MASTER

CONTINUATION OF STUDIES ON
THERMOREGULATION OF FISH AND TURTLES IN
THERMALLY STRESSED HABITATS

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ABSTRACT

A time dependent mathematical model accurately predicts heart, brain and gut temperatures of largemouth bass, Micropterus salmoides. Body diameter, insulation thickness, and tissue thermal conductivity are controlling variables in the transfer of heat between a fish and water. Fish metabolic rate and water velocity across fish surfaces do not appreciably affect heat transfer rates. These results are confirmed by laboratory experiments on live fish. Field experiments are now beginning to test the model. Multichannel temperature transmitters telemeter body temperatures of free swimming bass in Pond C on the Savannah River Plant while the behavior of those fish and other bass is recorded by an observer in an 8 m high tower.

Field studies of the home ranges and movements of turtles, Chrysemys scripta, in Par Pond on the Savannah River Plant are completed. We have marked and released over 400 turtles captured during 178,000 trap hours. We have recorded the movements of 30 individuals fitted with radio transmitters. Distinct differences are apparent in the behavior of turtles in areas affected by heated effluents as compared to those in control areas. Calculations and theoretical analysis of the transient energy exchange of C. scripta are continuing. We are now in the final stages of analyzing field and laboratory data. This fall we will begin writing our definitive paper on the behavioral thermoregulatory mechanisms of C. scripta.

Laboratory experiments using ^{133}Xe indicate that blood flow in the muscles and skin of alligators, Alligator mississippiensis, increases 2 to 6 fold during movement. Resting blood flow ranges from 0.002 to $0.030 \text{ ml g}^{-1} \text{ min}^{-1}$ in the muscle and 0.005 to $0.030 \text{ ml g}^{-1} \text{ min}^{-1}$ in the skin. Relative variation is similar in magnitude to that seen in human muscle.

Evaporative water loss from alligators decreases as body size increases.

The ratios of respiratory to cutaneous water loss are 1.80 at 5°C, 1.18 at 25°C and 0.85 at 35°C. Boundary layer resistances to evaporative water loss are 6 fold less than predicted by calculations of aerodynamic boundary layers.

Animals have evolved a variety of thermoregulatory strategies in response to selective pressures imposed on them by their natural environment. Body size is a primary factor in determining the thermoregulatory strategy that is to be used by a given animal.

Operative environmental temperatures (T_e) are as high as 60°C for a turtle basking on a log in the sun. In a rainstorm T_e drops to 18°C. Experiments to measure T_e for turtles in normal and thermally affected areas are now continuing on the Savannah River Plant.

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Introduction

The purpose of this research has been to determine quantitatively the mechanisms by which fish and turtles thermoregulate in response to thermal stress in their natural environment. During the current project year significant progress has been made in all areas of our research. In particular, we have successfully tested our mathematical model to predict the body temperature of a fish through time and have completed our field study of the movement and home ranges of turtles exposed to thermal effluents in Par Pond on the Savannah River Plant. Good progress has been made in analyzing data, writing manuscripts and in the development of energy budget theory.

Specific objectives to be accomplished in the current project year were to: 1.) Complete formulation of a transient energy budget for the turtle Chrysemys scripta, 2.) Complete field study of the effects of thermal effluents on the home ranges and movements of turtles in Par Pond on the Savannah River Plant, 3.) Continue theoretical calculations and attendant experiments on the effect of body size, physical characteristics and physiology on the thermoregulation of large ectotherms, 4.) Begin field experiments on the thermoregulatory behavior of largemouth bass, Micropterus salmoides, in Pond C on the Savannah River Plant, and, 5.) Begin field studies to measure the operative environmental temperatures of turtles in Par Pond and Pond C.

Significant progress has been made in meeting all these objectives. Details are given below.

Transient Energy Budgets of Turtles

We are presently completing our computer simulations of transient heat energy budgets for the turtle, C. scripta. Our plans to complete a manuscript on this topic have been delayed. At this time we still have two manuscripts

in the writing - review stages that are related to this topic. The first discusses the microclimate of Par Pond (Foley and Spotila 1979) and the second summarizes the response of turtles to thermal effluents in that reservoir (Spotila et al 1979). Both of these papers were submitted, returned and are now being rewritten.

This portion of our research effort has lagged behind our work on largemouth bass and our theoretical-laboratory studies on large ectotherms. We have conducted many laboratory and field experiments, and have analyzed much of the data, but have not gotten our findings into print. This has been the result of two factors. First, we have concentrated most of our efforts on the problem of fish thermoregulation. Second, the mechanisms by which turtles thermoregulate have proven to be much more complicated than we had originally anticipated. As a result we have decided not to publish our findings until we were able to provide an adequate theoretical framework for our data.

During the past year we have been proceeding with our calculations and theoretical analysis. Robert Foley, although no longer an employee of the college, has remained active in this research and has completed most of his analysis for the energy budget manuscript. Over the next few months Foley and I will continue this effort and hope to have a manuscript completed by the end of the current contract year (October, 1979).

Our efforts in this area are now coming to a critical junction. We must pull all of our information together and formalize conclusions. I am making this the Number 1 priority for the next project year. Maximum effort will be exerted in order to finish a definitive paper on the thermoregulatory mechanisms of C. scripta. Towards this end I am bringing Edward Standora to Buffalo as a research associate. Standora is completing his Ph.D. dissertation on the behavioral thermoregulation of C. scripta at the Savannah River Ecology Laboratory. His expertise will be invaluable in helping us to complete this phase of the project. More details are provided in the renewal proposal for the

next project year.

Par Pond Field Studies

Joseph Schubauer has completed his field studies on the response of turtles, C. scripta, to thermal effluents in Par Pond. He captured, marked and released over 400 turtles. These were caught during 178,000 trap hours using standard techniques. He constructed small radio transmitters and placed them on 30 individuals (15 males, 15 females) in the Hot Arm and West Arm of the reservoir (Fig. 1). Schubauer followed fifteen to twenty of these turtles simultaneously for up to one year. He plotted capture sites (trap data) and locations from telemetry sightings (triangulation of turtle locations using a radio receiver) on aerial maps. This allowed him to quantify movements and home ranges for these turtles.

There were twice as many C. scripta in the West Arm as in the Hot Arm (Table 1). While more turtles were captured in the Hot Arm, there were 3 times as many trap hours logged for the Hot Arm. Therefore, the number of captures per trap hour in the West Arm was more than twice that in the Hot Arm. The sex ratio in the West Arm was 1:1 while in the Hot Arm it was 3:1, male: female (Table 2). Since recapture rates were similar for the two areas trap bias did not appear to be a problem. Males in the Hot Arm moved significantly more than females (Table 3). Males and females moved similar distances in the West Arm. Some males appeared to have two home ranges in the Hot Arm and did more wandering than did turtles in the West Arm and females in the Hot Arm.

Turtles in the Hot Arm have adjusted to the presence of thermal effluents. They were excluded from the area near the Hot Dam, the point of entry for heated water from Pond C. Their exclusion may have been due in part to the lack of rooted aquatic vegetation in that area. Apparently the presence of

macrophyte beds is a necessary but not sufficient condition for the presence of turtles.

Schubauer is continuing to analyze his data and plans to complete his master's thesis this fall. He has published two technical reports and will have presented 3 papers at scientific conferences by the end of this project year.

Laboratory Experiments

Three laboratory studies provided information on blood flow in alligators (Alligator mississippiensis), the effect of body size on evaporative water loss in these animals and the role of size and boundary layer thickness in reducing evaporative water loss from egg shaped objects.

Blood Flow in Alligators

Our original objective was to define the role of the circulatory system in internal heat distribution and the role of tissue conductivity in heat flow through the skin and body wall of alligators. We began by measuring blood flow using the ^{133}Xe method of Morgareidge and White (1969). This research was conducted by Christina Weinheimer in the laboratory of Dr. David Pendergast of the Physiology Department of SUNY at Buffalo. We followed the protocol described in our research proposal for this year. Blood flow in the skin and muscle of an alligator's tail were greatly affected by movement (Fig. 2). Whenever an alligator moved, either struggling to escape or simply shifting position, blood flow increased 2 to 6 times. This was true for both the skin and muscle. Resting blood flow in the skin did not change with temperature (Fig. 3). Likewise muscle blood flow (resting) was stable from 24 to 35°C (Fig. 4). Flow rates greater than $0.030 \text{ ml g}^{-1} \text{ min}^{-1}$ were usually associated

with movement. Variation in resting flow was great, ranging from 0.005 to 0.03 ml g⁻¹ min⁻¹ in the skin and 0.002 to 0.030 ml g⁻¹ min⁻¹ in the muscle. These experiments suggest that blood flow in alligators is much more variable than previously reported (Grigg and Alchin 1976 and Smith 1976). Variability in blood flow in our experiments was similar to that found for humans (Pendergast, personal communication). Before we can quantify the role of blood flow in heat transfer in large ectotherms we will have to conduct many more experiments to ascertain the normal range of flow for different regions of the body under different environmental conditions. In addition, we will have to compare that data with data from other measurement techniques since we have indications that ¹³³Xe, while a good relative measure, may underestimate true blood flow by as much as 50%.

Evaporative Water Loss From Alligators

After completing our heat transfer analysis of the alligator (Terpin et al 1979) we found that the evaporative water loss process required further clarification. While a small component of an alligator's energy budget, evaporative water loss could be important in terms of its osmoregulatory ability.

Bogert and Cowles (1947) found an average weight loss of 0.83% per hour for the alligator at 38°C and 27% relative humidity. In our earlier study (Spotila et al 1972) we reported water loss rates of 0.45 mg cm⁻² hr⁻¹ at 10.5°C, 1.05 mg cm⁻² hr⁻¹ at 19.5°C, and 2.50 mg cm⁻² hr⁻¹ at 29°C. Bentley and Schmidt-Nielsen (1966) found that the major avenue of water loss in the crocodilian, Caiman sclerops, was through the skin, which contributed 87% of the total at 23°C. They also showed that cutaneous water loss was one third that of amphibians. Diefenbach (1972) found that at 26°C and 20% RH, 70% or more of the total

water loss was cutaneous for Caiman crocodilus and Crocodylus niloticus. In addition, he found that for the same species water replacement occurred only through drinking. Evans and Ellis (1977) examined sodium balance in hatchling American crocodiles (Crocodylus acutus) and found that hatchlings were intolerant even of dilute brackish water.

For our current experiments John Davis constructed a plexiglass, flow through chamber (110 x 48 x 20 cm) (Fig. 5) which was divided into respiratory and cutaneous sections by means of a plexiglass partition. Respiratory water loss was inversely related to body weight (Fig. 6). Respiratory water loss was $0.018 \text{ mg g}^{-1} \text{ hr}^{-1}$ at 5°C and $0.116 \text{ mg g}^{-1} \text{ hr}^{-1}$ at 35°C . Cutaneous water loss was $0.010 \text{ mg g}^{-1} \text{ hr}^{-1}$ at 5°C and $0.137 \text{ mg g}^{-1} \text{ hr}^{-1}$ at 35°C . Again as body size increased water loss decreased (Fig. 7). The ratio of respiratory to cutaneous water loss was 1.80 at 5°C , 1.55 at 15°C , 1.18 at 25°C and 0.85 at 35°C . The decrease in water loss with increase in body size raised a question as to the effect of the boundary layer of still air around these animals in retarding water loss. We addressed this question in another series of water loss experiments discussed below.

Body Size, Boundary Layer Thickness and Evaporative Water Loss

Differences in rates of evaporative water loss from small and large alligators may have been due to differences in the thickness of the boundary layers of air around these animals. A boundary layer is a layer of non-turbulent air which surrounds all terrestrial objects and organisms (Fig. 8). Fluid particles in the vicinity of the surface are slowed down by virtue of viscous forces so that air molecules adjacent to the surface of an organism stick to it and have zero velocity. Other air molecules sliding over them are slowed as a result of the interaction between faster and slower moving molecules.

Thus, a velocity gradient or profile exists such that there is a lower wind speed near the surface and an increasing wind speed with distance from the surface. Eventually, actually a relatively short distance from the surface, the velocity of the air molecules approaches that of the undisturbed free air stream. Therefore, the boundary layer is the region near the surface where air molecules passing the organism encounter a substantial velocity gradient. Kreith has defined the edge of the boundary layer as that point at which the local velocity reaches 99% of the external velocity.

Boundary layer divides a flow-field into two domains; a thin layer covering the surface of the body where the velocity gradient is great and the viscous forces are large, and a region beyond this layer where the velocity is essentially equal to the free air stream and the effects of viscosity are negligible (Kreith, 1973).

We have visualized the boundary layers around turtles (Bakken and Spotila 1971, Foley and Spotila 1978) using Schlieren photography. We hypothesized that larger animals had thicker boundary layers and thus slower rates of evaporative water loss. To test this hypothesis we needed a model system that was based on living organisms but avoided complexities of shape.

Bird eggs provided an ideal system for studying the effects of size on boundary layer thickness. Eggs ranged in size from the 0.2 g hummingbird egg (Trochilidae) to the 1.5 kg ostrich egg (Struthia camelus) and to the more than 10 kg egg of the extinct elephant bird (Aepyornis sp.). In these experiments Christina Weinheimer made agar and plaster replicas of eggs, soaked them in water (they then provided a free water surface) and measured their rates of evaporative water loss at several wind speeds.

Boundary layer resistance (r_b) is a measure of the thickness of the boundary layer. It is defined in units of sec cm^{-1} and is the time required for one molecule of water to diffuse one cm through the boundary layer

(Spotila and Berman 1976). In still air boundary layer resistance increased from 1.6 sec cm^{-1} for a 1 g egg to 5.65 sec cm^{-1} for a 12,690 g egg (Fig. 9).

Theoretical calculations by Tracy and Sotherland (1979) indicate that r_b for the large egg should be 36.1 sec cm^{-1} . The six fold difference between predicted and measured r_b for the large egg is potentially very important. The theoretical calculations are based on convection heat transfer theory and give an estimate of aerodynamic boundary layer. Our experimental results are a direct measure of the evaporative boundary layer. The large difference between our results and those of Tracy and Sotherland suggest that there is a fundamental difference between the two boundary layers (aerodynamic vs evaporative). Machin (1964) reported that the aerodynamic boundary layer thickness around a snail was 3 to 6 times greater than the evaporative boundary layer thickness measured around this animal. We are currently completing some additional experiments. If these results confirm our earlier findings we will have made a very important advance in the area of heat and mass transfer theory that will have a direct bearing on our understanding of the heat transfer process in large ectotherms.

Body Size and Thermoregulation

We have continued our theoretical analysis of the effect of body size on the thermoregulatory capabilities of large animals. We have found that an increase in body size isolates an ectotherm from its physical environment. Thus a large alligator enjoys some of the advantages of homeothermy due to its size alone. This has a direct bearing on its ability to adjust to thermal effluents. Freshwater fish and turtles are, in general, too small to take advantage of this form of homeothermy. They must rely more on behavior to compensate for the presence of a thermal effluent in their natural environment. Animals have evolved a variety of thermoregulatory strategies (Fig. 10).

in response to the selective pressures imposed on them by their natural environment. Body size is a primary factor in determining which thermoregulatory strategy will be used by a given animal. This is discussed at greater length in a current publication (Spotila 1979).

Thermoregulation of Largemouth Bass

Confirmation of the Model

Richard Kubb has completed his thesis (Kubb 1979) and we have prepared a manuscript for publication based on his research (Kubb and Spotila 1979). Kubb developed and tested a time-dependent model describing mechanisms of heat transfer in fish. The model predicted thermal time constants of largemouth bass (M. salmoides) (100-1600 g) and transient changes in body temperatures of fish experiencing step changes in ambient temperature (heating or cooling). (Fig. 11). It was a good predictor of heart, gut and brain temperatures for fish exposed to a change in water temperature through time (Fig. 12).

Model sensitivity analysis indicated that body diameter, insulation thickness, and tissue thermal conductivity were controlling variables in the transfer of heat between a fish and water. Fish metabolic rate and water velocity across fish surfaces did not appreciably affect heat transfer rates.

Results from experimental heating and cooling studies performed on M. salmoides indicated that body wall thicknesses for three anatomical compartments (mid-gut, brain and heart) were linear functions of body mass. Mid-gut and brain thermal time constants were dependent on body mass. Heart thermal time constants were independent of body mass indicating that the temperature of the heart may be a factor limiting the thermal exploitive behavior of different size fish. The mid-gut region exchanged heat at the slowest

rate and the heart region exchanged heat at the fastest rate. The cranial region exchanged heat at rates intermediate to those of the mid-gut and heart. We found statistically significant differences between deep body thermal time constants of live and dead M. salmoides indicating differential mechanisms of heat exchange for living and non-living fish.

Behavioral Thermoregulation - Field Experiments

We have put special emphasis in our field experiments on the behavioral thermoregulation of largemouth bass in Pond C on the Savannah River Plant. At this time (June 1979) Claire Ross has a multichannel temperature transmitter implanted in a largemouth bass in the aquatics facility at the Savannah River Ecology Laboratory. She has completed three transmitters and has three others partially constructed. We have established a grid system in Sanctuary Cove of Pond C and have mapped the location of submerged stumps, weed beds and channels. Our observation tower is in place and secured. Ms. Ross has already begun to record the behavior of bass and sunfish in her study area. We have perfected our surgical technique and eliminated the problem of Aeromonas infection by the use of tetracycline in the fish and its water.

This study is going very well. By the end of this project year I expect to have detailed behavioral data for fish in the study cove and temperature records for at least three telemetered largemouth bass. Next year will be spent analyzing that data, using it to "field test" our body temperature model and planning our next set of experiments.

Operative Environmental Temperatures of Turtles

Operative environmental temperatures (T_e) experienced by turtles (C. scripta) reach as high as 60°C when the turtles are exposed to the full

sun while basking. Kenneth Crawford is currently in the field at the Savannah River Plant and is measuring T_e for turtles this summer. He used electroplating techniques to construct 10 hollow copper turtle replicas of three sizes of C. scripta. He painted these to duplicate the solar absorptivity of real turtles. Now he is determining T_e under a variety of environmental conditions. A turtle basking during a summer rainstorm experiences a T_e of 18°C . If it was in the water it would be exposed to temperatures from 21 to 34°C . A cloud passing by the sun caused a drop in T_e of 8 to 10°C . The effect of an overcast sky is even more pronounced.

It appears that our T_e thermometers will be very useful in assessing the impact of microclimatic variables on the behavioral thermoregulation of turtles. We are proceeding to "map" the operative environmental temperatures available to turtles in their natural environment. We will compare them to operative temperatures available in areas affected by thermal effluents. This data should be available by the end of the current project year. Next year we will analyze our findings and use them to interpret our previous data on microclimates and turtle behavior.

Concluding Comments

During this year we have published seven articles (Foley and Spotila 1978, Foley et al 1978, Kowalski et al 1978, Paladino and Spotila 1978, Spotila and Paladino 1979, Terpin et al 1979, Spotila 1979), three articles are in press (Spotila et al 1979, Gibbons et al 1979a, Gibbons et al 1979b), three are in revision, and five are in preparation. Two masters theses were completed (Davis 1978 and Kubb 1979). In December 1978 we presented two papers at the American Society of Zoology meeting in Richmond, Virginia. We also presented a paper at the spring 1979 meeting of the Association of Southeastern Biologists. This summer we will present one paper at the Ecological Society meeting

and two papers at the American Society of Ichthyologists and Herpetologists meeting.

Cooperation with the Savannah River Ecology Laboratory (SREL) is becoming an even more important factor in our field research. During the past year we have worked very closely with Dr. J.W. Gibbons as well as with Edward Standora, Dr. John Giesy and Dr. I.L. Brisbin. By maintaining this cooperative effort we have increased the effectiveness of our research effort and contributed to the research aims of SREL. Joseph Schubauer was supported in part by a SREL graduate research support fellowship. This summer Claire Ross is supported in the same way while Kenneth Crawford is supported by this contract. One of the articles published this year was coauthored with Dr. John Giesy. Two of those in press are coauthored by Joseph Schubauer along with Dr. J.W. Gibbons and other members of the SREL staff. Several of those in preparation and revision are also coauthored with SREL staff.

The project director, James R. Spotila, spent 100% of his time on this project during 6 weeks of June and July 1979. He spent 33% of his time on this project during the 1978-79 academic year.

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Table 1. Trapping success for Chysemys scripta in thermally affected (Hot Arm) and control area of Par Pond on the Savannah River Plant

	HOT ARM	WEST ARM	TOTAL
NO. OF CAPTURES	157	119	276
NO. OF TRAP HR.	132,288	46,536	178,824
<u>NO. OF CAPTURES</u> <u>TRAP HR.</u>	0.0012	0.0026	0.0015

Table 2. Male, female and immature Chrysemys scripta trapped in heated area (Hot Arm) and control area (West Arm) of Par Pond on the Savannah River Plant.

	HOT ARM				WEST ARM			
	<u>♂♂</u>	<u>♀♀</u>	<u>I</u>	<u>TOT.</u>	<u>♂♂</u>	<u>♀♀</u>	<u>I</u>	<u>TOT.</u>
NO. OF ORIGINAL CAPTURES	67	19	10	96	27	35	2	64
PERCENT OF TOT.	69.8	19.8	10.4	100	46	51	3	100
RECAPTURE RATE (%)	40%	26%	40%	38%	59%	29%	0	41%

Table 3. Maximum straight line distance moved by Chrysemys scripta during the course of this study.

	HOT ARM		WEST ARM	
	♂♂	♀♀	♂♂	♀♀
$\bar{X}$	890.8	243.07	451.19	512.54
RANGE	249.09 - 1445.95	46.76 - 552.82	124.08 - 742.65	279.65 - 1108.13
N	7	5	4	7
t	2.5093		1.7996	
DF.	11		10	
P	P < .05		P > .10

Figure 1. PAR pond reservoir system on Savannah River Plant. PAR pond is 1120 ha and Pond C is 76 ha. Cove I (sanctuary cove) is located at the far northern end of Pond C. It remains near ambient while the rest of Pond C is $> 50^{\circ}\text{C}$ in the summer.

Figure 2. Typical data for blood flow in skin (circles) and muscle (squares) in the tail of alligators as measured with ¹³³Xe. Open symbols represent resting flow, closed symbols represent flow associated with movement. Experiments lasted up to 35 minutes.

Figure 3. Typical data for blood flow in the skin of alligators measured with ^{133}Xe at different temperatures. Closed circles represent flows associated with movement, open circles represent flows during rest.

Figure 4. Typical data for blood flow in the tail musculature of alligators as measured with ^{133}Xe at different temperatures. Closed circles represent flows associated with movement, open circles represent flows during rest.

Figure 5. Compartmentalization system used to separate respiratory and cutaneous water loss from alligators. An alligator was placed into a plexiglass chamber and a neoprene-plexiglass collar fitted on its neck to effect complete compartmentalization of water loss. Placing the chamber into an environmental room ensured temperature control at 5, 15, 25, and 35°C.

Figure 6. The effects of body weight on respiratory water loss in the American alligator, *Alligator mississippiensis*, at three temperatures (15, 25, and 35°C). There was no significant difference in the regression equations for 25 and 35°C.

Figure 7. The effects of body weight on cutaneous water loss in the American alligator, *Alligator mississippiensis*, at three temperatures (15, 25, and 35°C). There was a significant difference in the water loss at 15°C as compared to 25 and 35°C.

Figure 8. Laminar boundary layer, undergoing transition to turbulent condition along a flat plate. Connected arrows indicate velocity gradient as free air stream reaches the leading edge of the plate.

Figure 9. Boundary layer resistance (r_b) of bird eggs measured for agar replicas in still air. Line of best fit drawn by eye. Two large eggs are from ostrich and elephant bird.

STRATEGIES OF THERMOREGULATION

Figure 10. Evolution of homeothermism. Physical environmental factors place selection pressures upon animals. This results in the selection for thermoregulation "specialists". Thus there appear to be several "strategies" of thermoregulation that are due in part to the body size, insulation, and metabolism of animals and in part to characteristics of the physical environment.

Figure 11. Model prediction of body temperature vs actual data for three largemouth bass exposed to a step change in water temperature.

Figure 12. Model predictions and actual data for gut, brain and heart of a 1000 g large-mouth bass exposed to a step change in water temperature.