

Burst Swimming of Alligators and the Effect of Temperature

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ABSTRACT.—The swimming speed of alligators, like the locomotory speeds of many ectotherms, is significantly affected by temperature. However, temperature also affects alligators' swimming behavior. The effect of temperature on swimming speed appears to be partly the result of direct effects of temperature on muscle performance and effects of temperature on swimming behavior.

Speeds of locomotion among reptiles are strongly dependent upon body temperature (Bennett, 1980; Christian and Tracy, 1981), and are usually explained by a direct effect of temperature on the physiology of muscle (Bennett, 1980). The translation of muscle work into an animal's forward speed is a complex process that depends not only on the physiological performance of the locomotory muscles, but also on a number of other factors such as the specific muscle groups powering locomotion, the geometry and orientation of their muscle fibers and the numbers and types of active muscle fibers. If any of these other factors is itself affected by temperature, the performance curve (the relation between locomotory speed and body temperature) may reflect something other than a direct effect of temperature on the physiological performance of muscle.

In this paper, we report the effect of temperature on swimming speed of the American alligator (*Alligator mississippiensis*).

Specifically, we suggest that temperature affects swimming speed partly through effects on muscle performance, and partly through effects on the way an alligator swims.

MATERIALS AND METHODS

Animals.—The animals used in this study were small individuals of the American alligator, taken from a large collection of alligators maintained in our laboratory since 1977.

Speed and Behavior during Burst Swimming.—Burst swimming is the name given to a rapid burst of swimming which propels the animal away from some aversive stimulus—such as a pinch of the tail with the fingers, or a tap on the back with a stick. We used seven small individuals, 550-1170 g body mass.

Burst swimming trials were done in a large trough (7.3 m long × 1.2 m wide), constructed from heavy plywood, and lined with two layers of 6 mil black plastic. Water depth during trials was 15 cm. The trough was divided along its length into four sections (Fig. 1); a holding section, a starting section, a test section (itself subdivided into 3 segments 1 m long each) and a stopping section.

A bout of burst swimming was begun by placing the animal in the starting section, facing it in the direction of the test section. Burst swimming was induced by suddenly pinching the alligator's tail, and chasing it aggressively along the trough. After chasing it

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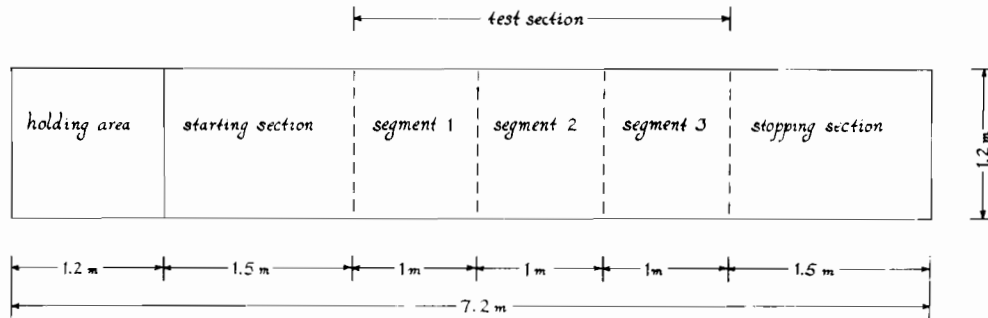


FIG. 1. Schematic top view of trough used for burst swimming trials, showing layout of the sections described in the text.

through the test section, harassment of the animal was broken off, allowing it to come to a stop in the stopping section.

During a bout of burst swimming, data on swimming speed and swimming behavior were recorded. Time (s) for the animal to traverse each 1 m segment of the test section was measured using three matched stopwatches. Burst speed (m s^{-1}) is the inverse of the time to traverse the 1 m segment. At the same time, the alligator's swimming behavior as it traversed each 1 m segment was classified according to two criteria: (a) whether the animal swam with the legs tucked at the side of the body, thus being propelled only by the tail, or swam using the legs as paddles in addition to the tail, and (b) whether the animal swam completely submerged in the water, or swam with the head breaching the surface. The criteria were chosen on the basis of preliminary observations, which indicated that swimming behavior varied in large part along these attributes.

At a single temperature, each animal was swum six times, broken down into three sets of two bouts each. Each alligator was swum once, followed after about 2 minutes by a second bout (immediate repetition). It was then placed back in the holding area and allowed to rest for about 30 minutes while the other alligators were swum in the same

way. After the 30 min rest, the alligator was swum again (delayed repetition). This was repeated three times, resulting in six bouts per animal per temperature. Temperatures used were 15, 20, 25, 30 and $35^{\circ}\text{C} \pm 1^{\circ}\text{C}$. So, for a single sequence of five temperatures, data on burst swimming speeds and behavior were gathered from 210 bouts of burst swimming (6 bouts per animal per temperature \cdot 7 animals \cdot 5 temperatures).

The entire sequence of five temperatures was repeated five times, with the order of temperatures in the sequence changed each time. Data on swimming behavior were not recorded for the first two temperature sequences. We report here only results from the three sequences for which data on swimming speed and swimming behavior were gathered coincidentally, totalling 630 bouts of burst swimming. Because each bout contained data from the three test segments of the test section, the total possible number of observations was 1890. Several data had to be excluded from analysis because of failure to observe the swimming behavior or failure to record a time. The number of observations for which both swimming speed and behavior were recorded is 1753.

Water temperature in the trough was adjusted by adding either hot or cold water drawn from a tap. When the desired water temperature was reached, the water level was restored to 15 cm,

and the water was vigorously circulated for 20–30 minutes to equalize temperatures through the trough. In some circumstances, later adjustments had to be made of the water temperature, particularly at the highest temperature. Burst swimming bouts were begun when the alligators' body temperatures were within 1°C of water temperature.

Behavior during Steady Swimming.—The results from the burst swimming trials raised the question: to what extent are the behaviors during burst swimming the result of the stressful situation or the effect of temperature *per se*? Therefore, we studied swimming behavior during presumably less stressful conditions, what we called "steady swimming."

Five small alligators (1–1.5 kg body mass) were used for this experiment. Steady swimming trials were carried out in a large recirculating flow tank, using the same temperatures as the burst swimming trials. Temperature of water in the flow tank was adjusted using immersible water heaters, or by dumping quantities of ice in the water.

Each alligator was trained to swim in the flow tank for several days before measurements were made. During experiments, water speed at the given temperature was adjusted to about $\frac{1}{3}$ the average burst speed recorded for that temperature in the burst swimming trials. In this way, we hoped to elicit more "casual" swimming than that during burst swimming.

Once water temperature in the flow tank was set, an alligator was placed in the flow tank, and its body temperature allowed to equilibrate for 30–60 min. During this time, the water in the flow tank was still. Steady swimming was induced by starting the water flowing. Sometimes, the alligator had to be gently prodded with a pencil or with the hand to start it swimming. A bout of steady swimming lasted 5 min. Every 15 s, an observation was made on whether the animal was swimming or not, and if it was swimming, an obser-

vation was made on its swimming behavior, using the same criteria as for burst swimming. If the animal was not swimming, it was gently prodded into swimming again (i.e., not pinched or poked as in burst swimming). This procedure was repeated for each of the five alligators, at which time temperature of the flow tank was changed and the experiment repeated.

Analyses of Data.—Data on burst speeds were analyzed using standard methods of analysis of variance. Differences among means were assessed using Tukey's multiple range comparison procedure. Level of significance was considered to be $P = 0.05$.

Burst swimming behaviors were analyzed also using analysis of variance, but with the independent variable being the percent frequency of occurrence for each behavior out of all observations for an animal at the given temperature. So, for a given behavior, each of the five temperatures contained one datum for each of the seven individuals used, a total of 35 data. Swimming behavior for steady swimming was analyzed in a similar way, but using the percent frequency of behaviors with respect to the number of times the animal was observed swimming at that temperature. The distributions of the percent frequencies were normalized using an arcsine transformation (Sokal and Rohlf, 1969).

RESULTS

Burst Swimming Speed.—From 15 to 25°C, average burst speed increased from 0.47 m s⁻¹ to 0.89 m s⁻¹. From 25 to 35°C, burst speed did not vary with respect to temperature (Fig. 2). Major sources of variation in the analysis of variance were temperature ($r^2 = 24.7\%$), repetition of temperature sequence ($r^2 = 27.4\%$) and individual ($r^2 = 7.9\%$). All other sources of variation (e.g., between segments in the test section, between bouts, etc.) accounted for less than 7% of the total variation in burst speed. Total explained variance for all

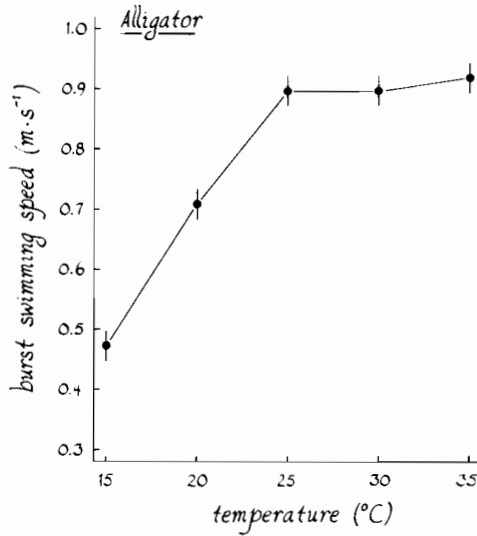


FIG. 2. Burst speeds of *Alligator* as a function of temperature. Symbols indicate mean burst speeds. Vertical bars are \pm one half the Honestly Significant Difference (H.S.D.), calculated from Tukey's multiple range test. Non-overlap of bars signifies a statistically significant difference between the means.

factors together was about 67% ($P < 0.0001$).

Behavior during Burst Swimming.— Temperature significantly affected how often alligators swam using the legs as paddles ($P < 0.0001$). At 15°C, the alligators swam using the legs as paddles an average of 79.7% of the time (Fig. 3). As temperature increased, the use of legs became less frequent, until at 35°C, the animals used the legs as paddles an average of only 15.4% of the time (Fig. 3).

Temperature also significantly affected the frequency that the animals swam breaching the surface of the water ($P < 0.0001$). At 15°C, the alligators swam with the head out of the water an average of 40.9% of the time (Fig. 3). At higher temperatures, the frequency of swimming in this way was less frequent, occurring only 14.7% of the time at 25°C. At temperatures higher than 25°C, swimming with the head out of the water was more frequent, occurring 37.7% of the time at 35°C.

Behavior during Steady Swimming.—

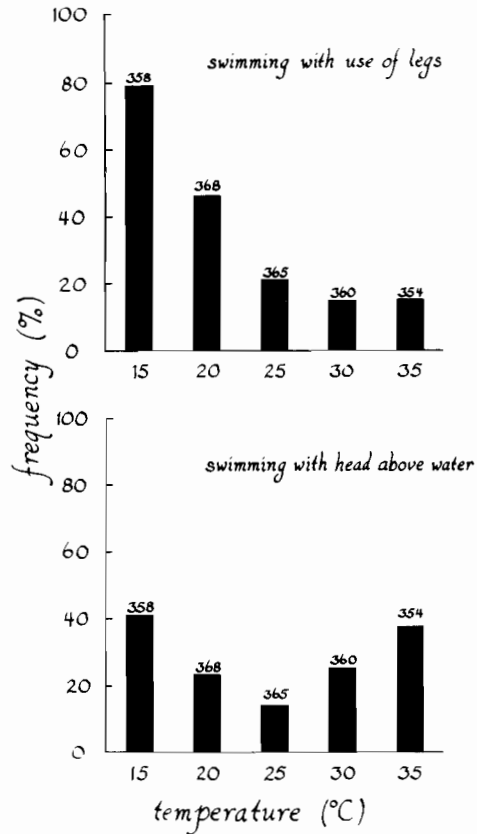


FIG. 3. Dependence of swimming behavior on temperature during burst swimming in *Alligator*. Numbers above each bar are the total number of observations for each temperature. Top panel: Frequency with which the alligators swam using the legs as paddles. Bottom panel: Frequency with which the alligators swam with the head breaching the surface of the water.

Temperature had a significant effect on the probability that an animal would swim. The alligators were seen swimming only about 70% of the time at 25°C, and at temperatures above and below this, they were less likely to swim (Table 1).

Among the observations in which the animal was swimming, the legs were used as paddles an average of 74% of the time (Table 1). Swimming with the head out of the water occurred an average of 76% of the time. Analysis of variance on the frequencies showed no

TABLE 1. Behaviors during steady swimming.

Temperature (°C)	Percent of observations (N = 200)		
	Swimming	Uses legs	Breaching
15	38.5	74.8	61.0
20	57.0	83.1	68.9
25	70.5	71.4	79.0
30	51.0	69.6	88.6
35	42.0	69.3	81.9

significant effect of temperature on steady swimming behavior. For use of legs, $P = 0.715$; for breaching, $P = 0.086$.

Swimming Behavior and Burst Speed.— Different ways of swimming were associated with different burst speeds (Table 2). The fastest burst speeds occurred when the animals swam completely submerged, and without using the legs as paddles. The slowest burst speeds occurred when the animals swam using the legs as paddles and breaching the surface of the water. In general, alligators swam faster when they did not use the legs as paddles, or when they swam completely submerged (Table 2). The differences in burst speeds are significant between each type of swimming.

Burst Speed and Effect of Repetition.— Immediate repetition of burst swimming did not slow the animals significantly at 15 and 20°C. At 25, 30 and 35°C, immediate repetition of a bout of burst swimming slowed the animals significantly. Delayed repetition of burst swimming did not consistently affect burst speeds over the range of temperatures used (Fig. 4).

DISCUSSION

It is reasonable to suppose that a faster speed of locomotion at higher body temperatures is due to an effect of temperature on muscle performance (Bennett, 1980). Indeed, numerous studies on isolated muscles from a variety of reptiles show that, within limits, force produced per contraction, speed of contraction and relaxation, stiffness in active muscle, rate of force production, and capacity to do work increase with

TABLE 2. Burst swimming speeds and swimming behaviors of *Alligator*.

Behavior	N	Burst swimming speed (m s ⁻¹)
Does not use legs Submerged	882	0.943
Does not use legs Head out of water	256	0.859
Uses legs Submerged	382	0.535
Uses legs Head out of water	233	0.467

temperature (Putnam and Bennett, 1982; Bennett, 1980; Fowler and Crowe, 1976; Washio, 1974; Licht et al., 1969; Licht, 1964). By almost all measures, performance curves for isolated muscles roughly parallel the performance curves for running speeds of lizards (Bennett, 1980). It may be, however, that the performance curve for burst swimming of alligators can be explained only partly by direct effects of temperature on muscle performance. The effect of temperature on the likelihood that an alligator will swim in a certain way may be equally important.

A rough estimate of the direct effect of temperature on muscle performance may come from examining the way burst speed varies with temperature *within* a given behavior. For example, if swimming behavior does not change with respect to temperature, probably the same groups of muscles are powering locomotion at all temperatures. A difference in speed then probably arises through a difference in speed and force of contraction of these muscle groups. If swimming behavior changes substantially, however, this may no longer be true. For example, a change from powering locomotion through oscillatory motions of the tail to using the limbs as paddles almost certainly changes the major muscle groups that are powering locomotion. This may in turn bring about variation in the transduction of muscle force into thrust, and hence for-

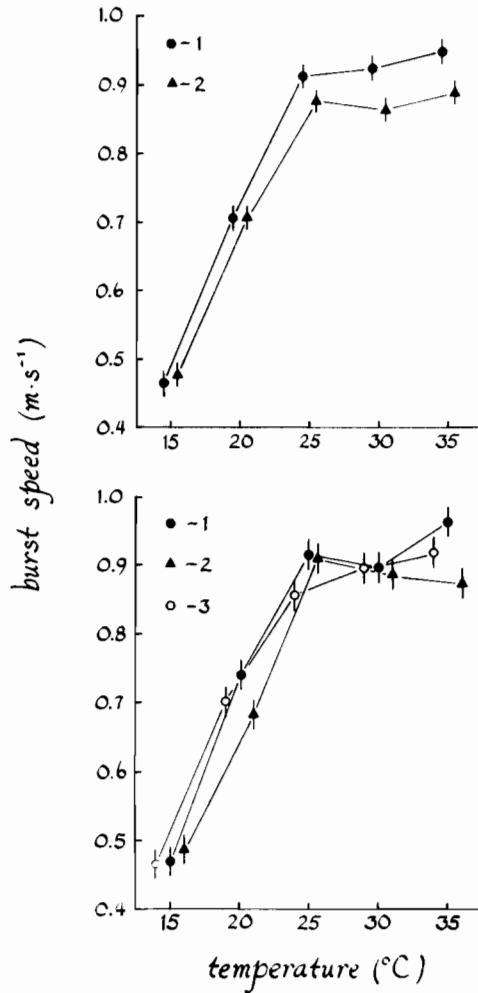


FIG. 4. Effect of repeated bouts of burst swimming on average burst speeds of *Alligator*. Top panel: Average burst speeds for the two bouts of burst swimming with about a 2 minute rest between the first and second bouts (immediate repetition). Circles signify the first bout, triangles signify the bout immediately following. Bottom panel: Average burst speeds for burst swimming after about 30 minutes rest (delayed repetition). Closed circles signify the first pair of bouts, triangles signify the second pair of bouts and open circles signify the third pair of bouts. Vertical bars are \pm one half the H.S.D.

ward speed, independent of any direct effect of temperature on muscle performance. Some variation in the drag forces the animal experiences also may result

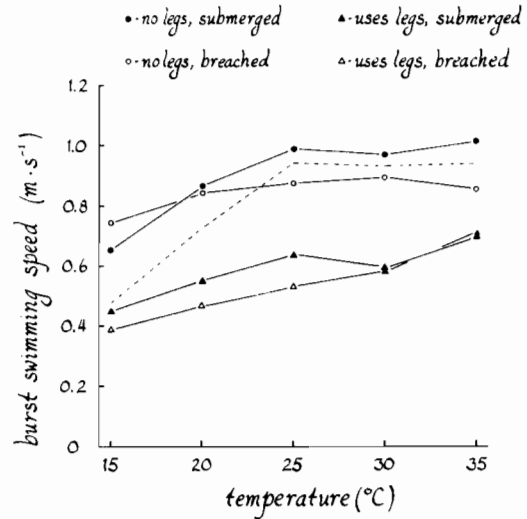


FIG. 5. Average burst speeds associated with different swimming behaviors of *Alligator*. The four possible combinations of the two criteria used to characterize burst swimming are shown. Closed circles: swimming without using the legs as paddles and submerged. Open circles: swimming without using the legs as paddles and breaching the surface. Closed triangles: swimming using the legs as paddles and submerged. Open triangles: swimming using the legs as paddles and breaching the surface. Dotted line plots the overall average burst speeds shown in Fig. 2.

from changes of swimming behavior, although these are likely to be small.

To what extent, then, do the observed variations in behavior with respect to temperature (Fig. 3) contribute to the overall performance curve for burst swimming (Figure 2)? Perhaps the easiest way to answer this question is to superimpose the overall performance curve for burst swimming (Fig. 2; dotted line in Fig. 5) over the performance curves of burst swimming for each behavior (solid lines in Fig. 5). Obviously, the overall performance curve is some average of the performance curves for each behavior. However, it is noteworthy that changes in swimming behavior have substantial consequences for the average speeds obtained, especially between 15 and 25°C. The alligators swim using the legs about 80% of the time at 15°C (Fig. 3), which corresponds to the

lowest speeds observed (Table 2). As temperature increases to 25°C, the use of legs during swimming declines to less than 20% (Fig. 3). The shift in behavior between 15 and 25°C corresponds to a change of burst speeds overall that is greater than for any behavior considered alone (Fig. 5). We may conclude, then, that the effects of temperature on the way an alligator swims are at least as important for shaping the performance curve as are the direct effects of temperature on muscle function, especially between 15 and 25°C (Fig. 5).

At first sight, this is a puzzling result, for it suggests that at both high and low body temperatures, an alligator escaping from attack often swims in ways that substantially reduces its speed. For example, at a body temperature of 15°C, the alligators were capable of average burst speeds as fast as 0.74 m s⁻¹, if they swam all the time without using the legs (Fig. 3). Yet, nearly 80% of the time, they swam using the legs as paddles, which reduced their average burst speeds by almost half, to 0.39 m s⁻¹. Similarly, at body temperatures of 35°C, the alligators swam 40% of the time with the head breaching the surface of the water (Fig. 3), resulting in burst speeds that averaged 16% less than the animals were capable of had they swam submerged all the time. This dependence of swimming behavior on temperature occurs only during the presumably stressful burst swimming trials; the same swimming behaviors were evident during steady swimming, but did not vary with temperature (Table 1). Why would alligators often swim in ways that reduce their average locomotory performance at both the upper and lower body temperatures? Curiously, why would this happen only when it would make most sense not to—while the animal is trying to escape from harassment?

Swimming more frequently with the head out of the water at temperatures greater than 25°C may reflect a greater tendency for warm alligators to breathe

while swimming. Among some lizards, burst activity results in an almost immediate increase in ventilation at high body temperatures, but not at cooler body temperatures (Bennett and Gleeson, 1976). In the case of the lizards, this reflects a greater aerobic capacity at higher body temperatures (Bennett and Gleeson, 1976). One may explain a greater tendency for warm alligators to breathe in a slightly different way. For example, locomotory activity lasted for no more than a few seconds for each bout of burst swimming. The initial stages of activity often are supported by incurring a so-called aerobic oxygen debt, tapping endogenous stores of oxygen bound to hemoglobin or dissolved in the tissues. Increased ventilation, or resort to anaerobiosis in any animal need occur only when these endogenous stores of oxygen are depleted. High body temperature will reduce the time these stores can support burst activity in at least two ways; overall levels of oxygen consumption will be greater at higher body temperatures and less oxygen will be in physical solution in the tissues of the body.

Perhaps endogenous stores of oxygen cannot support even the short bursts of activity that occur in burst swimming at high body temperatures, forcing the animal either to surface and breathe, or to incur an anaerobic oxygen debt. It is noteworthy, then, that immediate repetition of burst swimming resulted in slower average burst speeds only at 25, 30 and 35°C, but not at 15 and 20°C (Fig. 4). Thus, the limitation on performance at high temperature may not be a direct limitation of muscle performance, but a limitation in the delivery of oxygen to the active muscles. This does not, of course, explain why alligators swim more often with the head out of the water at low temperatures (Fig. 3).

At low temperatures, however, the main limitation on burst speed is not whether the animal swims with its head out of the water or not, but whether the

animal swims using its legs or not (Table 2, Fig. 5). In this case, the limitation on performance may be more behavioral than physiological. Also, swimming speed may not be an ecologically relevant measure of performance at low temperatures; there are other ways of escaping attack than trying to get away as quickly as possible. For example, some lizards at low body temperatures respond to harassment not by running away, but by standing ground and making an impressive threat display (Hertz et al., 1982). Also, some lizards are more "shy" at low body temperatures than at higher body temperatures (Rand, 1964). These strategies presumably are more effective against predators than fleeing when muscles are cool and not performing well.

A similar strategy may explain the behavior of the alligators during burst swimming at low body temperatures. We did not quantify this, but at 15°C, the alligator's response to a pinch of the tail often was not a burst of swimming, but an abrupt turning of the animal to nip the hand pinching it. During steady swimming, alligators had to be prodded into swimming more often at 15 and 20°C than at 25°C, suggesting that alligators with low body temperatures are more "reluctant" to swim than alligators at higher body temperatures (Table 1). It is conceivable that a more effective strategy for a cold alligator to avoid harassment is to not swim away, but to startle its molester by biting it. When it is forced to swim, it does so ineffectively (i.e., using the legs), for whatever proximate reason.

The performance curve for burst swimming of alligators may not be an ecologically relevant measure of physiological "state," as it often is thought to be for lizards. Rather, any presumed physiological interpretation of the performance curve is complicated by pronounced variation in locomotory behavior, which may have little relation to the animals' physiological perfor-

mance. Also, swimming speed may not be an ecologically relevant measure of alligator's performance at all temperatures. How else does one explain the curious result of cold alligators often swimming in ways that substantially impair their performance?

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