MASTER

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

Summary Progress Report
for Period
1 October 1977 to 30 September 1980

James R. Spotila
Department of Biology
State University College at Buffalo
1300 Elmwood Avenue
Buffalo, New York 14222

May, 1980

DISCLAIMER

This book was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

Prepared for the Department of Energy under Contract EY-76-S-02-2502

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency Thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

ABSTRACT

Biophysical-behavioral-ecological models have been completed to explain the behavioral thermoregulation of largemouth bass (Micropterus salmoides) and turtles (Chrysemys scripta).

Steady state and time dependent mathematical models accurately predict the body temperatures of largemouth bass. Laboratory experiments give validity to the model. Field experiments using multichannel radio transmitters have provided temperatures of several body compartments of free ranging bass in their natural habitat. Initial studies have been completed to describe the behavioral thermoregulation of bass in a reactor cooling reservoir.

Energy budgets, fundamental climate spaces, and realized climate spaces have been completed for the turtle, C. scripta. We have described the behavioral thermoregulation of C. scripta in Par Pond, S.C. and have measured its movements, home ranges and population levels in heated and unheated arms of the reservoir. Operative environmental temperature is a good predictor of the basking behavior of this turtle.

A new synthesis explained the evolution of thermoregulatory strategies among animals. Laboratory experiments clarified the effects of movement, diving and temperature on the blood flow of alligators. Other experiments defined the role of boundary layers in controlling the evaporation of water from the surfaces of turtles and alligators in still and moving air. Nutritional status may be an important factor affecting the thermoregulatory behavior of turtles.

Nineteen articles have been published and six master's theses have been completed. Fifteen presentations have been delivered at scientific meetings.

LEGAL NOTICE

This report was prepared as an account of Government sponsored work. Neither the United States, nor the Department of Energy nor any person acting on behalf of the Department

- A. Makes any warranty or representation, expressed or implied, with respect to the accuracy, completeness, or usefulness of the information contained in this report, or that the use of any information, apparatus, method, or process disclosed in this report may not infringe privately owned rights; or
- B. Assumes any liabilities with respect to the use of, or for damages resulting from the use of, any information, apparatus, method, or process disclosed in this report.

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. Overall objectives for the current renewal period (October 1977 - September 1980) were to: 1.) Continue to develop and perfect a mathematical model to predict the temperature of a fish in a heterothermal environment, for example, as it swims in and out of a thermal effluent, 2.) Determine specific physical and physiological adaptations by which large fish and other ectotherms adjust to changes in water temperature, 3.) Continue field studies on the biophysical ecology of turtles in thermally stressed environments on the Savannah River Plant, and, 4.) Continue energy budget modeling of heat transfer between large ectotherms and their environment.

We have met all of these objectives during the current three year renewal period. Specific goals were established for each year and detailed in our annual proposals. These were all met on schedule (see annual progress reports C00-2502-15, 16, 17). We have reported the results of our research in 19 scientific articles and notes in journals such as NATURE, PHYSIOLOGICAL ZOOLOGY, COPEIA, J. THERMAL BIOLOGY, and others; in six master's theses, and in 16 presentations at national meetings (see Appendix I). Considerable progress has been made in formulating biophysical-behavioral models to explain the behavioral thermoregulation of largemouth bass (Micropterus salmoides) and turtles (Chrysemys scripta). Our integrative approach of biophysical modeling, laboratory studies, and field experiments have proven to be a powerful method for studying the physiological ecology of these animals.

During the past three years we have concentrated on studies of the thermoregulation of fish and turtles with respect to their response to thermal effluents. We have also continued theoretical calculations (energy budget modeling) on the effect of body size and physical characteristics on the thermoregulation of large ectotherms.

Finally, we have conducted laboratory experiments on the effects of body size and physiology on the thermoregulation of alligators and turtles. Details of this research were given in articles and theses produced during this period. Annual progress reports discussed this research in terms of fulfillment of programmatic goals and milestones. The purpose of this summary report is to give an overall synopsis of this project for the 1977-80 renewal period. This report and the annual progress report for 1979-1980 (C00-2502-17) provide background for the renewal proposal for 1980-1983.

THERMOREGULATION OF LARGEMOUTH BASS

We set three goals for our bass research. These were: 1.) Formulate and test in the laboratory a mathematical model to describe the time dependent heat flow in a largemouth bass, Micropterus salmoides; 2.) Develop a system to simultaneously measure temperatures of several body compartments from free swimming largemouth bass, and 3.) Complete the first series of field studies on the behavioral thermoregulation of bass.

By 1977 we had developed a steady state energy budget model and measured the heat transfer coefficients for bass (Erskine and Spotila 1977). In 1977 and 1978 Richard Kubb developed a transient energy budget model to predict the body temperature of a bass exposed to a step change in water temperature. 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. Kubb also conducted heating and cooling experiments on a large number of bass at the Physiology Department of SUNY at Buffalo and at the Savannah River Ecology Laboratory (SREL). Anatomical measurements indicated that body wall thickness for three compartments (mid-gut, brain and heart) were linear functions of body mass. Mid-gut and brain

thermal time constants were dependent on body mass but the time constant for the heart was independent of mass. The heart region exchanged heat at the fastest rate, the cranial region next fastest and the mid-gut at the slowest rate. This quantitative assessment of transient heat flow through fish body tissues (laboratory studies) and conductive-convective heat exchange between fish body surfaces and the environment (heat transfer model) enabled us to make accurate predictions of deep body core temperatures of fish experiencing step changes in ambient temperature (Kubb and Spotila 1980).

From 1978 to 1980 Claire Ross accomplished the second and third objectives. She adapted the multichannel radio transmitter, developed by Standora (1977) for alligators, for use in bass. Temperatures were transmitted from five parts of a fish's body and from its surrounding water. The use of integrated circuits, miniature components, small batteries and, finally, hybrid circuits have allowed us to construct a small transmitter (7 x 2 x 1.5 cm) which, along with a 5 x 2 cm dia. battery, could be placed into the body cavity of a bass as small as 0.5 kg. Fish acted normally and did not appear any more stressed than those that received only a small "beeper" transmitter developed at Oak Ridge National Laboratory and used by Coutant and others (Rochelle and Coutant 1973). Fish were unrestrained and moved freely in their natural habitat in Pond C on the Savannah River Plant, Aiken, S.C. (Fig. 1). This system allowed us to follow fish while we were on shore or in a boat as far as 300 m away. To date, a total of five bass have been successfully implanted with multichannel transmitters, two at unheated temperatures and three at heated temperatures. Considerable data has been acquired relating body temperatures to water temperature. Heat lags have been documented in various body compartments of these bass. These lags are like those found by Kubb for fish in his laboratory experiments. These data will be useful in testing Kubb's time dependent model for fish moving in their natural environment. Details of these experiments have been reported in a thesis (Ross 1980).

We recently completed our first series of field studies on the behavioral thermoregulation of bass. Claire Ross examined the behavioral mechanisms which allow largemouth bass to survive under adverse temperature conditions in a South Carolina reservoir (Pond C, Fig. 1) receiving thermal effluent from a nuclear reactor. Water temperature was very important in determining the distribution of bass in the reservoir. Bass were restricted in range by lethal water temperatures and utilized a greater proportion of the reservoir in winter months as compared to summer months. Bass selected temperatures close to 30°C and avoided temperatures above 31°C .

Habitat selection by Pond C bass involved more than avoidance of lethal temperatures. Pond C bass were restricted in range by water temperature. Bass had to constantly respond behaviorally and physiologically to minimize adverse effects caused by physical stresses placed on them by this extreme and unpredictable environment while satisfying their biological requirements such as feeding, spawning, defense of territory, maintenance of position in dominance hierarchies, and avoidance of predation. The physiological effects caused by continuously fluctuating environments had to be offset by compensatory mechanisms.

Under normal, unheated conditions, bass dispersed throughout the reservoir but were concentrated in six main areas (two shoreline locations, three coves and one deep spring). During reactor operation hot water at temperatures lethal to fish ($\sim 55^{\circ}\text{C}$), forced bass to retreat to refuges in two of the coves and the deep spring. Distribution of bass varied seasonally. During winter bass occupied larger areas in the refuges than during the summer because more cool water was present. When confined to the refuge areas bass experienced a wide variety of temperatures. If they swam towards the main portion of the reservoir they quickly encountered lethal temperatures. If they remained in a refuge area they encountered considerable vertical and horizontal variation in temperature. Gradients of 15°C were common from the bottom to surface in water 0.5 - 0.9 m deep. A large bass

could easily experience 15°C at its ventral surface and 20°C or more at its dorsal surface while remaining motionless. By swimming a short distance, this bass could quickly go from a water temperature of 14°C to 32°C . Within the refuges bass occupied favorable locations that were determined in part by temperature and in part by other factors. They did not defend territories, although some individuals appeared to remain in particular locations. Other bass that entered such locations were not driven off or challenged. Under normothermic and heated conditions bass seemed to compromise and did not select a location based on optimum temperature alone but rather selected an optimal habitat that provided acceptable temperature, cover, food, etc. These results are contained in the Ross thesis (1980) and will be written for publication during the next year.

THERMOREGULATION OF TURTLES

The overall objective of this portion of our research was to continue field studies on the biophysical ecology of turtles in thermally stressed environments on the Savannah River Plant. Specific objectives were to: 1.) Complete laboratory testing of the climate space for Chrysemys scripta; 2.) Formulate a transient energy budget for this turtle; 3.) Complete a field study on the effects of thermal effluents on the home ranges and movements of turtles in Par Pond on the Savannah River Plant; 4.) Determine the operative environmental temperatures (T_e) of C. scripta; and 5.) Finish a definitive paper on the thermoregulatory mechanisms by which the turtle C. scripta adjusts to thermal effluents.

Energy Budgets and Realized Climate Spaces

By September, 1978 we had completed our laboratory experiments in a climate space simulation chamber that provided data required to test our steady state climate space for C. scripta. By the fall of 1979 we completed our analysis of the energy budgets and climate space of this turtle and prepared a working

manuscript. We also completed a manuscript on the behavioral thermoregulation of turtles in Par Pond (Spotila, et al. 1980) that is scheduled for submission in July, 1980. By June 1980 we completed analysis of our field data from 1974 - 1979 and calculated realized climate spaces for C. scripta. To produce a realized climate space Edward Standora superimposed the microclimatic conditions for which a turtle was actually above water basking ($Q_{abs} + T_a$), plus the water temperatures it occupied (as if it were operating along the blackbody line of the climate space), over the theoretical (or fundamental) climate space as given by Foley (1976).

This approach provided a clear picture of the actual ability of a turtle to exploit the thermal niches available in its environment. Standora, Foley and I are now combining this information with that in our working manuscript on energy budgets and climate spaces to produce a paper on the fundamental and realized climate spaces of C. scripta.

Par Pond Field Studies

Joseph Schubauer has completed his master's thesis (June 1980) and has several manuscripts in preparation on the response of turtles (movements and population structure) to thermal effluents in Par Pond (Schubauer 1980). Using standard techniques he captured, marked and released over 400 turtles during 178,000 trap hours. He constructed small radio transmitters and placed them on 30 individuals (15 males, 15 females) in the Hot Arm (heated) and West Arm (control) of the reservoir (Fig. 2). 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 directional antenna and 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, because 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. Males in the Hot Arm moved significantly more than females. 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.

Operative Environmental Temperatures

Operative environmental temperature (T_e) was a good predictor of the basking behavior of turtles. Kenneth Crawford has completed his analysis of the data from his T_e study of 1979 and has completed his thesis (Crawford 1980). We defined T_e as the "operative environmental temperature" of Bakken and Gates (1975, p. 261) and Bakken (1976, p. 351-352). It is the temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal and exposed to the same microclimate. It is also equivalent to the temperature of a blackbody cavity producing the same thermal load on the animal as the actual non-blackbody microclimate, and therefore may be regarded as the true environmental temperature seen by that animal (Bakken and Gates, p. 261, 1975). For an ectothermic turtle, with no pelage, T_e is the temperature of the environment as seen by the animal and is an index of the thermal load placed on the animal by its environment.

Crawford constructed and painted hollow copper turtles so that they duplicated C. scripta in size, shape, radiative properties (absorptivity and emissivity) and substrate contact area. These served as T_e thermometers since they experienced

the same T_e as real turtles. He placed them in the same positions in the environment as occupied by C. scripta and measured T_e on a continuous basis.

T_e was positively related to visible and thermal radiation and air temperature but it was not obviously related to wind speed. A multiple regression equation describes the relationship of T_e to these microclimatic parameters

$$T_e = 0.011R + 0.0025S + 1.53T + 0.0032V - 14.54 \quad (r^2 = 0.78)$$

where R = total radiation in Wm^{-2} ,

S = short wave radiation from 300-3000 nm in Wm^{-2} ,

T = air temperature in $^{\circ}C$ and

V = wind speed in ms^{-1}

Turtles, C. scripta, generally did not bask until T_e exceeded $28^{\circ}C$. This was not an artifact of our measurement system since we often measured T_e less than $28^{\circ}C$ and very few turtles basked at low T_e . Thus T_e was a good predictor of basking behavior. When we calculated T_e for other field data acquired when T_e was not measured, we found again that turtles did not bask until $T_e = 28^{\circ}C$. Since turtles behaved as we had predicted we have confidence in T_e as a predictive tool for turtle behavior. Thermoregulation appears to be the major factor determining the basking behavior of C. scripta.

Thermoregulatory Mechanisms

Field and laboratory data have been analyzed and realized climate spaces and fundamental climate spaces computed for C. scripta. We are now developing a theoretical framework on which to base a behavioral-biophysical-ecological model of the thermoregulation of C. scripta. In August we will review the status of our model and then set about writing a definitive paper on the behavioral thermoregulation of this animal. We will include an analysis that will predict the behavior of this species in response to a thermal effluent. This will complete all of the

objectives we established for our studies on the thermoregulation of turtles.

THEORETICAL CALCULATIONS

Some of our most exciting progress has been in the area of theoretical calculations on the effect of body size and physical characteristics on the thermoregulation of large ectotherms. The ability of animals to thermoregulate at a high constant body temperature is limited by the constraints imposed on them by their body size and physical characteristics and those of their environment. There may be more similarities between the thermoregulatory capacities of large reptiles and mammals than between large and small members of either class alone. The net heat production required to maintain a specific body temperature changes as the size of an ectotherm increases (Fig. 3). Metabolic requirements are reduced for all large animals and we expect to see a convergence of heat production and insulative capacities as the sizes of animals increase.

An increase in body size isolates an ectotherm from its physical environment. Thus a large alligator (Alligator mississippiensis) 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. It is not surprising that animals have evolved a variety of thermoregulatory strategies (Fig. 4) in response to the selective pressures imposed on them by their natural environment. Body size has been a primary factor in determining which thermoregulatory strategy would be used by a given animal. These findings are discussed in greater detail in Spotila (1980).

LABORATORY EXPERIMENTS

Four laboratory studies provided information on the effects of body size and behavior on the peripheral blood flow and evaporative water loss from alligators,

on the role of size on boundary layer resistance and evaporative water loss from turtle shaped objects and on the effect of nutritional status on the basking behavior of turtles.

Blood Flow in Alligators

Christina Weinheimer (1980) measured peripheral blood flow in the tails of six alligators using the ^{133}Xe technique described by Lassen (1964) and Clausen and Lassen (1971) using small Cd-Te detectors developed by Entine et al. (1974) and Cerretelli et al. (1978). This technique has been used on reptiles by Morgaridge and White (1969) and in crocodilians by Grigg and Alchin (1976), Smith et al. (1978) and Robertson and Smith (1979). Our research was completed in the laboratory of Dr. David Pendergast of the Physiology Department of SUNY at Buffalo.

Blood flow gradually decreased through time during all experiments. When an alligator was placed into water in a cage such that it could submerge and surface ad lib, it typically submerged for periods from a few seconds to two or more minutes with no change in the ^{133}Xe washout curves. When an alligator was involuntarily submerged blood flow to the tail dropped below $0.010 \text{ ml g}^{-1} \text{ min}^{-1}$, or essentially stopped. Standard BF from quiescent but restrained animals were combined for all the experiments in air. When muscle temperature (T_m) was less than 30°C muscle blood flow (MBF) ranged from 0.004 to $0.037 \text{ ml g}^{-1} \text{ min}^{-1}$ ($\bar{x} = 0.018$). When T_m exceeded 30°C MBF ranged from 0.006 to $0.049 \text{ ml g}^{-1} \text{ min}^{-1}$ ($\bar{x} = 0.017$). Skin temperatures (T_s) less than 30°C gave subcutaneous blood flow (SBF) of 0.006 to $0.023 \text{ ml g}^{-1} \text{ min}^{-1}$ ($\bar{x} = 0.012$). When T_s was greater than 30°C SBF ranged between 0.009 and $0.039 \text{ ml g}^{-1} \text{ min}^{-1}$ ($\bar{x} = 0.017$). Whenever an alligator moved, either struggling to escape or simply shifting position, blood flow greatly increased (two to eight times over resting values) both in the skin and muscle. After movement, blood flow gradually returned to resting levels. Variation in resting flow was great, ranging from 0.005 to $0.03 \text{ ml g}^{-1} \text{ min}^{-1}$ 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 et al. 1978). 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 newly acquired data with data from other measurement techniques since we have indications that ¹³³Xe, while a good relative measure, may underestimate true blood flow.

Blood flow determined with ¹³³Xe has been found to be in good agreement with simultaneous measurements by radioactive microspheres (Fisher et al. 1977). However, more recent studies (Pendergast, Pers. comm.) indicate that the ¹³³Xe method may in fact underestimate actual blood flow by one-half. Underestimates of BF could be caused by incomplete equilibration of ¹³³Xe between capillary blood flow and surrounding tissue (Bassinghwaight et al. 1968, Hirzel and Krayenbuehl 1974), and/or to intertissue back diffusion (Halsey et al. 1977, Hirzel and Krayenbuehl 1974). Thus, measurement of absolute flow values is not yet possible.

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 capabilities.

For these 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. Respiratory water loss was 0.018 mg g⁻¹ 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. 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. Using plaster replicas of each experimental animal we determined boundary layer resistance and then measured water loss and computed skin resistance of real alligators tested in a wind tunnel at air speeds of 200 cm s^{-1} . Boundary layer resistance ranged from 0.87 s cm^{-1} to 1.10 s cm^{-1} $\bar{x} = 1.05 \text{ s cm}^{-1}$. Skin resistance values ranged from 43.3 s cm^{-1} to 64.0 s cm^{-1} and were inversely related to rates of water loss. Mean skin resistance obtained for the alligator (54.7 s cm^{-1}) was within the range reported for other reptiles. These results are now in press (Davis et al. 1980).

Boundary Layer Studies

A boundary layer is a layer of non-turbulent air which surrounds all terrestrial objects and organisms. 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. At 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. While this is true, we have demonstrated, using bird eggs as a model system, that air movement quickly strips away the boundary layer from eggs, turtles and similar shaped organisms up to 10 kg in mass. At a wind speed of 100 cm s^{-1} the boundary layer resistance (r_b) of a 10 kg sphere is 15 times less than in still air and at 400 cm s^{-1} it drops to almost zero (Spotila et al. 1980). The same was true for alligators up to 1.5 m in length (Davis 1978, Davis et al. 1980). Thus, boundary layer resistance can be very important for larger organisms in still air but has little influence on evaporation from turtles, alligators and similar sized organisms in moving air.

In still air, boundary layer thickness is inversely related to the difference in water vapor density at the surface of an object and in the free air beyond the boundary layer. For bird eggs, turtles with dry shells, alligators and lizards this difference is small because internal resistance is large and the concentration of water molecules at the surface is small. Thus boundary layer thickness is greater and r_b is larger. Therefore, while agar replicas are excellent models for the measurement of boundary layer thickness and r_b for biological surfaces in moving air, they underestimate r_b and boundary layer thickness under conditions that are predominantly affected by natural convection. Boundary layer resistances for objects in still air can be computed using the formula of Tracy and Sotherland (1979).

Nutritional Status and Basking Behavior of Turtles

We have demonstrated that basking is an important thermoregulatory behavior

in turtles (C. scripta) under natural conditions (Spotila et al. 1980). Since Gatten (1974) reported that recently fed C. scripta had a higher preferred body temperature (29.1°C) than non fed individuals (24.6°C) we hypothesized that fed turtles should bask more often and/or for longer periods of time than non fed animals, and would have a higher body temperature through time. As a first step in testing this hypothesis we have completed one phase of a laboratory experiment to determine the effect of feeding on the basking behavior of C. scripta.

Ten C. scripta were held in each of two isolated enclosures (25°C) with free access to water, dry substrate and a light-heat source above the dry substrate. One group was fed a diet of meat and vegetables while the other was not fed. Behavior was filmed during the light phase of a LD 12:12 photoperiod during the six weeks of the experiment. Preliminary data analysis suggests that there was no difference in basking times between the fed and non fed groups during the first replication. The second replication is underway and definitive results will not be available until it is complete. However, it seems that our turtles are not acting as expected if feeding causes a thermophilic response.

This raises some important questions. Many authors have reported that lizards, snakes and turtles bask in response to feeding. Body temperatures are elevated above fasting levels for recently fed snakes, lizards, turtles and crocodilians. However, others have reported no thermophilic response in other lizards, turtles and crocodilians (see Lang 1979). Thus, the exact relationship between feeding, basking behavior and body temperature is unclear.

Parmenter (1978) reported that C. scripta had an optimum ingestion rate at 29°C , which is the preferred body temperature for fed animals. This suggests that feeding should cause a thermophilic response in turtles, although this response may be affected by other factors such as heterogeneity in the thermal environment, acclimation or water temperature, social interactions, past history, health, enzyme kinetics, etc. We plan to investigate the interrelationships of some of

these factors in the thermoregulatory behavior of C. scripta.

Our first action will be to complete the current experiment and analyze that data. Then we will conduct a series of experiments on the basking behavior and body temperatures of fed and non fed C. scripta acclimated to 10, 20, 30 and 35°C in an environmental chamber containing a heat-light source, dry substrate and water. We expect fed turtles to bask more often and have a higher body temperature than non fed animals, especially at lower ambient temperatures (10 and 20°C). Finally we will begin to study digestive efficiency and enzyme efficiency of turtles held at these temperatures. These experiments will be conducted over the next three years and are described in more detail in the renewal proposal that accompanies this report.

MAJOR ACCOMPLISHMENTS

We have demonstrated that an integrative approach including biophysical modeling, laboratory studies and field experiments is an effective method for studying the physiological ecology of animals. This approach has enabled us to determine quantitatively the mechanisms by which fish and turtles thermoregulate in response to thermal stress. Considerable progress has been made toward formulating biophysical-behavioral-ecological models to explain the behavioral thermoregulation of largemouth bass (M. salmoides) and turtles (C. scripta).

Steady state and time dependent mathematical models accurately predict the body temperatures of largemouth bass exposed to a step change in water temperature. Laboratory tests confirm the validity of the model. A multichannel radio transmitter provides the temperatures of several body compartments of free ranging bass in their natural habitat. These data can now be used to field test the model. Initial field studies on the behavior of bass in a reservoir receiving heated effluents at a lethal temperature indicate that these bass survive in refuge areas containing cool water. Their specific behavioral reactions in response to the onset

of the heated effluent remains to be studied as does their site specificity and the influence of social interactions on their thermoregulatory behavior in the refuges.

Energy budgets, fundamental and realized climate spaces have been completed for the turtle C. scripta. We have described the behavioral thermoregulation of C. scripta in Par Pond and have measured the movements, home ranges and population levels of turtles in a heated and unheated arm of the reservoir. We have also found that operative environmental temperature was closely related to microclimate variables and was a good predictor of the basking behavior of turtles. Thermoregulation appears to be the major factor determining the basking behavior of C. scripta. A biophysical-behavioral-ecological model is being finalized to predict the behavior of C. scripta in response to thermal effluents.

Mathematical modeling led us to propose a new synthesis of the evolution of thermoregulatory strategies among animals. Laboratory experiments clarified the effects of movement, diving and temperature on the blood flow of alligators. Other experiments demonstrated the importance of boundary layers in reducing the evaporation of water from the surfaces of turtles and alligators in still air. Boundary layer has little effect in moving air. Recent experiments indicate that nutritional status and acclimation temperature may be important factors influencing the basking behavior of aquatic turtles. New experiments are being planned to test this hypothesis.

During the course of this renewal period we have accomplished all of the research objectives set forth in our research proposals for 1977, 1978 and 1979. We have published 19 scientific articles and notes, have had six students complete their master's theses and have delivered 16 presentations at national scientific meetings (see Appendix I). We have extended our cooperative efforts with the Savannah River Ecology Laboratory, SREL, having continued our interactions with the research groups of Drs. J.W. Gibbons, J.P. Giesy and I.L. Brisbin. Several of

our presentations and articles were coauthored with members of the SREL staff.

Finally, we have asked several new questions, formulated hypotheses, and designed experiments to test these hypotheses. These are detailed in the accompanying renewal proposal. The experiments will be conducted over the next three year renewal period.

LITERATURE CITED

- Bakken, G.S. 1976. A heat transfer analysis of animals; unifying concepts and the application of metabolism chamber data to field ecology. *J. Theoret. Biol.* 60: 337-384.
- Bakken, G.S. and D.M. Gates. 1975. Heat-transfer analysis of animals; some implications for field ecology, physiology and evolution. Pages 255-290 in D.M. Gates and R.B. Schmerl, eds. *Perspectives of biophysical ecology*. Springer-Verlag, New York.
- Bakken, G. and J.R. Spotila. 1971. Schlieren photography and the energy budget. *Bull. Mo. Bot. Garden* 59 (4): 53-56.
- Bassingthwaighte, J.B., T. Strandell and D.E. Donald. 1968. Estimation of coronary blood flow by washout of diffusible indicators. *Circulation Res.* 23: 259-278.
- Cerretelli, P., M. Blau, D. Pendergast, C. Eisenhardt, D.W. Rennie. 1978. Cadmium Telluride ^{133}Xe clearance detector for muscle blood flow studies. *IEEE Transactions on Nuclear Science* NS-25: 620-623.
- Clausen, J.P., and N.A. Lassen. 1971. Muscle blood flow during exercise in normal man studied by the $^{133}\text{Xenon}$ clearance method. *Cardiovasc. Res.* 5: 245-254.
- Crawford, K.M. 1980. Basking behavior and operative environmental temperatures of the turtle, Chrysemys scripta. Master's thesis, State University College at Buffalo, July 1980.
- Davis, J.E. 1978. Evaporative water loss of the American alligator, Alligator mississippiensis: The relative importance of respiratory and cutaneous components and the regulatory role of the skin. Master's Thesis. 37 p. State University College at Buffalo.
- Davis, J.E., J.R. Spotila, and W.C. Scheffler. 1980. Evaporative water loss from the American alligator, Alligator mississippiensis: the relative importance of respiratory and cutaneous components and the regulatory role of the skin. *Comp. Biochem. Physiol.* In press.

- Entine, G., H.B. Serreze, and D.A. Garcia. 1974. High spatial resolution CdTe medical probes. IEEE Trans. Nucl. Sci. 21: 726-730.
- Erskine, D.J. and J.R. Spotila. 1977. Heat energy budget analysis and heat transfer in the largemouth blackbass (Micropterus salmoides). Physiol. Zool. 50: 157-169.
- Foley, R.E. 1976. Energy budgets and a climate space diagram for the turtle, Chrysemys scripta. Master's thesis, State University College at Buffalo. 51 p.
- Foley, R.E. and J.R. Spotila. 1978. Effect of wind speed, air temperature and body size on evaporative water loss from the turtle Chrysemys scripta. Copeia 1978: 627-634.
- Gatten, R.E., Jr. 1974. Effect of nutritional status on the preferred body temperature of the turtles Pseudemys scripta and Terrapene ornata. Copeia 1974: 912-917.
- Grigg, G.C. and J. Alchin. 1976. The role of the cardiovascular system in thermoregulation of Crocodylus johnstoni. Physiol. Zool. 49: 24-36.
- Halsey, J.H., Jr., N.F. Capra and R. McFarland. 1977. Use of hydrogen for measurement of regional cerebral blood flow. Problem of intercompartmental diffusion. Stroke 8: 351-357.
- Hirzel, H.O. and H.P. Krayenbuehl. 1974. Validity of the ¹³³Xenon method for measuring coronary blood flow (comparison with coronary sinus outflow determined by an electromagnetic flow-probe). Pflugers Arch. 349: 159-169.
- Kreith, F. 1973. Principles of heat transfer. 656 p. (3rd Ed.) Intext Educational Publishers, New York.
- Kubb, R.N. and J.R. Spotila. 1980. Mechanisms of heat transfer and time dependent modeling of body temperatures in the largemouth bass (Micropterus salmoides). Physiol. Zool., April, 1980.
- Lang, J.W. 1979. Thermophilic response of the American alligator and the American crocodile to feeding. Copeia 1979: 48-59.

- Lassen, N.A., J. Lindbjerg and O. Munck. 1964. Measurement of blood flow through skeletal muscle by intra-muscular injection of Xenon 133. *Lancet* 1: 686-689.
- Morgareidge, K.R., and F.N. White. 1969. Cutaneous vascular changes during heating and cooling in the Galapagos marine iguana. *Nature* 223: 587-591.
- Parmenter, R.R. 1978. Effects of food availability and water temperature on feeding electivity, growth, and body size of pond sliders (Chrysemys scripta scripta Schoepff). Master's thesis, University of Georgia.
- Robertson, S.L. and E.N. Smith. 1979. Thermal indications of cutaneous blood flow in the American alligator. *Comp. Biochem. Physiol.* 62: 569-572.
- Rochelle, J.M. and C.C. Coutant. 1973. Temperature sensitive ultrasonic fish tag, Q-5099. Oak Ridge National Laboratory. Report ORNL-TM-4438. 26 p.
- Ross, C.J. 1980. Behavioral thermoregulation of the largemouth bass, Micropterus salmoides. Master's thesis, State University College at Buffalo, 56 p.
- Schubauer, J.P. 1980. The ecology and behavior of an aquatic turtle, Chrysemys scripta, inhabiting a thermally altered reservoir, Par Pond, South Carolina. Master's thesis, State University College at Buffalo, July, 1980.
- Smith, E.N., S. Robertson, and D.G. Davies. 1978. Cutaneous blood flow during heating and cooling in the American Alligator. *Am. J. Physiol.* 235: R160-R167.
- Spotila, J.R. 1980. Constraints of body size and environment on the temperature regulation of dinosaurs. Chapter 8, pp. 233-254. In: R.D.K. Thomas and E.C. Olson, (Eds.) A Cold Look at the Warm Blooded Dinosaurs. AAAS Symposium Volume. 28. Westview Press, Boulder, CO.
- Spotila, J.R., R.E. Foley, J.P. Schubauer, R.D. Semlitsch, K.M. Crawford, E.A. Standora and J.W. Gibbons. 1980. Behavioral thermoregulation of turtles, Chrysemys scripta, in a nuclear reactor cooling reservoir. Manuscript.
- Spotila, J.R., C.J. Weinheimer, and C.V. Paganelli. 1980. Shell resistance and evaporative water loss from bird eggs. Effects of wind speed and egg size. *Physiol. Zool.* In press.

- Standora, E.A. 1977. An eight-channel radio telemetry system to monitor alligator body temperatures in a heated reservoir. pp. 70-78. In: Proceedings First International Conference on Wildlife Biotelemetry. F.M. Lang, (Ed.) Electrical Engineering Department, University of Wyoming, Laramie.
- Terpin, K.M., J.R. Spotila, and R.E. Foley. 1979. Thermoregulatory adaptations and heat energy budget analyses of the American alligator, Alligator mississippiensis. Physiol. Zool. 52: 296-312.
- Tracy, C.R. and P.R. Sotherland. 1979. Boundary layers of bird eggs: Do they ever constitute a significant barrier to water loss? Physiol. Zool. 52: 63-66.
- Weinheimer, C.J. 1980. Analysis of microcirculatory blood flow in the alligator, Alligator mississippiensis, using ^{133}Xe . Master's thesis, State University College at Buffalo. 27 p.

Figure 1 Distributions of fish in Pond C, June - November, 1979. Horizontal slashes indicate ambient distribution, vertical slashes indicate heated distribution.

Figure 2 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 3 Net heat production (M-E) required of ectotherms as a function of body size, body temperature and climate. Insulation (fat) thickness was a constant 10% of body diameter. Temperatures are in °C, wind speed is 100 cm s⁻¹ and radiation absorbed is in cal cm⁻² min⁻¹.

STRATEGIES OF THERMOREGULATION

Figure 4 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 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.

APPENDIX I

Scientific Presentations

Articles

- Erskine, D.J. and J.R. Spotila. 1977. Heat energy budget analysis and heat transfer in the largemouth blackbass (Micropterus salmoides). *Physiol. Zool.* 50: 157-169.
- Spotila, J.R., K.M. Terpin and P. Dodson. 1977. Mouth gaping as an effective thermoregulatory device in alligators. *Nature*. 265: 235-236.
- Bonin, J.D. and J.R. Spotila. 1978. Temperature tolerance of larval muskellunge (Esox masquinongy Mitchell) and F₁ hybrids reared under hatchery conditions. *Comp. Biochem. Physiol.* 59A: 245-248.
- Foley, R.E. and J.R. Spotila. 1978. Effect of wind speed, air temperature and body size on evaporative water loss from the turtle Chrysemys scripta. *Copeia* 1978: 627-634.
- Foley, R.E., J.R. Spotila, J.P. Giesy and C.H. Wall. 1978. Arsenic concentrations in water and fish from Chautauqua Lake, New York. *Env. Biol. Fish.* 3: 73-79.
- Kowalski, K.T., J.P. Schubauer, C.L. Scott, and J.R. Spotila. 1978. Interspecific and seasonal differences in the temperature tolerance of stream fish. *J. Thermal Biology*. 3: 105-108.
- Paladino, F.V. and J.R. Spotila. 1978. The effect of arsenic on the thermal tolerance of newly hatched muskellunge fry (Esox masquinongy). *J. Thermal Biology* 3: 223-227.
- Terpin, K.M., P. Dodson and J.R. Spotila. 1978. Ketamine hydrochloride as an effective anesthetic for alligators. *Copeia* 1978: 147-148. (Note)
- Gibbons, J.W., J.L. Greene and J.P. Schubauer. 1979. Variability in clutch size in aquatic turtles. *British J. Herpetology*. 6: 13-14.
- Gibbons, J.W., G. Keaton, J.P. Schubauer, J.L. Greene, D.H. Bennett, J.R. McAuliffe, and R.R. Sharitz. 1979. Unusual population size structure in freshwater turtles in barrier islands. *Georgia J. Science* 37: 155-159.

- Spotila, J.R. and F.V. Paladino. 1979. Toxicity of arsenic to developing muskellunge fry (Esox masquinongy). *Comp. Biochem. Physiol.*: 62C: 67-69.
- Spotila, J.R., K.M. Terpin, R.R. Koons, and R.L. Bonati. 1979. Temperature requirements of fishes from eastern Lake Erie and the upper Niagara River: A review of the literature. *Env. Biol. Fish.* 4: 281-307.
- Terpin, K.M., J.R. Spotila, and R.E. Foley. 1979. Thermoregulatory adaptations and heat energy budget analysis of the American alligator, Alligator mississippiensis. *Physiol. Zool.* 52: 296-312.
- Davis, J.E., J.R. Spotila, and W.C. Scheffler. 1980. Evaporative water loss from the American alligator, Alligator mississippiensis: the relative importance of respiratory and cutaneous components and the regulatory role of the skin. *Comp. Biochem. Physiol.* In press.
- Kubb, R.N., J.R. Spotila, and D.R. Pendergast. 1980. Mechanisms of heat transfer and time dependent modeling of body temperatures in the largemouth bass (Micropterus salmoides). *Physiol. Zool.*, April, 1980. pp. 222-239.
- Paladino, F.V., J.R. Spotila, J.P. Schubauer, and K.T. Kowalski. 1980. The critical thermal maximum: A technique used to elucidate physiological stress and adaptation in fishes. *Rev. Canad. Biol.* June, 1980.
- Schubauer, J.P., C.L. Scott, K.T. Kowalski, and J.R. Spotila. 1980. Effect of tetracycline hydrochloride treatment on the critical thermal maximum of common shiners. *Prog. Fish. Cult.* 42: 48-49.
- Spotila, J.R. 1980. Constraints of body size and environment on the temperature regulation of dinosaurs. Chapter 8, pp. 233-254. In: R.D.K. Thomas and E.C. Olson, (eds.) A Cold Look at the Warm Blooded Dinosaurs. AAAS Symposium Volume 28. Westview Press, Boulder, CO.
- Spotila, J.R., C.J. Weinheimer, and C.V. Paganelli. 1980. Shell resistance and evaporative water loss from bird eggs: Effects of wind speed and egg size. *Physiol. Zool.* In press.

Master's Theses

- Davis, J.E. 1978. Evaporative water loss of the American alligator, Alligator mississippiensis: The relative importance of respiratory and cutaneous components and the regulatory role of the skin. Master's thesis, State University College at Buffalo, 37 p.
- Kubb, R.N. 1979. Mechanisms of heat transfer and time dependent modeling of body temperatures in the largemouth bass (Micropterus salmoides). Master's thesis, State University College at Buffalo, 46 p.
- Crawford, K.M. 1980. Basking behavior and operative environmental temperatures of the turtle, Chrysemys scripta. Master's thesis, State University College at Buffalo, July 1980.
- Ross, C.J. 1980. Behavioral thermoregulation of the largemouth bass, Micropterus salmoides. Master's thesis, State University College at Buffalo, 56 p.
- Schubauer, J.P. 1980. The ecology and behavior of an aquatic turtle, Chrysemys scripta, inhabiting a thermally altered reservoir, Par Pond, South Carolina. Master's thesis, State University College at Buffalo, July, 1980.
- Weinheimer, C.J. 1980. Analysis of microcirculatory blood flow in the alligator, Alligator mississippiensis, using ^{133}Xe . Master's thesis, State University College at Buffalo. 27 p.

Presentations at National Meetings

- Foley, R.E. and J.R. Spotila. 1977. Shoreline microclimates of a reservoir receiving heated effluents from a nuclear reactor. Energy and Environmental Stress in Aquatic Systems, D.O.E. Symposium, Nov. 1977, Augusta, Ga.
- Schubauer, J.P., R.D. Semlitsch and J.R. Spotila. 1977. Influence of microclimate on the basking behavior of aquatic turtles. Amer. Soc. Zool. Toronto, Dec., 1977, Amer. Zool. 17(4): 895.

- Spotila, J.R., R.E. Foley and J.W. Gibbons. 1977. Response of turtles to heated effluents from a nuclear production reactor. Energy and Environmental Stress in Aquatic Systems, D.O.E. Symposium, Nov. 1977, Augusta, Ga.
- Kubb, R.N. 1978. Time-dependent modeling of heat transfer in the largemouth bass (Micropterus salmoides). Amer. Soc. Zool. Dec, 1978, Richmond, Va.
- Kubb, R.N. 1978. Time-dependent modeling of heat transfer in the largemouth bass (Micropterus salmoides): A predictive tool. Energy and environmental stress in aquatic systems, D.O.E. Symposium, Nov. 1977, Augusta, Ga.
- Schubauer, J.P. and J. Whitfield Gibbons. 1978. Home range and movement patterns of Chrysemys scripta (Reptilia:Emydidae) in a thermally altered lake in South Carolina. Assoc. Southeastern Biologists. April 1978.
- Weinheimer, C.J. and J.R. Spotila. 1978. Shell resistance and evaporative water loss from bird eggs: effects of wind speed and egg size. Amer. Soc. Zool. Dec. 1978, Richmond, Va.
- Schubauer, J.P. 1979. Exclusion of aquatic turtles from the heated portion of a reactor cooling reservoir (Par Pond). Ecol. Soc. of Amer. Oklahoma, June 1979.
- Schubauer, J.P. 1979. The influence of heated effluents on turtle populations in Par Pond, South Carolina. Assoc. Southeastern Biol. April, 1979.
- Schubauer, J.P. 1979. The response of Chrysemys scripta to heated effluents in Par Pond, S.C. Amer. Soc. Ichthyologists and Herpetologists, Aug. 1979, Orono, Maine.
- Spotila, J.R., E.A. Standora and R.E. Foley. 1979. Body temperatures of green turtles: free swimming and active on land at Tortuguero, Costa Rica. Amer. Soc. Zool. Dec. 1979, Tampa, Florida.
- Standora, E.A., J.R. Spotila, and R.E. Foley. 1979. Telemetry of movement and body temperature data from green turtles, Chelonia mydas, at Tortuguero, Costa Rica. Amer. Soc. Zool. Dec. 1979, Tampa, Florida.

- Crawford, K.M. 1980. Operative environmental temperatures of basking turtles, Chrysemys scripta. Herpetologists League - Society for the Study of Amphibians and Reptiles. August, 1980. Milwaukee, Wisc.
- Davis, J.E., J.R. Spotila, and W.C. Schefler. 1980. Evaporative water loss from the skin and respiratory tract of alligators, Alligator mississippiensis. Herp. League - S.S.A.R., August, 1980. Milwaukee, Wisc.
- Standora, E.A., M.J. Vargo and I.L. Brisbin, Jr. 1980. Body temperature profiles of free-ranging Chrysemys scripta obtained by multichannel telemetry. Herp. League - S.S.A.R., Aug., 1980. Milwaukee, Wisc.
- Weinheimer, C.J., D. Pendergast, and J.R. Spotila. 1980. Peripheral blood flow in alligators as affected by diving and fear. Herp. League - S.S.A.R., Aug., 1980. Milwaukee, Wisc.