

Crocodylian Thermal Selection

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CROCODYLIANS are among the largest living reptiles, being much larger than most lizards, snakes and turtles. The progression from hatchling to adult involves a considerable increase in size, and individuals undergo significant size-related changes in morphology, physiology and behaviour. Crocodylians are also amphibious. They live both on land and in the water, and respond differently in the two environments. Taken together, large size and an amphibious mode of life suggest that their thermal biology, which depends on heat exchange between an animal and its environment, may differ in important ways from that of their smaller terrestrial relatives. In addition, because many aspects of crocodylian behaviour are complex and unprecedented in other reptiles (see Lang Chapter 28) crocodylian thermal behaviour is likely to be distinctive.

This chapter discusses the thermal behaviour of crocodylians living in a variable thermal environment. Thermal selection is a complex behavioural response that varies not only with species, but also as a function of many influences on individual animals. The key features of reptilian energetics are discussed and then studies of crocodylian thermoregulation are briefly reviewed, with an emphasis on the functional significance of thermal selection. Experimental studies on particular thermal responses are then examined and their specific functions are discussed. Several examples of other thermal and non-thermal factors that affect thermal selection are also discussed.

The practical implications of these studies in terms of management are outlined in each section and are summarized in the conclusions. Thermal selection is important to crocodylians, and in most situations where crocodylians are maintained in captivity, pens and enclosures should incorporate variable thermal regimes (land, water, access to heat, shade, cool temperatures) that allow animals to regulate their body temperatures (between about 25°C and 35°C) by behavioural means. Juveniles of at least some species can be raised very successfully at reasonably high and stable temperature regimes during cooler periods of the year (see Joanen and McNease Chapter 32), but the correct feeding

regime is critical. There needs to be assurance that the mean temperatures do not increase above critical levels, and such conditions may simply not suit the more tropical species of crocodylians, which, in the wild, spend considerable portions of their time avoiding heat. Interspecific variation in thermal selection may be far more important than is generally recognised.

REPTILIAN ENERGETICS

Fundamental differences in lifestyle distinguish reptiles from both birds and mammals. A reptile consumes relatively small amounts of energy, yet is very efficient in converting that energy into biomass. For example, a free-ranging lizard converts about 40% of the energy ingested into new biomass (versus <3% for birds and mammals), but it consumes only 3-4% as much energy per day as a bird or a mammal of comparable size (Pough 1980). Rapidly growing alligators convert about 40% of the food eaten into body mass (Coulson *et al.* 1973). Two key physiological features are responsible for these dramatic differences in energy flow. Reptiles rely on anaerobic metabolism during activity and they depend on external sources of heat (they are ectotherms) to raise their body temperature (Pough 1983).

The resting and active metabolism of a reptile is only about one-tenth that of a bird or mammal of equivalent size. Consequently, a reptile's capacity for aerobic metabolism (oxygen consumption) is low (Bennett 1982). Alternate modes of energy generation permit a reptile to be as strong and as active as a mammal, albeit for a brief period. These anaerobic processes do not depend on how much oxygen is available and are also relatively independent of temperature. In comparison with mammals, reptiles have equivalent energy reserves and can mobilize energy just as quickly, but cannot sustain activity. Reptiles fatigue easily (see Seymour *et al.* Chapter 26) and recover slowly; during recovery, performance capacity is reduced (Coulson 1984; Gatten 1985).

Reptiles rely on external heat sources (ectothermy) to control their body temperatures, instead

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of generating heat metabolically (endothermy). The source of energy used to alter and regulate body temperature (T_b) is the important distinction between endothermy (internal heat) and ectothermy (external heat). A reptile raises and lowers its T_b principally by its behaviour, although this is augmented by physiological adjustments. The advantages of ectothermy are not only the ability to elevate T_b at comparatively minor energetic cost, but also to reduce T_b on a daily and/or seasonal basis. By lowering T_b , an animal reduces metabolic maintenance costs, thereby saving energy that may be channelled into growth and/or reproduction.

Thermal relations of vertebrate ectotherms are typically complex, because energy utilization is a function of variable T_b as well as variable food supply. In fish, a bioenergetic approach that integrates analyses based on optimal foraging theory and on models of behavioural thermoregulation appears to be a better predictor of behaviour than either analysis alone (Crowder and Magnuson 1983). Similar approaches that combine heat energy budgets and food energy budgets have recently been outlined for ectothermic vertebrates (Spotila and Standora 1985).

CROCODILIAN THERMOREGULATION

Biophysical studies indicate that heat exchange is strongly influenced by solar radiation and by conduction in the water. Water is very important because it serves alternately as a heat source as well as a heat sink. Large animals are tightly coupled to the radiant environment and are relatively independent of the convective environment (ambient air temperatures). As size decreases, convective transfer of heat via circulating air increases (Spotila *et al.* 1972; Terpin *et al.* 1979).

Physiological mechanisms may alter heat production, heat flow within the body and heat exchange between an animal and its environment (Bartholomew 1982). In small American alligators *Alligator mississippiensis*, metabolic heat production is negligible in terms of its potential impact on T_b , but may be significant in very large ones (Turner and Tracy 1985). Heat flow within the body may be altered by shunting blood between the head and body or between the appendages or tail and the body. Various organs within the body heat at different rates. Cardiovascular changes alter heating and cooling rates and may have regional or local effects. The osteoderms of *A. mississippiensis* are highly vascularized and may have a thermal function. Mouth gaping may function at times to alter heat exchange in the head versus the body (Fig. 1). The relative importance of these various mechanisms under natural conditions awaits further study, particularly in the light of the well-documented and very subtle responses of crocodilians to the stress of laboratory manipulations (Gans 1976).



Fig. 1. *Tomistoma schlegelii* basking with mouth open, which may function to alter heat exchange in the head versus the body.

Crocodilians are not passive recipients of a thermal environment. Their behaviour, particularly land-water movements, have long been noted and attributed a thermal function. Radiotelemetry studies of crocodilians living in natural and semi-natural surroundings indicate that T_b s are regulated by specific heat-seeking and heat-avoidance behaviours on land and in the water. These studies confirm the importance of solar radiation and water temperature as the principal determinants of T_b and also demonstrate significant differences between species in thermal behaviour and in the corresponding patterns of T_b (Spotila 1974; Smith 1975; Lang 1975, 1977, 1980; Loveridge 1984).

For example, *A. mississippiensis* actively seek heat in the morning by moving onto land, and later in the day by assuming exposed positions in the water. Body temperatures are elevated to 31–33°C while on land and these levels are maintained throughout the afternoon. In the evening and at night, the animals remain in the water and T_b s drop gradually; they are near water temperature by early morning, when basking is initiated again. Saltwater crocodiles *Crocodylus porosus*, exhibit a very different pattern of behaviour and T_b when in similar conditions. Generally, in non-tidal areas, after a brief period at the water surface early in the morning, *C. porosus* submerge and remain underwater for most of the day, and in the evening, they move onto land where they remain all night. In the southern parts of its range, in mid-winter, they may remain out of the water for longer periods during the day, and in cooler areas all day. Body temperatures rise slowly from 28°C at sunrise to 30°C at sunset, and then drop at night. In contrast to *A. mississippiensis*, *C. porosus* avoid daytime heating by submerging, and then cool on land at night. As a consequence, *C. porosus* T_b s are low and variable during the day whereas *A. mississippiensis* T_b s tend to be stable and at levels considerably above ambient air and water temperatures.

These observations and additional field studies on other species of crocodylians inhabiting warm, tropical environments have led me to suggest that a crocodylian's thermal preference is inversely related to its thermal environment. Thermoregulation is pronounced in species living in thermally-variable habitats whereas a strategy of thermoconformity typifies forms living in thermally-equable habitats (Lang 1980).

Although initial studies on *A. mississippiensis* emphasized heat-seeking behaviour and thermoregulation at high and constant levels, there is evidence from field studies that *A. mississippiensis* and other species sometimes select thermal regimes that result in voluntary cooling and lowered T_b s, even when there are opportunities to be warmer. For example, *A. mississippiensis* in southern Florida moved onto land at night during the warm summer months, and T_b s cooled below ambient water temperatures (Lang 1977). Hatchling American crocodiles *Crocodylus acutus*, inhabiting coastal mangrove habitats in the Everglades, chose microhabitats and activity patterns that coincided with the lowest available ambient temperatures in the water and on land (Mazzotti 1983). Juvenile Nile crocodiles *Crocodylus niloticus* captured on land at night had T_b s below water temperatures during both the hot and cold seasons; those captured during the hot season had T_b s below ambient air temperatures (Loveridge 1984). During the warmer months, *C. porosus* and *Crocodylus novaeguineae* (New Guinea freshwater crocodile) in Papua New Guinea, *Caiman crocodilus* (spectacled caiman) in Venezuela, and *Gavialis gangeticus* (gharial), *Crocodylus palustris* (mugger crocodile) and *C. porosus* in southern India, all moved onto land at night and cooled below ambient water temperatures by early morning (Lang 1980; additional unpublished observations).

Studies of *A. mississippiensis* living in thermally altered habitats are instructive. When heated water was available throughout the winter months, animals moved between areas of warm ($>25^\circ\text{C}$) and cool ($<15^\circ\text{C}$) water, but frequently moved out of warm and into cool water, sometimes over distances >19 km (Murphy 1977). Although they tended to spend more time during the winter in warm water, some individuals remained in adjacent areas where water temperatures were low (Murphy 1977; Crouch 1977).

Despite numerous studies of thermoregulation in crocodylians (Avery 1982; Bartholomew 1982), only a few investigations have focused on the T_b s selected by animals under controlled conditions. Selected T_b s are those maintained by an animal in a thermal gradient that allows the animal to extend its T_b above and below its activity T_b s, which are those of a free-living animal engaged in its normal daily routine

(Pough and Gans 1982). Thermal selection (thermal preference) as used in this chapter, refers to the behavioural responses that result in a particular T_b being maintained or "selected" from a range of available environmental temperatures, either in the laboratory or in the field.

In nature, crocodylians move between land and water in response to light-dark cycles as well as temperature cycles (Lang 1976). Consequently, an appropriate thermal gradient for such studies must provide opportunities for animals to be on land and in the water over the entire range of available temperatures. Previous studies have often involved animals confined to dry land [*A. mississippiensis* (Colbert *et al.* 1946; Johnson *et al.* 1978)] or subjected to heating trials [*A. mississippiensis* (Johnson *et al.* 1978); *Caiman crocodilus* (Diefenbach 1975c)]. The T_b s reported in these studies are at the upper end of T_b s voluntarily selected by animals living in gradients or in the field, and do not include representative lower values (Lang 1975, 1977, 1980; additional unpublished observations).

Internal and external factors modify reptilian thermal behaviour and T_b (Regal 1980; Huey 1982). In crocodylians, there is evidence that circadian rhythms, climatic conditions, social interactions and reproductive state all influence thermal behaviour (Lang 1976, 1977). Selected T_b s are altered by nutritional status, age, infection, social context and the temperature that a particular animal was incubated at when an embryo (Lang 1979, 1981, 1982, 1984, 1985, this chapter). Additional factors (reproductive state, acclimation, light regimes and exercise) affect the selected T_b s of other reptiles (Regal 1980; Huey 1982; Cannon and Kluger 1985) and may also affect those of crocodylians. Some of the factors that modify the crocodylian thermoregulatory system are in Figure 2.

When individuals of comparable age are tested under identical conditions, significant individual differences in selected T_b s are evident (Lang 1979, 1981; this chapter). Species differences in selected T_b s as well as differential responses to modifying factors are also apparent. For example, yearling *A. mississippiensis* select higher T_b s than *C. acutus*, and exhibit more pronounced heat-seeking behaviour when fed (Lang 1979).

Holding reptiles at constant temperatures and not providing opportunities for thermal selection can be detrimental. Although some lizards and snakes survive in captivity at nearly constant temperatures, chronic exposure to constant temperatures, especially high temperatures near the upper end of selected T_b s, may cause stress or injury (Regal 1980; Huey 1982; Avery 1984). Various species of crocodylians that have been tested in thermal gradients select mean T_b s in the range of 25 - 35°C . Constant temperatures below 25°C result in reduced feeding

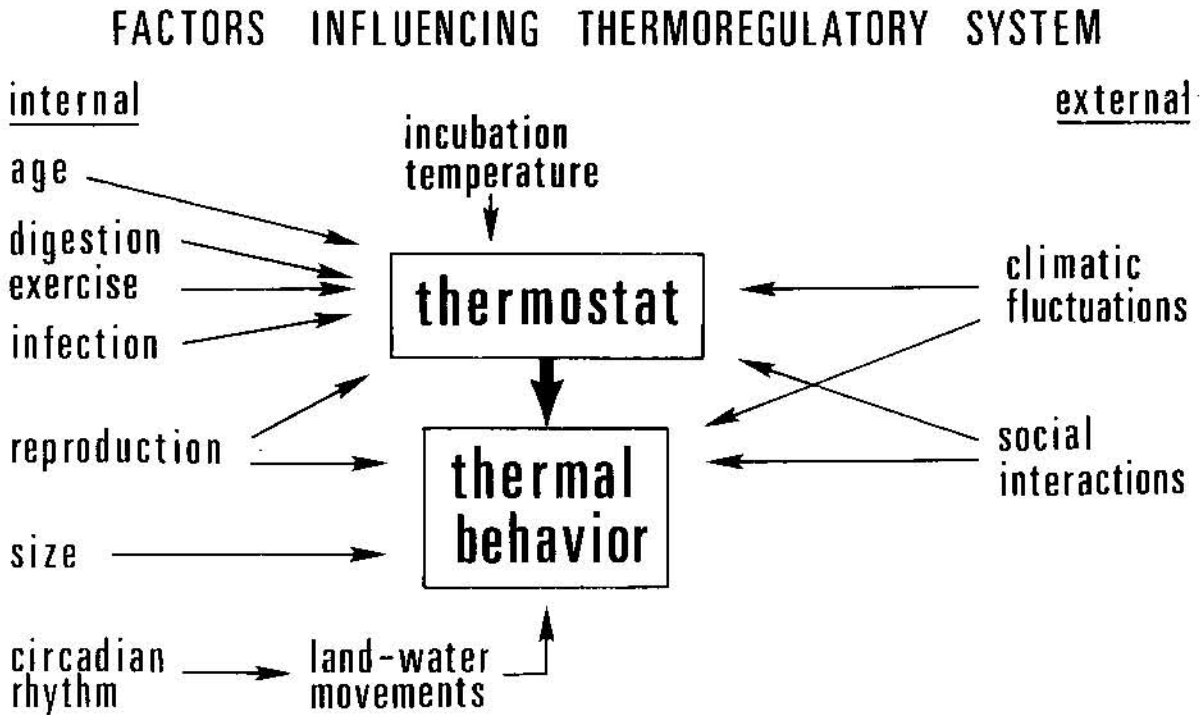


Fig. 2. Internal (left) and external (right) factors modify the thermoregulatory system of reptiles. The thermostat represents multiple controllers, and thermal behaviour is a composite of multiple responses (Crawshaw 1980). Body temperature is regulated by appropriate thermal behaviour. Each factor has varying effects on the thermostat and/or the thermal behaviour. Exercise, reproductive state, and social interactions are known to alter the thermostat in other reptiles, but the influence of these factors is yet to be demonstrated in crocodilians.

and limited growth. Most species, particularly those living in tropical habitats, do not tolerate T_b s below 15–20°C for prolonged periods (Coulson and Hernandez 1983; personal observations).

The ability of reptiles to thermoregulate is well documented (Avery 1982; Bartholomew 1982). However, thermoregulation is not an end in itself, but rather a complex trait that affects an individual's fitness by influencing how it feeds, grows, avoids predators and reproduces (Huey 1982). Unfortunately, the complexities of thermal selection and the multiplicity of factors that influence it have obscured demonstrations of its functional significance. Attempts to resolve this dilemma have led to ecological analyses of how temperature affects the performance of reptiles (Huey and Stevenson 1979). In particular, attention has focused on whole-animal processes that vary in the time scale of the response. Some responses are short term (metabolism, locomotor ability), others intermediate term (digestion, learning) and yet others are long term (growth, recovery from disease). The long term responses are especially interesting, but are difficult to study (Huey 1982).

Investigations in temperature effects on the physiological and behavioural performance of crocodilians are relevant. In *A. mississippiensis*, temperature has a minimal effect on circadian periodicity, but a significant effect on the pattern of locomotor activity. The daily activity is bimodal at

32°C and unimodal at 22°C (Kavaliers and Ralph 1980). The aerobic metabolism of crocodilians is temperature dependent, but the thermal dependence (Q_{10}) of metabolic rate is minimal or reduced at T_b s normally encountered in the field or selected by animals in a laboratory (Brown and Loveridge 1981; Lewis and Gatten 1985). In *Caiman crocodilus*, hearing responses are reversibly shifted toward lower frequencies and higher intensities with cooling, but important parameters (single unit thresholds, tuning sharpness, cochlear potentials) are unaffected by temperature changes between 17–35°C (Kauffmann 1974; Smolders and Klinke 1984). The spectral composition of *C. crocodilus* vocalizations and the repetition rate of calls also remain unchanged over 13–33°C. However, call duration and the interval between calls decreases with increasing temperature (Garrick and Garrick 1978). Brain activity (EEG) in *C. crocodilus* is temperature dependent, but state of arousal and slow wave sleep are independent of temperature at the upper end of selected T_b s (Parsons and Huggins 1965; Huggins *et al.* 1968; Meglasson and Huggins 1979). In the same species, digestion is directly affected by temperature: increasing temperatures result in increases in appetite, gastric contraction frequency and amplitude, and peptic activity. The thermal dependence (Q_{10}) of peptic activity is highest at low temperatures, and is reduced at high temperature (Diefenbach 1975a, b). In *A. mississippiensis*, gastric contractions in undisturbed animals are

most frequent during the coolest part of the daily thermal regime (Pugh 1978).

Taken together, these studies demonstrate that many responses are temperature dependent, although temperature affects different aspects of performance in different ways. Of particular interest are responses that exhibit non-linearity with temperature and/or a significant degree of thermal independence. For example, temperature has varied effects on the "burst" swimming of *A. mississippiensis*. Temperature influences how fast an animal swims, how it swims and whether it swims or exhibits defensive behaviour. Swimming speed *per se* does not appear to be an ecologically relevant measure of performance; performance as a function of temperature is complicated by qualitative changes in behaviour (Turner *et al.* 1985).

Why do crocodilians thermoregulate? Smith (1975) has suggested that *A. mississippiensis* function best within only a narrow portion of the temperature range found in their environment. But crocodilians differ from many reptiles that are active during the day; they tend to be inactive and thermoregulating, basking or avoiding heat. Field studies indicate that locomotor activity is most frequent at dawn, dusk and at night when T_b s are low (early morning) or declining (evening and at night). Loveridge (1984) noted that *C. niloticus* are most active in the evening, when they move about and hunt. During the breeding season, *A. mississippiensis* engage in social interactions that include chases, bellowing, territorial displays, courtship and mating behaviour. These activities peak in frequency in the early morning when T_b s are lowest, prior to daily basking (Lang 1977). Similar observations on other species (*C. porosus*, *C. novaeguineae*, *C. palustris*, *Caiman crocodilus*), suggest that contrary to Smith's (1975) suggestion, high T_b s are not a prerequisite for many of the activities crocodilians engage in. In many respects, cool crocodilians appear to function just as effectively as warm ones. If so, are there specific functions that are enhanced by thermoregulation?

Although it is clear that thermal selection is complex and modified by various internal and external factors, there are indications that particular thermal responses serve specific functions. In the following sections, recent experimental studies are summarised that illustrate how thermal selection is altered by feeding, infection, size and age, developmental temperatures and social factors (experimental methods are summarised in Appendix I). For each of these, the consequences and probable functions of particular thermal responses are discussed, and the practical implications of these and related studies are emphasized. There is a fundamental need to provide captive crocodilians with an adequate thermal environment.

THERMAL SELECTION, FEEDING AND GROWTH

Alligator mississippiensis respond to feeding by seeking heat (thermophily) and raising T_b s above fasting levels. When animals housed in a thermal gradient (20-40°C) are fed, they spend more time in the warm end of the gradient, and this results in significant increases in mean T_b s (1.5-4.0°C). When not fed, the same animals select lower T_b s by moving to the cool end of the gradient. This response to feeding and fasting is evident in hatchling and juvenile *A. mississippiensis* living in thermal gradients and also in adults living in natural settings (Lang 1977, 1979, 1982).

Elevated T_b s following feeding facilitate digestion. The time required for protein digestion and absorption in *A. mississippiensis* is twice as long at 20°C as it is at 28°C (Coulson and Hernandez 1983). The rate of digestion (passage of food through the gut) is three times faster at 30°C than at 15°C in *Caiman crocodilus* (Diefenbach 1975b). In contrast, digestive efficiency (the amount of energy extracted from the food) does not change appreciably (<5%) over a wide range of temperatures in other reptiles (Avery 1984) and presumably does not change significantly in crocodilians. Thus, the major effect of thermophily following feeding appears to be a decrease in the time required to process food, rather than an increase in the total amount of energy extracted from a meal (Greenwald and Kanter 1979). The primary benefit would be time saved rather than energy gained (per unit of food consumed).

Digestion entails considerable energy expenditure for food processing and conversion. The major cost is associated with increased rates of protein synthesis (Coulson and Hernandez 1983; Jobling 1983). At 28°C, the metabolic rate of *A. mississippiensis* increases three times following feeding (Coulson and Hernandez 1979). The metabolic increment associated with feeding is dependent on the quality and quantity of food ingested and on the frequency of feeding (Coulson and Hernandez 1983). In essence, eating a large meal commits an animal to a major metabolic investment in processing and assimilating that food.

Temperature clearly has major effects on the dynamics of digestion and assimilation (Coulson *et al.* 1978; Coulson and Hernandez 1983), and increased T_b s following feeding presumably:

1. Augment stomach acid production initially and subsequently accelerate neutralization of an alkaline tide;
2. Maintain osmotic balance of plasma amino acids;
3. Promote protein synthesis; and,
4. Increase thyroid activity.

An important adjunct of elevated T_b s may be an increase in the metabolic scope of recently-fed animals. It is not known if replete *A. mississippiensis* tire more easily or require additional time to recover from sustained activity, but the quiescent behaviour of animals following feeding suggests that performance capacity may be reduced in recently-fed individuals. In a recent study, Lewis and Gatten (1985) delineated the effects of temperature on the oxygen consumption of resting and spontaneously active *A. mississippiensis*, but comparable measurements for feeding alligators over a range of temperatures are not available. In brief, by selecting higher T_b s following feeding, *A. mississippiensis* is able to process a meal quickly, thereby reducing the time required for digestion. The savings in time mean that an animal can feed again soon if food becomes available. In addition, if performance is compromised by feeding, this effect would be minimized by digesting a meal rapidly.

If higher T_b s are beneficial, why do *A. mississippiensis* select lower T_b s when they are fasting? Metabolic rate increases as T_b increases (Lewis and Gatten 1985), thus the energy expenditure for maintenance alone may increase rapidly as T_b rises. The selection of lower T_b s reduces energy expenditure on maintenance, and energy savings are presumably then available for increased growth and/or reproduction. Observations on fish strongly suggest that they also behave in a way that maximises net energy gain (Brett 1971; Caulton 1978).

An essential component of these scenarios is the selection of lower environmental temperatures, resulting in lowered T_b s and reduced metabolic expenditure, during part of the diurnal cycle. On this basis, a crocodilian that remains at high T_b s when it is fasting, incurs additional maintenance costs that could otherwise be applied to growth (if it were able to reduce T_b).

In experiments I conducted with hatchling *A. mississippiensis*, 10 individuals were housed in thermal gradients and alternately fed then fasted for 10 day intervals, over a period of 90 days. Body temperatures were measured 4-5 times daily (see Appendix I), and thus a mean T_b could be computed for each animal for each feeding and fasting period. Feeding resulted in increased T_b s relative to fasting (Fig. 3), and there were significant differences between individuals in the selected T_b s (both fed and fasted). Some consistently selected high T_b s (No. 11, squares on Fig. 3) while others maintained low T_b s (No. 6, circles on Fig. 3). There were also individual differences in the magnitude of the thermal responses to feeding (the difference between fed versus fasted T_b s; Fig. 3). For some, the thermal response to feeding was large (4-5°C) whereas for others, the response was small (1-3°C).

Regression analysis was used to determine the extent to which the variation in growth (difference between initial and final mass) could be explained by food consumption (expressed as a percentage of body weight), mean T_b (overall average of fed and fasted treatments), and thermal response (the cumulative difference between successive rationing treatments; variables are described more fully in Appendix I). There was a very significant relationship (Fig. 4) between cumulative growth and the cumulative thermal response ($r^2 = 0.80$, slope = 2.83; testing for slope = 0, $t = 5.33$, $p = 0.001$), but the slopes of none of the other regressions were significant. Maximum growth occurred in the individuals whose accumulated thermal response to feeding was highest, and minimum growth in those whose response was lowest. There was no consistent relationship between growth and either relative food consumption or overall mean T_b .

The manner in which the thermal response affects growth can be seen by example. Number 12 selected an overall mean T_b (fed and fasting combined) of 29.8°C, whereas No. 6 selected 28.3°C. Mean food consumption for the two animals (18.6% per feed for No. 12 and 21.8% per feed for No. 6) was similar. However, accumulated thermal response (Fig. 4) differed greatly (+3.2°C for No. 12 and +9.8°C for No. 6). Animal No. 12 grew 32 g, whereas No. 6 grew 52 g during the test period. Nine months later under the same feeding regimen, No. 12 was only one fourth the size of No. 6 (252 g versus 991 g). In other words, individuals that selected a narrow range of T_b s irrespective of feeding, grew less than those that responded to feeding by elevating T_b s and then subsequently reducing T_b s during fasting.

The results described above have important practical implications for the maintenance of crocodilians in captivity:

1. The *A. mississippiensis* used in the study behaved so as to maximize net energy gain when feeding was limited to discrete periods. This behaviour was dependent on the availability of a range of suitable temperatures that permitted an animal to select T_b s appropriate to its feeding status. The study highlights a need to provide an adequate source of heat as well as a thermal mosaic of environmental temperatures. Land and water areas should be available at various temperatures, some of which are cool (<30°C) and others that are warm (>32°C).

2. If animals are held at high temperatures (no access to cooler temperatures), food must be available at frequent intervals. If not, then the additional maintenance costs associated with high T_b s may result in reduced growth.

3. Access to heat is beneficial because higher T_b s following feeding facilitate digestion and promote growth. If animals are maintained exclusively at cool

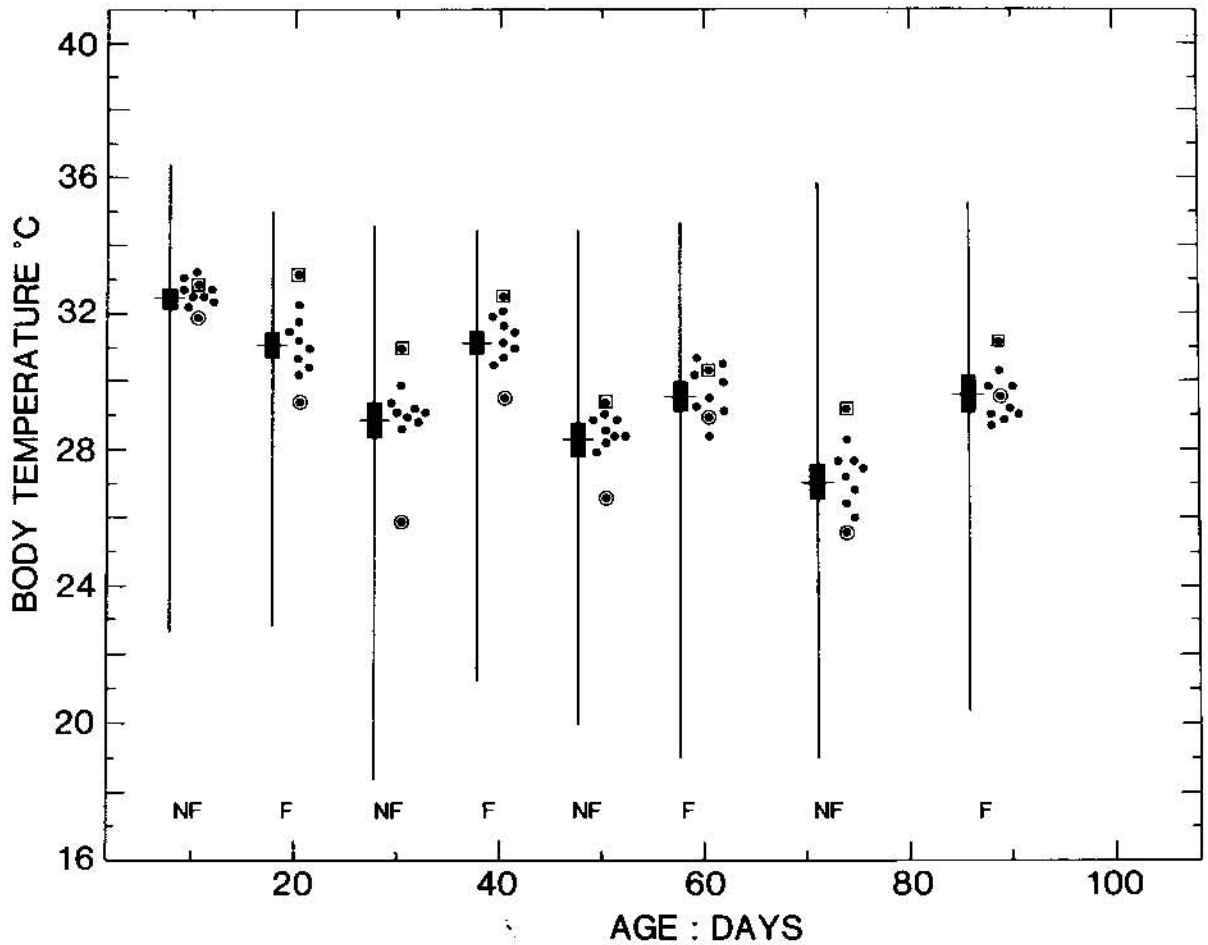


Fig. 3. Body temperatures (T_b 's) selected by young *Alligator mississippiensis* living in a thermal gradient. Animals were fasted (NF) or fed (F) for alternating 10 day periods from 0-90 days of age. For each treatment, pooled mean T_b 's ($N = 350$; 10 animals \times 35 T_b 's/animal) are indicated by horizontal lines \pm 2SE's (boxes) and ranges by vertical lines. Spots are mean T_b 's for each animal and values for No. 6 (circle) and No. 11 (square) are identified separately. Initial T_b 's were high, and then declined to fasting values within 30 days. Feeding resulted in elevated T_b 's relative to fasting.

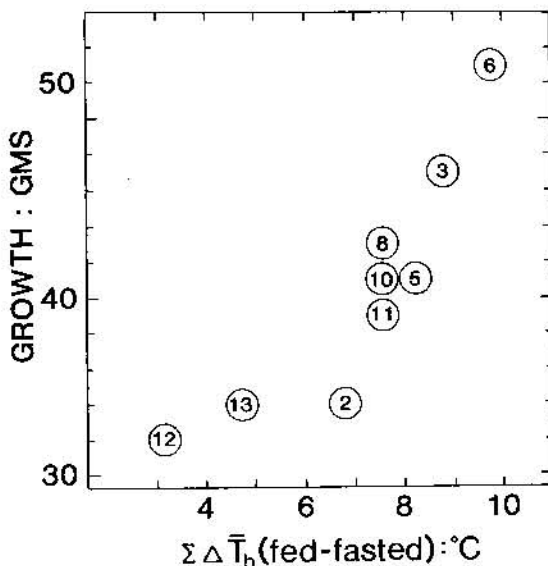


Fig. 4. Growth of young *Alligator mississippiensis* as a function of thermal response — the difference between selected body temperatures when fed and fasted (see Appendix I for methods).

temperatures, feeding will diminish and growth will be compromised.

Appetite appears to depend on the ultimate availability of heat, rather than on proximate temperatures. In other words, an animal will feed even when it is cool (for example at night) if it anticipates that warm temperatures will be available in the near future (the next day). Seasonal changes in appetite may reflect such anticipated ambient thermal regimes. For example in the spring, when ambient temperatures are increasing, *A. mississippiensis* feed more readily than in the fall when ambient temperatures are decreasing. Ultimately, appetite is temperature dependent. In *A. mississippiensis*, feeding ceases at temperatures below 22°C (Coulson *et al.* 1973). *Caiman crocodilus* regurgitate food if thermal regimes are unsuitable for digestion (Diefenbach 1981). In captivity, predictable access to heat is important. If thermal regimes are erratic, it is likely that animals will feed less often and grow less rapidly.

Thermophily following feeding has been noted in other species of crocodylians, but the response is not as pronounced as in alligators (Lang 1979, 1982). I reported that this response was absent in hatchling *C. novaeguineae* (Lang 1981), but subsequent studies on hatchling Siamese crocodiles *Crocodylus siamensis* indicated that a longer period of fasting (10 rather than five days) was needed before fasting values were lowered significantly (Lang 1985; see later, Fig. 6). Diefenbach (1975c) reported that this response was absent in *Caiman crocodilus*, but subsequent testing has indicated a significant increase of T_b s in fed versus fasted animals (unpublished data). Species comparisons indicate that in general, thermophily following feeding occurs in all species so far tested, but the response is diminished in *Crocodylus* and *Caiman* relative to *Alligator*.

What then is the optimum temperature range for growth in crocodylians? Extensive studies of fish have demonstrated that growth depends on a balance between temperature and food rationing. If food is limited, high T_b s mean high maintenance costs but without the attendant benefits of rapid food processing. Consequently, maintenance is expensive and the potential for growth is reduced. As rationing increases, the temperature for optimum growth increases (Brett 1979; Brett and Groves 1979). The T_b for maximum growth occurs at the T_b that a fish chooses in a thermal gradient (final preferendum) when food is not limited (Jobling 1981; McCauley and Casselman 1981).

Crocodylians are less dependent on ambient water temperatures than are fish, because they can move between land and water. However, their T_b s are still strongly influenced by water temperature. Thus, the selected T_b s of crocodylians are probably a useful guide for establishing the boundaries for thermal regimes that will maximize growth. On the basis of limited studies, young crocodylians select T_b s of 25-30°C when fasting and T_b s of 31-35°C when feeding (Lang 1979, 1981; Figs 3 and 6); the controlled temperature conditions used to raise *A. mississippiensis* successfully in Louisiana (see Joanen and McNease Chapter 32) are within the lower part of this selected T_b range. Narrower boundaries for any given species ideally requires an analysis of that species' selected T_b s in a thermal gradient. In addition to the factors mentioned above, variables such as infection and age may also influence thermal selection (see below).

THERMAL SELECTION, INFECTION AND HEALTH

In addition to its important role in energy utilization, reptilian thermal selection serves many other functions (Dawson 1975). When birds or mammals are infected with pathogens, such as bacteria, viruses or parasites, a fever often develops that is fuelled by

internal metabolic heat production. Fever is defined as an elevation in an organism's thermoregulatory "set point" that results from appropriate changes in its physiology and/or behaviour.

Recent research has revealed that ectotherms, including fish, amphibians and reptiles, are capable of developing and maintaining a behavioural fever in response to infection. The pioneering studies of Kluger and associates, using desert iguanas *Dipsosaurus dorsalis*, demonstrated that infected lizards thermoregulated at elevated T_b s and that high T_b s following infection enhanced survival. When infected lizards were held at high, normal and low temperatures, those at high temperatures survived whereas survivorship was reduced at normal and low temperatures (Kluger 1978).

Fever appears to be a common feature of the vertebrate thermoregulatory system, and probably has an ancient evolutionary ancestry (Kluger 1978). Behavioural fever has been demonstrated in some lizards and turtles, but not in other reptiles. Crocodylians are of interest because their phylogeny distinguishes the order from the other reptiles and allies them more closely with the birds, in which endothermy evolved independently. In addition, the survival value of behavioural fever is now evident from studies on lizards. If crocodylians respond similarly, then it would be possible to show how thermal selection functions in another context to promote health.

In experiments I conducted with 9 month old *A. mississippiensis*, 10 individuals housed in a thermal gradient were treated first with sterile saline as a control and then with live cultures of *Aeromonas hydrophila*, a pathogenic bacterium known to cause infections in other vertebrates. The animals responded to infection by selecting high T_b s within hours and maintaining a behavioural fever for two days. By days 3-4, T_b s had returned to normal levels. Mean T_b s were elevated above baseline levels by +4.9°C on the first day and by +2.1°C on the second day after the infection was induced. In contrast, the saline control resulted in a negligible rise of +0.2°C above previous levels (Fig. 5). The T_b of one individual (monitored continuously with a temperature sensitive radio transmitter) increased from 30.1°C before infection to 34.0°C within 4 hours of treatment; it peaked at 37.5°C after 7.5 hours, then declined to near-normal levels within the next 24 hours. There were also significant individual differences in the thermal response to infection. The mean difference in T_b before and after treatment ranged from +1.6°C to +7.8°C. None of the animals used in these experiments showed ill effects from the treatment; they all subsequently behaved normally and continued to grow at normal rates (Lang 1984).

This experiment clearly demonstrated that *A. mississippiensis* responded to infection by

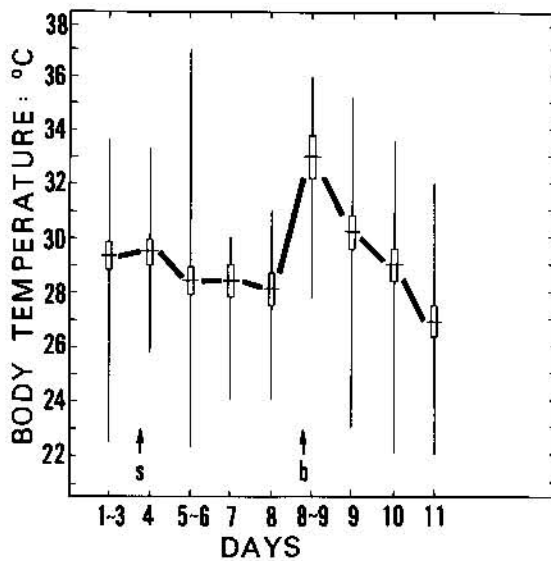


Fig. 5. Behavioural fever in young *Alligator mississippiensis* ($N = 10$; 9 months old) in response to peritoneal injections of live bacterial suspension (b; *Aeromonas hydrophila*) versus sterile saline (s). Selected body temperatures in a thermal gradient are indicated by range (vertical lines), means (horizontal lines) and $\pm 2SE$'s (boxes). Sample sizes (N) = 90 (1-3 days), 70 (4 days), 120 (5-6 days), 30 (7 days), 30 (8 days), 60 (9 days), 70 (10 days), 90 (11 days).

developing a behavioural fever. Body temperatures were elevated rapidly to high levels that persisted for several days. The results are interesting because other studies indicate that:

1. The bacterium used in these experiments is commonly found on the surface and in the tissues of healthy *Alligator mississippiensis* in the wild and in captivity (Gorden *et al.* 1979); and,
2. Under unusual conditions, this pathogen causes death in wild *A. mississippiensis* (Shotts *et al.* 1972; Brisbin 1982). In these cases, abnormally high temperatures and/or the stress of capture and handling were also implicated in the deaths of infected animals.

In a parallel study, the responses of *A. mississippiensis* to infection by *Aeromonas hydrophila* and to thermal stress were investigated (Glassman and Bennett 1978). The dosage was equivalent to that used in the behavioural experiments described above. Juvenile animals responded to infection with an increase in white blood cells, an immune-defense reaction seen in other vertebrates. When treated animals were held at constant temperature (20°C, 25°C, 30°C and 35°C), the maximum increase in white blood cells and neutrophilic macrophages occurred at 30°C. At this temperature, recovery of infected animals was optimum, but infected animals held at 35°C died within three weeks; death was attributed to an ineffective immune-defense response, an increase in the growth of bacteria and the stress of chronically high temperatures.

These results are particularly significant because they contrast sharply with my experimental findings of behavioural fever in *A. mississippiensis* discussed above. Infected *A. mississippiensis* living in a thermal gradient selected high T_b 's, ranging from 30.9-35.1°C (individual mean T_b 's; individual maxima = 33.2-36.0°C; grouped mean = 33.0°C) for several days and then behaved normally and continued to grow — those held at constant high temperature (35°C) died.

Alligator mississippiensis free to select appropriate T_b 's from a range of available temperatures were able to resist infection by selecting suitable thermal regimes. As similar responses occur in other reptiles and in other ectothermic vertebrates, most crocodilians probably respond like *A. mississippiensis*. The importance of the behavioural response to temperature is obvious, and again highlights the need to provide a thermal mosaic of environmental temperatures to promote good health and growth.

Adequate thermal conditions are essential for the health of reptiles. The immune response is temperature dependent; antibody synthesis is highest at an optimum temperature and reduced at higher and lower temperatures (Cooper *et al.* 1985). Therapy with heat is often an important adjunct or alternative to chemotherapy. For example, parasitic infections in snakes have been treated by increasing ambient temperatures to 35-37°C for 1-2 days, a treatment which augments the host immune response (Deakins 1980). Viral and bacterial infections are often exacerbated by low temperatures, that make reptiles more susceptible to disease, and by high temperatures that stress animals and promote the growth of pathogens (Jacobson 1980; Kleese 1980; Marcus 1980). Lack of adequate temperature control is a major predisposing cause of disease in captive crocodilians (see Foggin Chapter 36). Health and disease, particularly in captivity where stress is an additional factor, are the result of complex interactions between a reptile and its environment (Cowan 1980). Allowing crocodilians to thermoregulate rather than imposing unnatural (especially constant) thermal regimes upon them, can be expected to improve health.

THERMAL SELECTION, SIZE AND AGE

Crocodilians are the largest living reptiles. An adult may be 100 times longer and 2000-20,000 times heavier than a hatchling. Theoretically, the magnitude of such differences should result in major ontogenetic differences in physiology and behaviour. For example, the maintenance costs per gram of tissue are much lower for a large versus a small *A. mississippiensis*, but the performance capacity of a small *A. mississippiensis* is much greater. For large animals, recovery from activity requires days rather than hours (Coulson 1984). Heat exchange with the environment and the transport of

heat within the body also vary with body size (Bartholomew 1982; Smith *et al.* 1984; Turner and Tracy 1985). In the light of these size-related differences in thermal physiology, it is reasonable to ask whether thermal selection (thermal preference) varies as a function of size and/or age in crocodilians.

In a variety of ectotherms, ontogenetic (developmental) changes have been documented with respect to thermal tolerance and thermal selection. In many species of fish, juveniles prefer warmer temperatures than adults (McCauley and Huggins 1979; Shrode *et al.* 1983), and similar results have been reported for some species of amphibians, but not for others (Dupre and Petranka 1985). In reptiles, the absence of size-dependent changes in the T_b s selected by certain lizards and snakes has been noted, yet differences in the thermal behaviour of juveniles versus adults have also been reported [see references in Lang (1981) and Huey (1982)]. The selected T_b s of blue-tongue skinks (*Tiliqua scincoides*) were highest in the youngest animals and declined with size and age (Phillips 1983).

In crocodilians, comparisons of thermal selection between different sized individuals are limited. In several studies, a direct relationship between size and selected T_b s (thermal preference) has been reported among juveniles [*Caiman crocodilus* (Diefenbach 1975c); *A. mississippiensis* (Johnson *et al.* 1978)]. However, the T_b s in these studies were derived from animals during heating trials or that were otherwise exposed to steep temperature gradients; the reported T_b s reflect size-dependent differences in heating rates. These studies were not based on the daily records (24 hours) of individuals free to thermoregulate in aquatic-terrestrial gradients.

In fact, studies of crocodilians in natural settings or in thermal gradients indicate that different sized juveniles and adults do not maintain appreciably different T_b s. *Crocodylus niloticus* ranging in size from 0.5-38 kg body weight had similar T_b s (30-34°C) while basking, and a bimodal pattern of daily basking behaviour was evident in animals of all ages (Loveridge 1984). *Alligator mississippiensis* ranging in size from 0.3-245 kg body weight maintained nearly equivalent T_b s (27-33°C) in thermal gradients (juveniles) and in large natural enclosures (adults). Differences within juveniles (Lang 1979) and within adults (Lang 1977) were greater than between-group differences. Daily T_b s of juvenile and adult *C. novaeguineae* were monitored in large natural enclosures, and they did not differ from each other despite a 100 times difference in body weight (Lang 1981). In telemetry studies of *Caiman crocodilus* (3-50 kg), *C. novaeguineae* (37-110 kg) and *C. porosus* (97-750 kg), daily T_b s (integrated over 24 hours) did not vary as a function of body weight over a wide range of sizes (Lang 1980). In a similar study of

A. mississippiensis (59-245 kg), thermal behaviour rather than size was the major determinant of heating rates among different sized alligators. Daily T_b s varied considerably between individuals, but did not correlate with body size (Lang 1977).

Despite the lack of correspondence between T_b s and size in juvenile and adult crocodilians, young in a number of species select high T_b s for several weeks immediately after hatching. Thereafter, T_b s decline to levels that approximate those of juveniles and adults. In *C. novaeguineae*, hatchlings in a thermal gradient selected T_b s of 33-34°C, which were significantly higher (by 1.5-3.0°C) than later levels. Limited observations suggested that *C. porosus* hatchlings behave in a similar fashion (Lang 1981).

Hatchlings of several other species are now known to have a pronounced thermophily immediately after hatching (Lang 1982, 1985). *Alligator mississippiensis* hatchlings initially selected T_b s of 32.5°C that declined to 27-28°C (when fasting) within a month. Some individuals selected very high T_b s (36-37°C) during this period (Fig. 3). Hatchling *C. siamensis* responded similarly. Initial T_b s were 33-34°C and subsequently declined to 29-30°C (when fasting) within 30-40 days. During this period, some individuals selected T_b s of 38-39°C (Fig. 6).

These observations suggest that an initial period of thermophily may be a characteristic of crocodilian hatchlings. Crocodilian embryos typically hatch with a large "residual" yolk store in the body cavity (10-20% of body weight), and the heat-seeking behaviour and high T_b s probably facilitate its early digestion. Hatchlings do not always accept food immediately, but may take 1-4 weeks before beginning to feed at levels (15-30% of body weight) that occur in juveniles several months later (see references in Lang 1981). Rapid assimilation of yolk would promote growth and would enable young to begin feeding soon after hatching. For *A. mississippiensis* hatchlings, increasing ambient temperatures by 2-4°C (to 31°C) during the initial two weeks results in better survival and earlier acceptance of food (Joanen and McNease 1976).

These results have important implications for the maintenance of crocodilians in captivity. Providing adequate sources of heat (for example heat lamps, warm water, direct sunlight), should increase survival during the immediate post-hatching period. Low temperatures retard the digestion of residual yolk, delay the initiation of feeding, retard growth and increase susceptibility to disease. Inadequate temperatures are an important predisposing cause of disease in hatchlings (see Foggin Chapter 36). Unassimilated yolk compacts in the yolk sac, becomes infected and causes death.

Because some hatchlings may select very high T_b s (37-39°C) within thermal gradients (Fig. 6), a pen or

enclosure design that allows access to temperatures between 35–40°C in the immediate post-hatching period may be beneficial. However, cooler land and water temperatures, in the range of 25–35°C, should also be provided. Raising ambient temperatures to 31–32°C may increase survivorship, but constant higher temperatures may also increase the risk of thermal stress and disease. As indicated previously, a range of suitable temperatures is preferable because it permits an animal to select appropriate T_b s behaviourally in response to specific conditions.

DEVELOPMENTAL TEMPERATURES AND THERMAL SELECTION

Prior temperature experience generally has little or no effect on thermal selection in reptiles (Crawshaw 1980; Crawshaw *et al.* 1980). Holding an animal at low or high ambient temperatures does not alter the T_b s that it selects subsequently. The reptilian thermostat is labile and influenced by various factors, but it is also species-specific (Regal 1980; Huey 1982). When thermal responses differ among closely related species, these differences are usually attributed to genetic differences which have been acquired through natural selection (Huey and Webster 1976).

On the other hand, certain physiological differences may result from the environmental induction of physiological responses during early life. This effect has been variously referred to as: irreversible acclimation; phenotypic acclimation; physiological imprinting; and, thermal imprinting. Previous studies have demonstrated that salinity and/or temperature experiences during the early life stages can have irreversible effects on the later physiological responses of invertebrates and fish. Winkler (1985) describes such an effect on the thermal tolerance of a fish population and discusses the implications of this phenomenon on interpretations of physiological differences between individuals and populations.

The temperatures at which embryos are incubated has a profound effect on embryonic growth and development in reptiles (Gans and Billett 1985; Gans *et al.* 1985). For example, developmental temperatures have dramatic effects on scalation in some snakes (Fox 1948; Osgood 1978). The temperatures during critical periods of embryonic development determine phenotypic sex in some reptiles, notably in turtles and crocodylians (Ewert 1985; Ferguson 1985; Standora and Spotila 1985; see Webb *et al.* Chapter 50). In light of these observations, developmental temperatures may also produce irreversible physiological changes. For example, thermal imprinting during development may be manifest in post-hatching physiological performance, for example, in thermal selection.

I examined the possible effects of the incubation temperature of eggs on the thermal behaviour of the resulting hatchlings, using *C. siamensis*. Eggs from the same clutch were incubated at high (32.5–33.5°C) and low (27.5–28.0°C) temperatures. Males (14/14; 100%) were produced at high temperatures and females (11/11; 100%) at low temperatures.

Hatchlings (four males; two females) were introduced into thermal gradients immediately after hatching and were maintained on a feeding regime (fed versus fasted in 10 day cycles) identical to the procedure used with hatchling *A. mississippiensis* described above. Selected T_b s were monitored 4–5 times daily for each individual throughout the experiment (experimental method — Appendix 1).

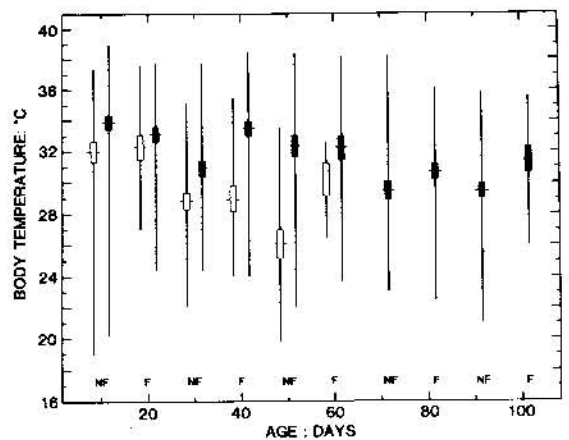


Fig. 6. Influence of incubation temperature on subsequent thermal behaviour of young *Crocodylus siamensis* siblings housed in a thermal gradient. Hatchlings incubated at 32.5–33.0°C (dark bars; N = 4 males; pooled N = 160/treatment) selected consistently higher body temperatures than those incubated at 27.5–28.0°C (open bars; N = 2 females; pooled N = 80/treatment). Ranges (vertical lines), means (horizontal lines) and $\pm 2SE$'s (boxes) are presented for ten day feeding (F) and fasting (NF) periods.

Incubation temperature had a definite influence on the subsequent thermal behaviour and selected T_b s of these young crocodiles. Hatchlings incubated at high temperatures selected consistently higher T_b s in comparison with those incubated at low temperatures. The magnitude of the difference averaged 3.3°C, ranging from 1.2–7.4°C. Differences were evident regardless of whether the animals were fed or fasted, but were greater during fasting (+4.9°C) than feeding (+2.6°C). This effect may be related in part to the larger volume of residual yolk in hatchlings from the high temperature incubation (Webb *et al.* Chapter 50), but it persists after yolk is likely to have been completely absorbed (for example 40–50 days on Fig. 6). These data are limited because the number of animals tested was small, but they do demonstrate that thermal selection is affected directly or indirectly (perhaps through sex?) by incubation temperature.

Some constant incubation temperatures produce hatchlings of both sexes in varying proportions [*A. mississippiensis* (Ferguson 1985); *C. porosus* (see Webb *et al.* Chapter 50)], and in some species [*C. johnstoni* (Webb and Smith 1984; Webb *et al.* Chapter 50)], at least some females are produced at all constant incubation temperatures so far tested. Thus it is possible to compare the thermal selection of hatchlings of the same sex incubated at different temperatures, and therefore to isolate a temperature effect from a sex effect. Similarly, shifting eggs from high to low incubation temperatures (or vice versa) at different stages of development, should allow any critical embryonic period when thermal selection is affected to be identified. Perhaps it coincides with the critical periods for sex determination. Experiments designed to answer these and related questions are currently underway with *A. mississippiensis*.

If the results of this initial study are confirmed and extended to other species, the effect of incubation temperature on subsequent thermal selection would have important consequences for the growth of hatchlings. Animals that select low temperatures would grow less rapidly, but would be at an advantage when climatic conditions are relatively cool and/or food is limiting. Under such conditions, maintenance costs would be lower at low temperatures. On the other hand, animals that select high temperatures would grow rapidly, particularly if climatic conditions were favourable and food was abundant. Differences in thermal selection should result in differences in the growth rates of hatchlings incubated at different temperatures. The size of *A. mississippiensis* hatchlings (relative to egg size) and their post-hatching growth rates within constant environment chambers, are both influenced by the temperature of egg incubation (see Joanen *et al.* Chapter 51).

Thermal regimes during development not only determine the sex and growth of embryos, but incubation temperatures also appear to alter the physiology and behaviour of hatchlings. Investigations are needed that focus on how incubation temperatures may modify hatchling performance. It would be particularly instructive to examine how feeding, thermal response and growth, change as a function of developmental temperature.

THERMAL SELECTION VERSUS NON-THERMAL BEHAVIOURS

Reptiles thermoregulate to live, but do not live to thermoregulate. Numerous non-thermal factors influence thermal behaviour, and other behaviours, such as foraging, escaping predators and social interactions, may compete with and sometimes take precedence over thermally-directed behaviours. Social factors have various influences on how, where and when ectotherms thermoregulate [fish (Medwick

et al. 1981); amphibians (Gatten and Hill 1984)]. In reptiles, dominant individuals may exclude subordinates from access to heat (Bruton 1977; Done and Heatwole 1977; Saint Girons 1977) or otherwise alter patterns of heat-seeking behaviour by subordinates (Regal and Connolly 1980). Alternatively, the presence of a subordinate may stimulate heat-seeking by a dominant animal (Regal 1970). In crocodylians, dominant animals may restrict subordinates from access to water or shade (personal observations with *C. porosus*) or influence heat-seeking by subordinates in various ways [*A. mississippiensis* (Lang 1977)].

Young crocodylians are gregarious and tend to associate closely with siblings or other hatchlings. This behaviour was evident in small *A. mississippiensis* housed in the thermal gradients; during experimental studies, they were often found together. A simple experiment was conducted to determine if social interactions affected the thermal selection of these animals.

Ten young *A. mississippiensis* housed together in a thermal gradient were removed and fed in plastic tanks. Nine were then transferred to another room and the remaining individual was fed a miniature, temperature-sensitive radio transmitter before being returned to the gradient alone. The T_b of this individual was monitored automatically each half hour for the next 10 days. During this period, the nine siblings were fed again on day 4 and were returned to the home gradient on days 5-6 (48 h), removed on day 7, fed on day 8, and returned to the home gradient a second time on day 9 (24 h), and then removed on day 10.

This study demonstrated that the presence of social companions significantly altered the thermal behaviour of the experimental animal. In isolation, its T_b s were initially elevated following feeding and then declined by days 3-4 to fasting levels. In the company of fed companions on days 5-6, it selected high T_b s typical of fed animals, even though it had not been fed. When the siblings were removed on days 7-8, the isolated animal's T_b s declined to near fasting levels. A second introduction of fed companions into the gradient (day 9) again resulted in elevated T_b s, which again declined to fasting levels (day 10) when they were removed. The unfed experimental *A. mississippiensis* maintained low T_b s when it was alone, but it selected high T_b s when it was in a social group selecting high T_b s, even though it had not been fed (Fig. 7).

This experiment demonstrates how another activity (gregarious behaviour), can take precedence over thermal selection. In this case, the experimental animal "chose" to associate with its companions even though such an association entailed high T_b s and increased maintenance costs. In contrast, when alone it reduced its energy expenditure by

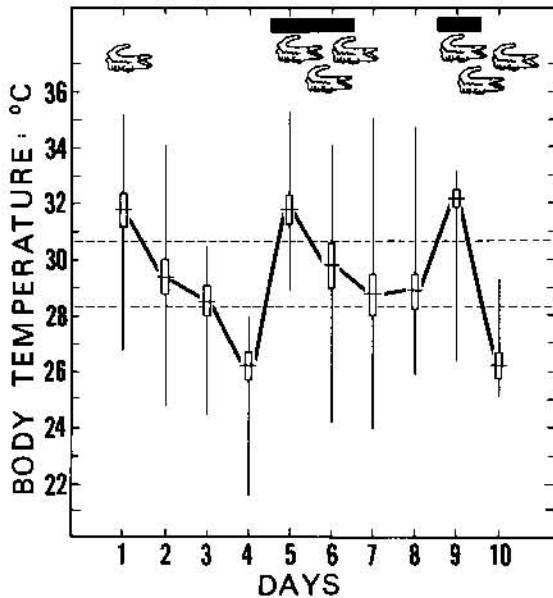


Fig. 7. Social influences on the selected body temperatures ($T_{b,s}$) of a juvenile *Alligator mississippiensis* living in a thermal gradient. $T_{b,s}$ were monitored with telemetry (stomach transmitter; readings every 30 minutes; $N = 48/\text{day}$). Ranges (vertical lines), means (horizontal lines) and $\pm 2SE$'s (boxes) are presented for each day. The animal was fed on day 0 and placed in the gradient alone, where $T_{b,s}$ declined to fasting levels by day 4. Although still unfed, $T_{b,s}$ increased to "fed" levels when fed siblings were placed back in the gradient (black bars at top of graph; days 5-6, 9) and decreased when they were taken out (days 7-8, 10). Dashed lines indicate fasted (lower) and fed (upper) mean $T_{b,s}$ selected by hatchling alligators (Fig. 3).

selecting lower $T_{b,s}$. The cost of group association (in terms of increased maintenance) was apparently outweighed by the benefits of joining a group.

Group living presumably benefits an individual by decreasing its risk of predation and/or increasing its efficiency of feeding (Bertram 1979; Morse 1980). Field studies with *A. mississippiensis* indicate that hatchlings disperse at dusk to forage alone or in small groups and then reassemble later in the night and early morning in loosely-organized sibling groups. Individuals spend the daylight hours closely associated while basking on land or in the water (Deitz 1979). In most other species, young are found together in groups for varying periods after hatching [see references in Garrick and Lang (1977) and Ferguson (1985)] with some notable exceptions (Mazzotti 1983).

Predation on young crocodilians is a major source of mortality, and protective behaviour by adults towards hatchling groups is well developed. It is likely that a decreased risk of predation is the ultimate factor promoting gregarious behaviour among young crocodilians. However, proximate behaviours, such as responding to vocalizations by approach, appear to be responsible for maintaining group cohesiveness (Deitz 1979). The "normal" condition for most young is probably one of

close association with other hatchlings for a period of time. In this regard, it is interesting to note that young *Caiman crocodilus* maintained in a colony exhibited a set pattern of alertness and behavioural sleep. Isolated individuals remained alert for unnaturally long periods of time, finally becoming exhausted, yet failing to display normal patterns of behavioural sleep (Warner and Huggins 1978).

In most captive situations, young animals are housed and raised in groups. The above studies suggest that group associations play a major role in the lives of young crocodilians and thus may be important in captivity. If young crocodilians are isolated, individuals may not behave normally, may be subject to increased stress, and may fail to feed and grow. Perhaps most important, the study illustrates that thermal selection can be modified at times, by non-thermal factors.

CONCLUSIONS

Behaviour is the principal means by which crocodilians control their body temperature (T_b). Thermal selection entails specific heat-seeking and heat-avoidance behaviours that raise or lower T_b in response to internal and external modifying factors. Feeding results in an increase in heat-seeking behaviour and in elevated T_b that facilitate digestion and energy assimilation. During fasting, animals that select lower T_b are able to reduce the energy demands associated with high T_b . The thermal response to food availability maximizes net energy gain and promotes growth.

Animals infected with pathogens select high T_b that enhance resistance to disease. Hatchlings initially select high T_b , a thermophilic response, to facilitate yolk assimilation which in turn fosters early acceptance of food. Other factors, both thermal (for example, incubation temperatures) and non-thermal (for example, social interactions), influence an animal's thermal behaviour and the T_b it selects. Taken together, these studies illustrate that thermal selection in crocodilians is a complex behavioural response which varies with species and as a function of many influences on individual animals.

Clearly, the thermal environment and the animal's response to it play major roles in determining growth, health and well-being. Consequently, careful consideration of thermal requirements is warranted in any captive facility. On the basis of limited data, crocodilians select T_b of 25-35°C when permitted to do so in a variable thermal environment. Pens and enclosures should be provided with thermal conditions within this range in order to allow individual animals to regulate T_b by the appropriate behaviour.

Requisites include adequate land and water areas at varying temperatures, access to heat on a daily

basis, and access to shade or low temperatures throughout the day. Deep water (>1 m) serves as an effective buffer against hot, daytime ambient temperatures. Ample sunlight and/or heat lamps provide suitable heat sources when ambient temperatures are low. If thermal conditions are stable relative to daily ambient temperature fluctuations (indoor enclosures or covered outdoor pens), or if facilities are maintained at near constant temperatures, then caution is needed to prevent thermal stress from continual exposure to high or low temperatures.

Raising *A. mississippiensis* hatchlings under controlled temperature conditions has proven remarkably successful (see Joanen and McNease Chapter 32). However, that success is dependent on the provision of the right compromise between food availability, temperature, hygiene and husbandry, which has been derived through research. In addition, *A. mississippiensis* may be more amenable to constant warm conditions than are other more tropical species of crocodylians. In the absence of equivalent data for most species, allowing crocodylians to thermoregulate by providing a suitable, yet variable thermal environment is probably the best raising strategy.

ACKNOWLEDGEMENTS

These studies were supported by grants from the Faculty Research Grants Committee at the University of North Dakota. Additional support and logistic assistance was provided in numerous ways by the faculty and staff of the Biology Department at the University of North Dakota. I thank Cecil Clemons at Gatorama, Ted Joanen at Rockefeller Refuge and Ron Magill at the Metro Zoo, Miami for providing alligator and crocodile eggs, and Paul Pickett, Kathryn Lofthus and Leroy Gravseth for assistance with experiments and with animal care. I am grateful to Grahame Webb, his colleagues and the staff at the Conservation Commission of the Northern Territory, for the opportunity to attend and present this paper at the Technical Conference on Crocodile Conservation and Management, held in Darwin, Australia, in January 1985.

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APPENDIX I

Experimental Methods

Studies were conducted with American alligators (*A. mississippiensis*) and Siamese crocodiles (*C. siamensis*) hatched from eggs transported to and incubated at the University of North Dakota.

Alligator mississippiensis eggs were obtained from a breeding facility in south-central Florida, and were incubated at $30.0 \pm 0.25^\circ\text{C}$. All of the hatchlings were females, verified at 2 years of age by cloacal examination. Upon hatching, they were permanently housed in thermal gradients. Each gradient was constructed from a large tank (2.5 x 1 x 1 m high) outfitted with platforms, baffles, heaters and heat lamps, thermostats, water circulators and water level valves. This arrangement provided an aquatic-terrestrial thermal gradient (20-40°C) in which heat was continuously available 24 hours/day. The photoperiod was 12L:12D. The gradients were reversed periodically to control for position effects and were housed in a room at $18.0 \pm 1.0^\circ\text{C}$.

Animals were marked individually. Body temperatures (T_b 's) were monitored 4-5 times daily at intervals of 2-3 hours (day and night) with a cloacal thermometer calibrated against a certified, standard thermometer. Body temperatures in some individuals were also monitored with small temperature-sensitive radio transmitters placed in the stomach and monitored automatically every 30 minutes. The transmitters were calibrated before and after each use with a standard thermometer, and were accurate to $\pm 0.1^\circ\text{C}$. The presence of the transmitter in the animal's stomach had no detectable effect on its T_b .

Limited rationing was provided by alternating periods of fasting versus feeding (10 days/treatment). During each feeding period, animals were removed from the gradients and placed in plastic tanks with food and heat available for 4-8 hours. Animals were allowed to feed voluntarily on *ad libitum* quantities of chopped fish and vitamins each second day, and typically consumed 15-25% of their body weight at each feeding (5 feedings/10 day feeding period).

For the analysis of growth as a function of food consumption, mean T_b and thermal response, the following values were determined for the last five measurement periods (40-90 days; fed = 40, 60, 80 days; fasted = 50, 70 days). The first three periods were excluded from the analysis because newly-hatched young exhibited a pronounced thermophily for 0-30 days [see Discussion, p. 310, and Lang (1981) for a similar response in *C. novaequinae*]. Growth was expressed as the difference in mass (in grams; measured in post-absorptive animals 48 hours after feeding) of each animal at the start and finish of the analysis period (initial = 40 days; final = 92 days). For each animal, the food consumed at

each feeding was expressed as a percentage of pre-feeding body weight, and was averaged for each of the three feeding periods (five feedings/10 day period). The mean food consumption for the three feeding periods (at 40, 60 and 80 days) was used for the analysis.

For each animal, body temperatures were averaged for each of the five measurement periods (two fasting and three feeding; plotted as individual points on Fig. 3). These values were used to calculate the mean T_b and the thermal response for each individual. The mean T_b was the overall average of the fed and fasted values (combined) for the analysis period. To calculate the thermal response, the magnitude of the difference between successive treatments (fed versus fasted) was determined for the last five measurement periods: fed at 40 days versus fasted at 50 days; fasted at 50 days versus fed at 60 days; and, the same for 60 versus 70 days and 70 versus 80 days. These differences were then summed (irrespective of sign) to provide a measure of thermal response to alternate fed versus fasted treatments. Thus the thermal response of each animal (as plotted on Fig. 4) is the cumulative change between successive treatments for the analysis period. It is used here simply as an index of how T_b varied as a function of the rationing treatments.

Behavioural fever was induced by injecting a suspension of live *Aeromonas hydrophila*, a gram negative bacterium, in a dose of 1 ml/100 g body weight into the peritoneal cavity. Controls received an equivalent dose of sterile saline. Animals were tested at fasting T_b (10 days after feeding).

The *C. siamensis* eggs, from a single clutch, were obtained from a breeding facility at the Metro Zoo in Miami, Florida. The eggs were placed in incubators ($\pm 0.25^\circ\text{C}$) within 48 hours of laying and were incubated in moist vermiculite. Two incubation temperature treatments were used, "high" (temperatures varied between 32.5°C and 33.0°C) and "low" (27.5 - 28.0°C). Hatchlings were individually marked at the time of hatching and were then introduced into the thermal gradients. Sex was determined by cloacal examination at 2 years, and was confirmed by dissection of gonads. Monitoring of T_b and feeding procedures were as described above for *A. mississippiensis*.

Statistical analyses were conducted by computing descriptive statistics for individuals and pooled T_b measurements for each treatment. Statistical procedures followed those in the Statistical Analysis Systems (SAS).

Significance was determined at a level of $p < 0.05$ (two-tailed).