 1944).

**Appetite.**—Although crocodilians are able to digest food over a wide range of temperatures (Diefenbach, 1975a), temperature influences appetite. When young alligators are held at 28–30 C, they feed daily and ingest about 20% of their body weight per week (Coulson et al., 1973; Joanen and McNease, 1976); but, at low ambient temperatures (10–20 C), alligators, *Caiman*, and Nile crocodiles in captivity cease feeding (Coulson et al., 1973; Diefenbach, 1975a; Pooley, 1962). Field observations of alligators and Nile crocodiles indicate that feeding is curtailed during periods of seasonally low temperatures (McIlhenny, 1935; Joanen and McNease, 1973; McNease and Joanen, 1975; Pooley and Gans, 1976).

Despite favorable ambient temperatures, Nile crocodiles refused food prior to brief periods of cool weather that were apparently signalled by falling barometric pressure (Pooley and Gans, 1976). Thus, appetite appears to be dependent, at least in part, on the ultimate availability of heat rather than on proximate temperatures. Consequently, in a climatic regime of cool nights and warm sunny days, crocodilians may feed even at night (when ambient temperatures are low) in anticipation of sufficient heat availability the following day. This suggestion is supported by two field observations. Immature alligators in coastal Louisiana are active and presumably feeding during the spring and fall when nights are cool, but days are warm enough to permit heating (McNease

and Joanen, 1975); and I observed that immature alligators in south Texas actively forage at  $T_b$ s of 16–17 C.

Small crocodilians apparently accept food over a wider range of temperatures than do large animals (Joanen and McNease, 1972; Diefenbach, 1975a; Pooley and Gans, 1976). Small individuals heat more rapidly than large animals (Colbert et al., 1946; Smith, 1976), and should be able to utilize available warm microhabitats more readily. Consequently, small crocodilians may be able to attain thermal levels that favor digestion when this is not possible for large animals. In this regard, McNease and Joanen (1975) found that immature alligators in nature were more active over a wider range of air and water temperatures and for a longer period of the year than were adults.

It seems unlikely that there is a difference in thermal preference between individuals of different sizes. The daytime  $T_b$ s selected by juvenile alligators in the present study (fasted = 28.7 C; fed = 31.4 C) are consistent with the values reported for adults in natural settings (Smith, 1975; Lang, 1975a). The daytime  $T_b$ s of juvenile American crocodiles (fasted = 27.9 C; fed = 29.5 C) are comparable to those (28–32 C) selected by wild hatchlings in Florida Bay (Lang, 1975b), but values for adults are lacking. Size-dependent differences in thermal preference have been reported for *Caiman* in a laboratory gradient (Diefenbach, 1975c) but such differences have not been found in lizards (Bogert, 1949; Wilhoft, 1958; Hirth, 1963; Brooks, 1968).

#### DIFFERENCES IN THERMAL RESPONSES TO FEEDING

**Individual variation.**—Commenting on the variable responses of the lizard *Scincella lateralis*, Regal (1966) noted that certain animals utilized warm areas only after feeding while others were seen in these areas regularly but more often when fed. In subsequent studies, however, individual differences have been largely ignored. In the present study, individual animals responded differently to feeding. For some,  $T_b$ s were elevated substantially above fasting levels, but not for others. Likewise, there were differences in the variability of  $T_b$  before and after feeding.

A number of factors may have contributed to these differences. Variation in appetite and/or competition for food may have affected the

amount of food ingested by each animal, resulting in differing thermal preferences. Variation in appetite has been noted in snakes (Vinegar et al., 1970; Gehrman, 1971b), and food competition has been documented in lizards (Greenberg, 1976a; Done and Heatwole, 1977) and turtles (Boice, 1970; Froese and Burghardt, 1974). In addition, thermal responses may have been affected directly by social factors, as in some lizards (Regal, 1968, 1971; Bruton, 1977; Done and Heatwole, 1977; Saint Girons, 1977) and crocodilians (Modha, 1968; Lang, 1977). However, I did not witness any obvious competitive or social interactions during the study. Crocodilians housed and fed together grow at variable rates (Pooley, 1962; Coulson et al., 1973), and competition for food and/or access to heat may contribute to this variation.

**Alligators vs. crocodiles.**—Alligators had higher and less variable  $T_b$ s than crocodiles when they were fed. There is a possibility that the crocodiles ingested less food than the alligators, and this might account for their diminished responses. Yet, there were no apparent differences in appetite; crocodiles were observed feeding as often as alligators. During the fasting period, alligator  $T_b$ s were more variable than those of crocodiles. The lowest  $T_b$  recorded for a fasting alligator was 13.0 C compared to 18.2 C for a crocodile. Other authors have noted that alligators are more cold-tolerant than crocodiles (Neill, 1971, for *C. acutus*; Coulson and Hernandez, 1964, for *C. niloticus*).

These interspecific differences may reflect a more labile thermoregulatory strategy for alligators. In particular, they appear to be more responsive than crocodiles to factors that influence  $T_b$ . Because alligators inhabit a warm temperate climate with definite seasonal changes in temperature, it would be advantageous for an alligator to engage at times in distinctly thermophilic behavior in the face of considerable fluctuations in ambient temperature. Thus, they probably seek heat in aquatic situations, as well as on land. Such behavior may help explain why the alligators in this study were more aquatic than the crocodiles, especially during the daytime following feeding. They also positioned themselves more often under the heat lamp when fed.

In contrast to alligators, American crocodiles inhabit essentially tropical environments where seasonal temperatures are less variable and am-

bient temperatures closely approximate the levels of  $T_b$  at which they normally function. Consequently, a crocodile might be expected to show a decreased propensity to seek heat or to respond to factors that promote heat-seeking. If, as Diefenbach (1975c) has suggested, tropical *Caiman* do not show a thermophilic response to feeding, such evidence would further support this interpretation. Similarly, other tropical crocodilians might not exhibit thermophily to feeding to the extent that alligators do. Studies on species from diverse thermal habitats should clarify the ecological significance of these differences.

#### THERMAL PREFERENCES: FIXED OR ADJUSTABLE?

In reptiles that are active over a wide range of  $T_b$ s, it is likely that distinct  $T_b$ s are associated with different activities. Thermophily following feeding has been demonstrated in certain species that are nocturnally active (crocodilians: Lang, 1975a and present study) and/or semi-aquatic (turtles: Moll and Legler, 1971; Gatten, 1974). Similarly, the preponderance of studies reporting thermophilic responses in snakes (cited in introduction) is understandable because many snakes are active over a wide range of temperature (Brattstrom, 1965). Marine iguanas (MacKay, 1964; Bartholomew, 1966; White, 1973) and nocturnal geckoes (Licht et al., 1966; Bustard, 1967; Pianka and Pianka, 1976) are active and forage at  $T_b$ s 10–15 C lower than those maintained during basking. In these forms, a thermophilic response following feeding might be predicted. If this is the case, then the "puzzling" preferences of nocturnal geckoes for  $T_b$ s that were 5–20 C higher in a thermal gradient than in nature (Licht et al., 1966) could be explained, in part, by thermophilic behavior promoting digestion during the day, as Bustard (1967) and Pianka and Pianka (1976) have suggested.

For some reptiles, such as the heliothermic desert lizards, in which activity coincides with typically high  $T_b$ s, thermophily following feeding may not be pronounced because these species normally operate at  $T_b$ s close to the optimal  $T_b$  for efficient digestion. However, even in these species, digestion is presumably enhanced as  $T_b$  approaches the upper limit of tolerated  $T_b$ s. For example, the digestive efficiency of *Dipsosaurus dorsalis* is 7% greater at 41 C than at 37 C (Harlow et al., 1976). However,

the thermal preferendum for this species is alleged to be 38.5 C (DeWitt, 1967a) even though  $T_{bS}$  of 43–44 C have been recorded for free-ranging individuals (Norris, 1953; DeWitt, 1967a, b). Unfortunately, the thermal response of *Dipsosaurus* to feeding has not been reported, but  $T_{bS}$  above the thermal preferendum might be functional on the basis of the data on digestive efficiency.

The generalization that reptilian digestion requires  $T_{bS}$  near or identical with the thermal preferendum (Dawson, 1975) may be valid for certain species, but it does not take into account the definite changes in thermal preference evident in other species. The notion that reptiles possess a "single" preferred  $T_b$  ignores the observations that a reptile at times may actively select a particular  $T_b$  for a specific activity or function (Regal, 1966) whereas, at other times, it may simply conform its  $T_b$  to the range of thermal levels within its habitat (Greenberg, 1976b). Perhaps a more useful approach is to consider that the reptilian thermostat is adjustable (Hammel, 1968) and that the setting is dependent on various interrelated factors. Regal (1978) has postulated some of the possible functional relationships of these factors in the control of body temperature.

The benefits and associated costs of behavioral thermoregulation have been modeled recently for lizards by Huey and Slatkin (1976). Lizards are categorized as thermal specialists vs. generalists ("careful" vs. "less careful" regulation), and optimal thermal strategies (ranging from no regulation to perfect regulation) are predicted for lizards living in differing thermal environments. In the model, physiological benefit is defined as a function of a single optimum temperature, but this assumption does not allow for two or more thermal optima, e.g., one distinct  $T_b$  for activity and another for digestion. On the basis of the evidence reviewed here, certain reptiles appear to regulate  $T_{bS}$  "more carefully" during digestion. In effect, ingestion seems to promote a switch in strategy from that of thermal generalist to specialist. Thus, caution is indicated in comparisons based on the model because an individual reptile's thermal strategy may be a function of its internal state as well as its thermal environment.

Thermophily following feeding is probably more widespread among reptiles, particularly lizards, than the limited number of studies cited here would indicate. It also occurs in fish (Javid and Anderson, 1967; Brett, 1971) and am-

phibians (Lillywhite et al., 1973), groups in which a variable thermostat is suggested as an appropriate model to explain multiple influences on thermal preference (Crawshaw, 1977; Lillywhite et al., 1973; Feder and Pough, 1975). In most ectotherms that show a thermal response to feeding, well-defined behavioral orientations are responsible for changes in thermal levels.

However, in some "ectotherms," digestion may be accompanied by endogenous heat production. For example, the blue-fin tuna is able to regulate its  $T_b$  considerably above water temperature. One individual showed a marked rise in stomach temperature (+7.0 C) while presumably feeding and digesting food (Carey and Lawson, 1973). In the snake *Python molurus*, recently-fed individuals exhibited  $T_{bS}$  that were elevated 1–4 C above fasting values and ambient temperature levels in the absence of environmental sources of heat (Benedict, 1932; Van Mierop and Barnard, 1976). In light of the capacity for endogenous heat production this species (Benedict et al., 1932; Hutchinson et al., 1966; Vinegar et al., 1970), the increased  $T_{bS}$  in response to feeding suggest a condition of temporary endothermy during digestion. Some heat may be generated by chemical decomposition of the food, and this possibility cannot be excluded on the basis of these limited observations.

How are thermophilic responses modulated by ingestion and digestion? The mechanisms remain obscure. In toads, the ingestion of glass beads to simulate food failed to evoke heat-seeking; thus, the stimulus promoting thermophily was not solely a mechanical one (Lillywhite et al., 1973). Clearly, additional studies of physiological as well as behavioral alterations in the thermal states of ectotherms during digestion are warranted. In particular, investigations are needed that relate differing energetic requirements to particular thermal strategies.

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