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Constraints of Bioenergetics on the Ecology and Distribution of Vertebrate Ectotherms

Final Report

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ABSTRACT

The constraints of bioenergetics on the ecology and distribution of vertebrate ectotherms were quantified. During this project we conducted studies: 1) to determine the role of incubation temperature on the post- hatching growth rate of the snapping turtle, *Chelydra serpentina*, 2) to establish the rate of energy expenditure of the slider turtle, *Trachemys scripta*, in the field, 3) to determine the field metabolic rates, body temperatures and selected microclimates of the box turtle, *Terrapene carolina*, and 4) to measure the effect of diet type on the consumption rate, digestion rate and digestive efficiency of adult *T. scripta* . We also completed our research on the three-dimensional bioenergetic climate space for freshwater turtles. In addition, we produced two reviewed volumes, one from our symposium on the Constraints of Bioenergetics on Animal Population Dynamics and one from our workshop on Biophysical Ecology: Methods, Microclimates, and Models that were held at meetings of the American Society of Zoologists in 1987 and 1989.

We reached our research goals for this project and published 16 articles and three master's theses, and presented three papers at scientific meetings.

INTRODUCTION

The purpose of this research during 1988-1990 was to quantify the constraints of bioenergetics on the ecology and geographic distribution of vertebrate ectotherms. We used turtles (*Trachemys scripta, Terrapene carolina, and Chelydra serpentina*) and other reptiles as representative species and employed an integrative approach of mathematical modeling, laboratory studies and field experiments to develop an understanding of the role of bioenergetics in the adaptation of these animals to climate change and local environmental disturbances.

The overall objectives of this period were to:

1) Formulate a unified energy budget model for a turtle. This shall include development of a three-dimensional climate space diagram and computation of annual energy and mass balance budgets to determine the potential for growth, reproduction and storage under different climate regimes.

2) Compare the bioenergetics of herbivorous, omnivorous and carnivorous turtles.

3) Make quantitative predictions of the effects of climatic change and thermal alterations on the ecology, behavior, and biogeography of turtles.

The objectives to be accomplished in the 1988 project year were to:

1) Complete the effort to develop a three-dimensional bioenergetic climate space for a turtle, including both heat energy transfer and food energy transfer processes.

2) Determine the role of incubation temperature in the post-hatching growth rate of *C. serpentina.*

3) Complete analysis of data from experiments to determine the energy expenditure of *T. scripta* in the field by measuring heart rate as an indicator of metabolic rate and by constructing time budgets.

4) Complete experiments to determine the field metabolic rates, body temperatures, and field microclimates of *T. carolina* .

5) Determine the effect of diet type on the consumption rate, digestion rate and digestive efficiency of adult *T. scripta*.

Research generally followed these directions.The experiments on *T. carolina* in the field at the Savannah River Plant went very well and we acquired a large data base on the biophysical ecology of this turtle. The experiments on *T. scripta* were more complicated than anticipated, but produced a wealth of data on the effect of behavior on heart rate and metabolic rate in this turtle. In the fall, this study moved into the field to obtain data on the metabolic rate of free ranging turtles in a pond within a fenced enclosure. The experiments on *C. serpentina* and the diet experiments on *T. scripta* were completed.

This research was conducted at Drexel with some of the projects finishing up in Buffalo during the fall of 1988. David Penick is now pursuing his Ph.D. degree at Drexel, and the University provided a postdoctoral fellowship to Dr Michael O'Connor from Colorado State University. He produced the unified energy budget models and three-dimensional climate spaces for our turtles. Thus, all of the objectives for this project year were completed. The move to Drexel University increased our ability to reach our objectives because of the greater support base provided here and the ability to attract better graduate students because of the Ph.D. program. Some of the projects remained in Buffalo during the latter half of 1988, providing greater continuity and allowing us to maintain momentum while our new laboratory was being completed at Drexel. This allowed us to complete the growth study on *C. serpentina* and field metabolic rate study on *T. scripta* during the transition period to Drexel University.

The first set of experiments we completed was to determine the role of incubation temperature in the post-hatching growth rate of *C. serpentina* . In a series of experiments, Kathy Ryan incubated snapping turtle eggs at 26 °C and 30 °C to produce 60 male and 60 female hatchlings. Then she placed groups of 25 male and 25 female hatchlings at 25°C and 35°C and fed them a high protein (meat/fish) diet. Each turtle was housed in a separate clear plastic container (30 x 15 x 13 cm) containing 3 cm of water. Turtles were weighed and measured once each week. We maintained them under these conditions for several months. Most of the turtles at 35°C died after a few weeks. The survivors were placed into a fluctuating environment of 25°C at night and 35°C during the day. These animals survived and we compared their growth rates to those turtles held at 25°C. In general, the turtles grown at 25°C grew fastest, although those in the fluctuating environment also had a high growth rate. There was no effect of these two incubation conditions on the post-hatching growth rate of *C. serpentina* . When eggs were switched from 30°C to 26°C and then back to 30°C in another experiment, however, there was an effect on both hatchling size (smaller) and posthatching growth rate (slower). This suggests that fluctuating thermal conditions in the nest (Wilhoft et al. 1983) might have an effect, not only on the incubating embryonic turtle but also on the hatchling during the first few months of its life. These results will be important in determining the climatic limits for this species, since the egg stage is often a critical life history stage for reptiles (Gibbons and Nelson 1978).

The activity patterns, time budgets, and active metabolic rates of *T. scripta* were studied by Diane Mann, who used cardiac rate as an index of energy expenditure. The first portion of this research was a study testing the strength of the relationship between cardiac rate and oxygen consumption at various activity levels and ambient temperatures in the laboratory. The second portion was a field study in which we measured the turtle's activities and time allotments while simultaneously monitoring cardiac rate and body temperature using biotelemetry. Field metabolic rates were calculated from the regression equation for cardiac rate vs metabolic rate that was developed in the laboratory. Earlier experiments by Standora and Congdon (unpublished data) indicated that the doubly labeled water technique would not work to measure the field metabolic rate of this turtle due to the turtle's high water flux rate.Thus, a different technique was needed to measure field metabolic rate.

The use of cardiac rate as an index of energy expenditure has been an important approach in studies to predict the active metabolic rates of free-ranging animals (Renecker and Hudson 1985). The application of cardiac rate as an indirect measure of metabolic rate has been examined using biotelemetry on birds (Ferns et al. 1980 and Gessaman 1973), mammals (Morhardt and Morhardt 1971, Lund 1974, Renecker and Hudson 1985, among others), and reptiles (Bartholomew and Tucker 1963,1964; Huggins et al. 1971, and Gatten 1974). Results have been diverse, with some studies exhibiting a high correlation and others a low to modest correlation between heart rate and metabolic rate. Mann, in this study, had good success in the laboratory in relating cardiac rate to metabolic rate. Correlation coefficients for the relationship of heart rate to metabolic rate ranged from $r^2 = 0.40$ to 0.74. The overall regression equation of metabolic rate as a function of heart rate for three turtles under a variety of laboratory conditions was

$$MR = 0.0034\ (HR) - 0.009$$

where MR is metabolic rate in ml/g•h and HR is heart rate in beats/ min (Fig. 1). The correlation coefficient (r^2) was 0.62. Once she completed her laboratory experiments on turtles in air and in the water, she moved her experiments outside to the experimental pond and enclosure that she constructed at the Aquatic Biology Field Station of the State University College on the shore of Lake Erie.

In the field portion of this study, during the fall of 1988, Mann placed several turtles in the experimental pond (8 x 8 x1.5 m deep). Two of the turtles in a group were fitted with cardiac and temperature transmitters so that these variables could be recorded on a continual basis. Several other turtles were placed in the pond without any transmitters attached. These turtles were behavioral controls. After the turtles were placed into the pond, they were observed from an observation blind while activity, telemetric and microclimatological data were recorded. Activities and the corresponding cardiac rate and air-water temperature were recorded at specific time intervals. Details of the experimental procedures will be presented in Mann's master's thesis which will be completed soon. An initial description of the experiments was presented in the renewal proposal for 1988.

The results of this research should make it possible to use cardiac rate as an index of energy expenditure in these turtles. While the correlation between metabolic rate and heart rate is not absolute (Gatten 1974), it appears to be sufficient for the purposes of this study. This, combined with behavioral time-budget analysis, will allow the calculation of energy budgets for this species. Then energy budgets can be used to determine the amount of energy expended by this turtle in a year. This will allow us to test the unified energy budget model developed for this species, compute annual energy and mass balance budgets, and confirm the turtle's predicted bioenergetic space.

David Penick measured seasonal changes in water balance, energetics, daily behavior, body mass, body temperatures, and microclimates of the box turtle, *Terrapene carolina,* using doubly labeled water (DLW), radiotelemeters, microclimatological instrumentation, and field observations. The main objectives of this study were to determine the field metabolic rates (FMR), body temperatures, and water flux rates of the box turtle so that a complete unified energy budget could be developed for this species.

The DLW technique is a method for predicting the FMR of animals by measuring the production of carbon dioxide and thus the oxygen consumption. The rates of CO_2 production can be measured in free living vertebrates by injecting amounts of labeled hydrogen and oxygen molecules as water into the animal. Oxygen-18 and tritium (^3H) are the labels normally used. The oxygen-18 in the body water of a labeled animal is in isotopic equilibrium with the oxygen of CO_2 in the blood due to the action of carbonic anhydrase (Lifson et al. 1949). The principle behind this method is that oxygen molecules are lost as water and as carbon dioxide, while hydrogen molecules are lost only as water. The specific activity of ^{18}O in the body water declines faster than that of ^3H because ^{18}O is lost in the form of CO_2 as well as in the form of H_2O. The difference in the rates of decrease of ^{18}O and ^3H is a measure of the CO_2 production rate, thus the difference in the proportion of labeled oxygen lost to the amount of labeled hydrogen lost can be used as an index of carbon dioxide production. The DLW method has been used successfully with birds (Walsberg 1977, Ricklefs and Williams 1984, and Ricklefs et al 1986), mammals (McClintock and Lifson 1958, Nagy and Martin 1985, and Nagy 1987), lizards (Congdon et al. 1978, Bennett and Gleeson 1979, Mautz 1979, Nagy 1984, and Nagy et al. 1984) and the desert tortoise (Nagy and Medica 1986). Penick's study followed the protocols developed in the laboratories of Nagy, Williams and Congdon. He determined the equilibration time for the isotopes within the body of the turtle, validated the DLW method for box turtles in the laboratory by simultaneously measuring O_2 consumption and CO_2 production, in a metabolic chamber, of turtles that were injected with doubly labeled water, and measured the field metabolic rates of box turtles throughout the year. These experiments took place in the Upper Three Runs Creek drainage basin (Tinker Creek) at the Savannah River Plant in South Carolina. He quantified the daily energy expenditure and behavior of *T. carolina* in the field for four periods of the year: mid-summer (late July-early August), fall (late October- early November), winter (late January- early Febuary), and spring (late April- early May).

Details of the protocols used in these experiments were described in the renewal proposal for 1988. This portion of our research could not have been accomplished without the close cooperation of Dr. Justin Congdon and the rest of the Savannah River Ecology Laboratory staff. We relied on Dr. Kenneth Nagy at UCLA for the isotope analysis. The experiments were completed in late summer 1988 and Penick moved to Drexel University where he analysed his data and wrote his thesis. The large amount of data acquired in this study should allow us to construct bioenergetic climate spaces and annual energy budgets and to assess how changes in the environment will influence the energy exchange of these turtles.

Harold Avery (1988) determined the digestive assimilation rate of juvenile *T. scripta* fed different levels of crude diet protein at different temperatures. A review of the literature and details of Avery's results are found in the progress report for 1987 and in his thesis (copies submitted with 1989 proposal).

We are continuing our efforts to develop a three-dimensional climate space for a turtle, including both heat transfer and food energy transfer processes (**Objective 1**). We concentrated on this effort in 1988 and 1989. To accomplish this objective we added a postdoctoral fellow to this project in the fall of 1988. Dr Michael O'Connor joined us from Dr. C.R. Tracy's laboratory at Colorado State University. Dr. O'Connor is an expert in mathematical modeling and is concentrating on the climate space project. Drexel University provided him with a fellowship for the last four months of 1988 and first two months of 1989.

Symposium and Workshop

In December 1987, we held a symposium on "Constraints of Bioenergetics on Animal Population Dynamics" at the American Society of Zoologists meeting in New Orleans. During 1988, we edited the manuscripts and they were published in an issue of *Physiological Zoology*. This will serve as a basis for research in this area of ecology for the next several years. We believe this was an important part of our effort during this project year. In December 1989, we held a workshop on Biophysical Ecology: Methods, Microclimates, and Models at the American Society of Zoologists meeting in Boston. During 1990, we edited the manuscripts and they were published in the American Zoologist in 1992.

CONCLUDING COMMENTS

This research was designed to determine the constraints of bioenergetics on the ecology and distribution of vertebrate ectotherms Ectotherms such as turtles appear to play an important role in the functional coupling of the land-water interface of wetlands. They process plant and animal material acquired in the water (*T. scripta and C. serpentina*) and on land (*T. carolina*) and transfer productivity to aquatic (fish) and terrestrial (fox,raccoon, etc.) carnivores in the form of eggs (to fox, raccoon, etc.), hatchlings (fish, alligators, fox, raccoon, etc.) and juveniles and adults (alligators, raccoons, and other terrestrial predators). They may be particularly important reservoirs for elements such as calcium and radioactive isotopes of uranium, strontium and cesium. They also serve as reservoirs and vectors for parasites, algae, seeds, and other organisms resulting in the colonization of new wetlands and the preservation of fauna and flora when wetlands dry up (Congdon and Gibbons 1988). Thus, the information we generated on the bioenergetics and ecology of turtles is important in any effort to predict the micro- and macro-distribution of these animals in wetlands and their capacity for processing organic and inorganic materials.

This research benefitted from our close cooperation with researchers at the Savannah River Ecology Laboratory. Justin Congdon and John Aho served as members of the thesis committees for Harold Avery and Cindy Vernale. Congdon was on the thesis committee for David Penick as well. We continue to work closely with Drs. Congdon and Aho as well as Dr. J.W. Gibbons. We also cooperate with Dr. Rebecca Sharitz and Ken McLeod with regard to wetland processes and with Dr. I.L. Brisbin on box turtle ecology and biophysical ecology. By maintaining this cooperative effort we have increased the effectiveness of our research effort and contributed to the research goals of SREL. We believe it is important to maintain a vertebrate perspective in the overall study of wetland processes.

The project director, James R. Spotila, spent 25% of his time on this project during the academic year and 100% of his time on this project during June-July 1988- 1989. Edward A. Standora spent 25% of his time on this project during 1988. Michael O'Connor spent 100% of his time on this project during September - December 1988 and until 1989.

SIGNIFICANCE

This research combines and integrates theoretical (mathematical modeling), laboratory and field studies to make quantitative predictions of the effects of climate change and thermal alterations on the ecology, behavior and biogeography of vertebrate ectotherms. Powerful predictive tools (unified energy-budget models) were developed that describe in both a qualitative and quantitative manner the mechanisms by which turtles adjust to multiple stresses in their natural environments. During this project we formulated annual energy and mass balance budgets for two species of turtles. Laboratory and field experiments were designed to obtain the data necessary to complete these budgets. Now that this project is completed we better understand the constraints of bioenergetics on the ecology and geographic distribution of vertebrate ectotherms.

Over the next several decades energy related activities will continue to have potentially serious effects on aquatic organisms. At present the impact of various energy alternatives (nuclear, fossil fuel, solar, etc.) on vertebrate ectotherms such as turtles is to a large extent unpredictable. There is a critical need to understand exactly how energy technology will affect these animals. A good approach that allows us to determine the reactions of these vertebrates to stress is to study their bioenergetics. Since turtles rely on the environment for maintenance of their body temperatures, as well as for food, they operate in such a way that we can model their bioenergetics using a series of mathematical equations. Unified energy-budget models provide a holistic set of equations that can be solved in an iterative fashion to predict the body temperatures and resource utilization of an animal. These models will be useful in defining the mechanisms whereby animals allocate energy to various life processes.

If we can obtain a clear understanding of the mechanisms by which vertebrate ectotherms are constrained by the interaction of their bioenergetic requirements and by the conditions of their physical environment, we can then predict how they will respond to changes in their aquatic habitats caused by a combination of natural and human stresses. By anticipating potential problems before they arise we will be able to develop adequate energy supply systems while retaining the economic, ecological and aesthetic values of our aquatic ecosystems. This is especially true in the eastern United States where turtles occupy an important position in the trophic structure of lakes, ponds, swamps and rivers. This research is especially important in light of the continued addition of thermal effluents into aquatic ecosystems and the potential for serious disruption of climates due to the warming of the CO_2 greenhouse effect.

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