MASTER

Energy Budgets of Animals:

Behavioral and Ecological Implications

Progress Report

Report No. AT(11-1) - 2270 - 7

Contract EY-76-S-02-2270.A002

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PROGRESS REPORT

This past year, with D.O.E. support we have published one major paper in Ecological Monographs, two major papers in Copeia and have two papers in press in Copeia, one in press in Ecology, and one submitted to Physiological Zoology. Reprints of the published papers, those in press and the manuscript are enclosed.

ENDOTHERM GROWTH AND REPRODUCTION RESEARCH

We have been able to predict the potential for reproduction and growth in any physical environment for the deer mouse, *Peromyscus maniculatus*, an animal that we have been using to establish the feasibility of such an approach. We have been able to verify the predictions experimentally for those environments we have tested. We are in the process of writing it up and it will be included in the progress report next year as a manuscript either submitted or in press.

We have also been able to successfully extend the fractional factorial designs we described in Science (1978) to include the period before copulation all the way through to weaning. We have found a much greater sensitivity to the sensitive variables in the Science manuscript when the longer duration is used. We are also finding a substantial individual variation in the tolerance to deprivation of food and/or water. The physiological basis for this is unknown at present. Food type, quantity, water and sprout availability affect the amount, size and number of offspring at weaning, but not at birth. In further tests of the robustness, accuracy and sensitivity of fractional factorial designs using eight variables, we changed the confounding patterns substantially. We still obtain the same results, showing the same variable far outweigh the effects of other variables or possible hidden interactions. We plan to write at least two, possibly three papers on all those experiments this year. We've had to invest a significant effort to get all the data into computer format this year, since the volume of data has grown so large. The data is now on file, and programs are nearly completed that sort, plot and analyze the data. We have a superb baseline data set with nearly 2000 pregnancy and birth events of normal wild animals, in addition to all the experimental data that will be presented to cover environmental variable effects over the entire reproductive and growth cycle in deer mice.

We have been able to show that the predictions of metabolic rate using our new general fur model (Kowalski, 1978; Gebremedhin, Porter and C mer (1980) accepted; McClure and Porter, in MSS) agree within 5-10% of metabolic rates we measure on resting animals in metabolic chambers. Since we now feel we can predict the maintenance costs for any endotherm in any climate, and we have been able to establish the maximum food processing capacity for two species so far, the difference between food available and that needed for survival is the amount that can go into growth and reproduction. Thus, we feel that by next year we will be able to predict a great deal about the potential population dynamics of the deer mouse in a variety of climates throughout the country and have completed a major step in moving from empirical studies to mechanistic predictions that can be reliably used to assess impact of environmental change on a species from first principles.

We have been assembling climatic data for those calculations. Next year we would like to test the predictions at different altitudes in the Colorado Rockies or the White Mountains of California, where extensive climatic records and biological stations are available.

MICROCLIMATES AND ECTOTHERM GROWTH AND REPRODUCTION

1. Pitcher plant mosquitoes: microclimate modifications and tests; reproduction in heterogeneous environments

Until recently, our general microclimate model had only been developed and tested in the deserts of the United States and in tropical Cape Coast, Ghana. Now we have extended the model to include wet areas, such as bogs (Kingsolver, 1979). We also explored the consequences of environmental variability and uncertainty for ectotherm reproductive success in that paper, which are important questions for persistence of populations of animals outdoors. The thermal and hydric components of environmental variation may play an important role in the maintenance of fitness variation in animals. Kingsolver's results support the hypothesis of Istock (1978) that environmental uncertainty favors mixed life history strategies in Wyeomyia, Kingsolver's research animal, and probably animals in general. The wide variability we are finding in our deer mice physiology may be part of a similar mixed life history strategy. We intend to explore questions similar to Kingsolver's but with deer mice as soon as we can obtain sufficient physiological data during mice growth and reproduction. Maintenance physiology is now being obtained.

2. Desert iguanas -- reproduction and limits to distribution

Our ectotherm reproduction and growth research on desert iguanas has reached publication stage, as the four enclosed manuscripts attest. We are concluding the first phase of growth experiments on our desert iguana hatchlings. These experiments are intended to establish quantitatively how food, temperature and photoperiod can accelerate laboratory growth rate and the onset of reproduction by a factor of 4-7 times that seen in the field. We had expected to do much more of that this year, but for some unknown reason this year, like two years ago, there has been very little egg laying. One year ago we had about 200 eggs. It may be that there is a two year breeding cycle, which has been undetected until now. We will know that this coming winter and spring. The results of the egg incubation research thus far have allowed us to predict where and when eggs should be laid and at what depths. That needs to be tested in the field now. We have an area in San Gorgonio pass, near Palm Springs, California, where we know the sharp limits of their distribution. There are areas where superficially they could be, but aren't, that are contiguous with desert iguana inhabited regions. We would like to go to the field and determine with microclimate and soil measuring equipment and radio telemetered gravid females captured in the field where they are laying their eggs. All phases of this field research, except the actual location of egg sites have already been done in nearby areas where there are lizards (Muth, 1977, 1980a,b,c,d). Field verification of laboratory experiments and theoretical predictions should help settle any remaining doubts about the role of egg microhabitat requirements in the distribution of a vertebrate ectotherm laying shelled eggs (see especially Muth, 1980; Physiological ecology of desert iguana (<u>Dipsosaurus dorsalis</u>) eggs: Temperature and water relations, Ecology, in press).

3. Galapagos land iguanas: larger size animals, new microclimate model additions and tests

In collaborative work with C. Richard Tracy at Colorado State University, we have been able to extend the ectotherm model to much larger animals, the Galapagos Land iguana in the Galapagos islands. We have successfully added transients and appendage-torso interactions to the animal model and have shown that we can predict animal temperatures in the field to within 2° or less for any transient. We have also added slope effects to the micrometeorology model and have been able to predict changes in home range utilization related to slope or flat ground in different seasons and document those predictions with a year round field study on Santa Fe, Galapagos (Tracy, Christian and Porter; Porter, Tracy and Christian, in preparation).

4. Side blotch lizards: microclimate, physiology and social systems effects

We have begun a systematic effort to incorporate some social effects into our animal-microenvironment calculations

Uta stansburiana was studied in western Colorado during the summer months of 1976 (the study area location and description is given in Waldschmidt 1979) and in eastern New Mexico during the summer of 1978. Tinkle (1967) gives a description of the habitat; the location of the study area was 50 km east of Carlsbad, N.M. In both locations individual lizards were marked and their locations in the habitat recorded on a daily basis. These location data were later analyzed using a nearest neighbor analysis (Clark and Evans, 1954). This type of analysis is capable of detecting random and non-random patterns in location data.

The results of the analysis, given in Table 1 are consistent with each population's social structure. Throughout the summer the agonistic southern population was composed of individuals which were maximally dispersed from each other whereas in June and July the less agonistic northern population was composed of individuals which were significantly clumped. In August northern *Uta* were randomly dispersed.

These results are consistent not only with the lizards' social structure but also with the differences in the physical structure of the habitat between populations. The habitat along with the physical environment creates microenvironments in which *Uta* can carry out their normal daily activities. Microhabitats in the sun during a large portion of the day are often characterized by lethal temperatures and are thus avoided by the lizards (Porter et al., 1973). At these times the size and distribution of shaded microhabitats determine where lizards can be active. In the desert-grassland ecotone of eastern New Mexico the shade patches are relatively small and scattered throughout the habitat. When rival lizards encounter each other in the same shade patch the displaced individual can flee to a nearby shaded patch to either hide in the vegetation or burrow into the loose sandy soil. The availability of nearby patches of shade and the agonistic nature of the lizards probably combine to produce the dispersed spatial pattern.

In western Colorado *Uta* were only found along rocky hillsides where shade patches occur in relatively large clumps. Patches of shade were produced by extremely large boulders and a few widely scattered juniper trees. Here lizards disperse within a patch of shade not between patches as southern Uta do. Because of the lack of vegetation along the rocky hillsides and the hardpacked soil lizards cannot readily escape an agonistic neighbor, there are few places to hide. Hiding from neighboring lizards is rarely a problem for northern Uta because of their low levels of agonism. Their confinement to barren rocky hillsides and their low level of agonism probably combine to produce this population's clumped spatial pattern.

The physical structure of the habitat and the local social structure are complimentary. When a southern Uta must flee from an agonistic neighbor it has a place to flee to. Northern Uta don't have a place to flee to but then they don't need one. If land altered by strip mining was to be reclaimed, the size and distribution of shaded microhabitats should match the existing social structure. It might be a mistake to try to force agonistic southern populations to live in an area offering few but large shade patches with few places to hide. On the other hand northern Uta might do well with more but smaller shade patches offering many places to hide.

In summary, this year we have been able to:

1) extend the general microclimate model two ways: a) to incorporate wet ground surfaces (bogs), and b) to incorporate slope effects. Tests of the model in a Michigan bog (Kingsolver, 1979) and the Galapagos Islands (Porter, Tracy and Christian, 1980, AIBS meetings, in preparation) show temperature accuracies to within 4°C at worst at any soil or air location, which is about a 2% error in estimation of metabolism (Porter and James, 1979).

2) the addition to ectotherm modeling an analysis of: a) reproduction in heterogeneous and uncertain environments; b) prediction of distribution limits due to egg incubation requirements (Muth, 1980a,b,c,d); c) addition of appendage-torso modeling and tests on large ectotherms (Tracy, Christian and Porter, AIBS paper, and 1980 in preparation); d) social systems interactions with environmental and physiological variables.

3) continue the endotherm (deer mouse) experimental research and extend the growth and reproduction studies to include the entire reproductive and growth cycle in the deer mouse.

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