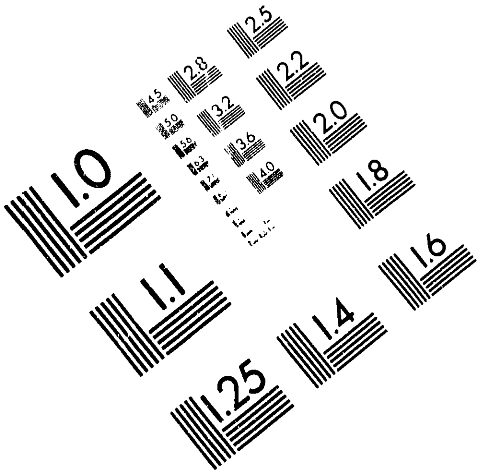

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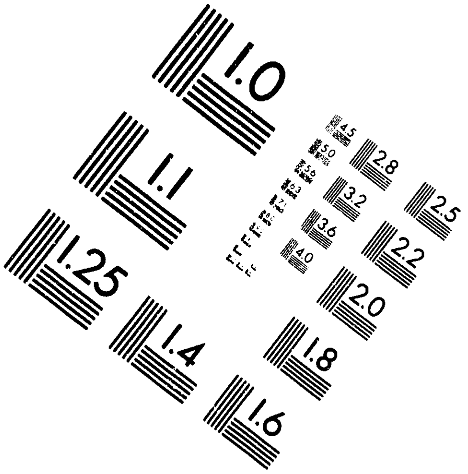

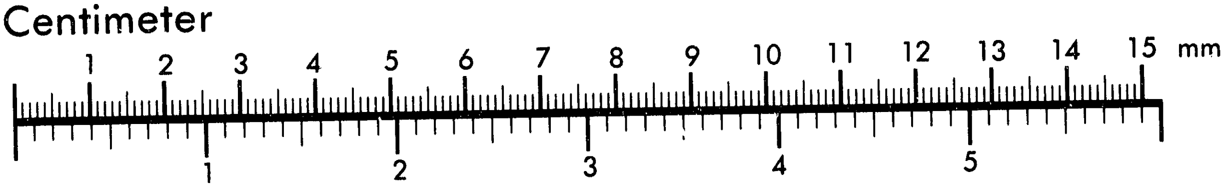

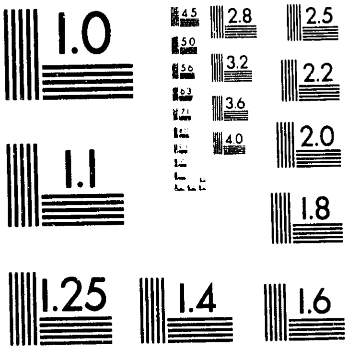

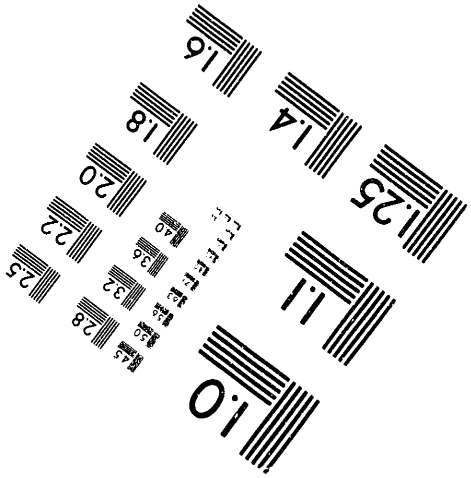

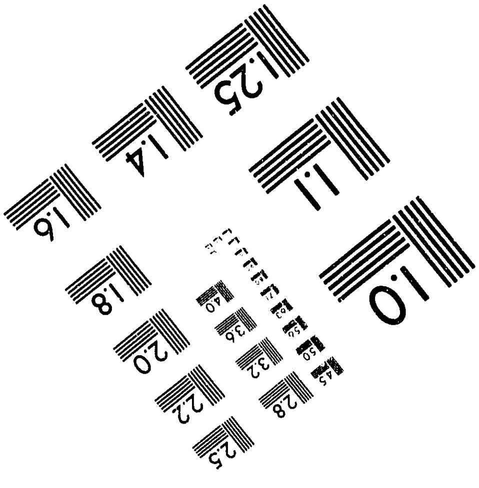

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MASS AND ENERGY BUDGETS OF ANIMALS: BEHAVIORAL AND ECOLOGICAL IMPLICATIONS

ANNUAL TECHNICAL PROGRESS REPORT

for Period
1 April 1992 to 31 March 1993

Warren P. Porter
University of Wisconsin
Madison, Wisconsin 53706

May 1993

Prepared for

The U.S. DEPARTMENT OF ENERGY GRANT NO. DE-FG02-88ER60633

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I. A. Summary

This report summarizes our research and publications during the past year of support from DOE. The common goal of these diverse projects is to understand the mechanisms of how animal populations respond to the continual changes in their environment in both time and space. Our models are mechanistic (rather than descriptive); this has allowed us to explore how a wide array of environmental variables may determine individual performance. For example, Fig. 1 shows a map of the maximum number of eggs that could be produced by the lizard *Sceloporus merriami* in the climatic range found in Texas in 1976. Weather and geological data were collected from 19 sites, and maximum possible egg production was calculated with the microclimate and lizard heat and mass balance models. These calculations illustrate which populations will be affected most strongly by specific changes in climate. In a check of the model's accuracy, our calculations for one site (Big Bend) compared favorably with field data collected at Big Bend by our collaborators, Drs. Art Dunham and Karen Overall, for ten successive years (summarized in last year's report).

The basic research and model development that DOE has supported in our laboratory is directly applicable to climate change. Large scale climate change and its effect on animal populations can be seen as quantitative extensions of biological responses to smaller scales of environmental variability. Changes in developmental rates or reproductive levels of individuals, extension or contraction of geographic ranges, and modification of community organization have all been documented in response to previous changes in habitats. We know from our biophysical work that some changes in function are driven by microclimate conditions directly, and some are mediated indirectly through ecological parameters such as the food supply.

Our research is guided by a comprehensive conceptual scheme of the interaction of an animal with its environment (Fig. 2). Animals live in a set of microclimates whose thermal and hydric properties are determined in part by the influence of the macroclimate, in part by behavioral modifications by the animal itself. The physical and physiological properties of the organism, and the range of available microclimates, set bounds on the performance of organismal function, such as growth, reproduction, storage, and behavior. To leave the most offspring over a lifetime, animals must perform those functions in a way that maximizes the amount of resources devoted to reproduction. Maximizing the total size of the budget and minimizing those budget items not devoted to reproduction (i.e. maintenance) are both crucial. Animals can also trade off among expenditures for current and future reproduction. Both water and energy are important, potentially limiting resources (Fig. 3).

Projects described here include empirical studies, theoretical models, and combinations.

B. Key papers published during the past year (with synopses)

Adolph, S. C. and W. P. Porter. 1993. Temperature, activity, and lizard life histories. American Naturalist (in press). We found that geographic variation in lizard survivorship and reproduction can be explained in terms of climate and physiology, rather than invoking evolutionary arguments.

Carmi, N., B. Pinshow, W. P. Porter, and J. Jaeger. 1992. Water and energy limitations on flight duration in small migrating birds. The Auk 109(2): 268-276. This paper challenges the contention that bird migration flight duration is energy limited. Our new integrated flight energetics-heat and mass balance model predicts that water loss is the primary constraint.

Grant, B. W. and W. P. Porter. 1992. Modeling global climatic constraints on animal energy budgets. American Zoologist 32: 154-178. We found that optimal foraging behavior is different in the two sexes of *Sceloporus merriami*, apparently because of different criteria for optimality in males than females. We also showed that environmental constraints on optimal behavior are more applicable when energy reserves are high. On a daily basis, the availability of suitable microclimates is far more important than food availability or predation levels in affecting optimal behavior.

Reynolds, P. S. 1992. Behavioral and biophysical ecology of beaver (*Castor canadensis*) in North-Central Wisconsin. Dissertation, University of Wisconsin. showed that climate

variation can explain seasonal differences in activity and feeding in the beaver, *Castor canadensis* (Chapter 2), and developed a heat transfer model for the beaver (Chapter 4). Other chapters are in press (below).

Reynolds, P. S. 1993*a*. Time-series analysis of radiotelemetry data. *In* Case studies in biometry, ed. N. Lange, et al. John Wiley, N. Y (in press). This article demonstrates that sequential radiotelemetry data of body temperatures (for estimating energetics) have been improperly analyzed in the literature by many investigators, and proposed a new suitable analysis for such serial data.

Reynolds, P. S. 1993*b*. Size, shape, and surface area in beaver (*Castor canadensis*), a semi-aquatic mammal. Canadian Journal of Zoology (in press). This analysis shows that beaver, although partly terrestrial, are as streamlined morphologically as highly aquatic pinnipeds.

C. Additional publications by our lab group, supported in part by DOE awards

1. Published, in press, or accepted

Curtin, C. G. The Gothic earth flow revisited: a chronosequence examination of recolonization on a disturbed subalpine earth flow. Vegetatio (accepted).

Curtin, C. G. Do ecosystems recover? Long-term evidence from disturbed subalpine plant communities. Biological Conservation (accepted).

Curtin, C. G. Effect of soil type on the recovery process of disturbed subalpine ecosystems. Restoration and Management Notes (accepted).

French, J. B., Jr., W. L. Schell, J. J. Kazmierczak, and J. P. Davis. 1992. Changes in population density and distribution of *Ixodes dammini* (Acari: Ixodidae) in Wisconsin during the 1980s. Journal of Medical Entomology 29:723-728.

Price, J., B. Yandell, and W. P. Porter. 1992. Chemical ions affect survival of avian cholera organisms in pondwater. Journal of Wildlife Management 56:274-278.

Reynolds, P. S. 1992. White blood cell profiles as a means of evaluating implant surgery in small mammals. Journal of Mammalogy 73:178-185.

Reynolds, P. S. 1992. Effects of body size and fur on heat loss of collared lemmings. Journal of Mammalogy (in press).

2. Submitted manuscripts

Curtin, C. G. An examination of the secondary effects of changes in land use on native species, Wisconsin, USA. Conservation Biology.

Padilla, D. K., K. L. Cottingham, S. C. Adolph, and D. W. Schneider. Predicting the ecological consequences of the invasion of a novel ecological type in an aquatic food web. Canadian Journal of Fisheries and Aquatic Sciences.

Porter, W. P., J. C. Munger and J. Jaeger. A biophysical model of metabolic expenditure in a mammal: the model and three empirical, independent tests. Physiological Zoology.

Porter, W. P., S. Green, N. L. Debbink, and I. Carlson. The interactive effects of low-level concentrations of groundwater pesticides on mammalian endocrine function. Journal of Toxicology and Environmental Health.

Sinervo, B., and S. C. Adolph. Growth plasticity and thermal opportunity in *Sceloporus* lizards. Ecology.

Steudel, K., W. P. Porter, and D. Sher. The biophysics of Bergmann's rule: a comparison of the effects of pelage and body size changes on metabolic rate. Journal of Zoology.

I. D. Breakthroughs and major developments

We have made more progress in the last year than originally proposed. Major unanticipated developments include the following:

1) Habitat fragmentation is probably the most important variable governing the impact of climate on populations of box turtles. Disturbed and fragmented sites are less diverse topographically and vegetationally, and therefore are less thermally heterogeneous. As a result, box turtles in fragmented habitats appear to have shorter activity periods, longer egg incubation periods, smaller clutch sizes, and higher adult mortality.

2) A mechanistic explanation of Bergmann's rule, which has been confused in the literature because of conflicting empirical results. Body size change with increasing latitude is much more effective in reducing mass-specific metabolic rate for small mammals partly because of multiple constraints in fur design. These constraints reduce the effectiveness of insulation in small mammals, leaving body size as the only major avenue of modifying energy expenditure across latitude and altitude.

3) A mechanistic explanation for the mouse-to-elephant curve relating metabolic rate to body size. Using our endotherm model, we examined the relative importance of fur properties, postural changes, and body size for metabolic rate. We have also discovered that there are optimality constraints on fur properties that change with body size.

4) Satellite imagery for estimating photosynthetic productivity on the ground in arid regions may be seriously in error.

5) Developing a first principles model for dew deposition on rocks of any size in the Negev Desert. Dew formation and duration controls nitrogen availability, activation of lichens to photosynthesize and incorporate nitrogen, and feeding time available for rock-eating snails to graze the lichens. Rainfall controls snail reproduction, migration to new rocks and nitrogen release from the snail feces. Thus, in this model, portable, RLS (rock-lichen-snail) system we have primary and secondary producers and ecosystem nutrient flux that is driven by climate. This small ecosystem with its nonlinear feedbacks can be completely mechanistically modeled and experimentally studied in the lab and in the field.

II.A.1 **Global variation of climate change driving local microclimate models** (Dr. Warren Porter; collaborators: Pat Behling and Dr. John Kutzbach, Climate Research Center, Space Science & Meteorology, University of Wisconsin, Madison)

Specific Aims:

Extending multi-site simulations of climate and physiological constraints on potential growth and reproduction to continent-wide simulations for multi-year sequences.

Setting up the model to accept macroclimate data input at grid locations coincident with the forthcoming global climate simulation models, which have 1° (latitude/longitude) resolution.

Run the model for selected ectotherms and endotherms with known physical and physiological properties to explore potential climate effects on potential for growth and reproduction and present the results as a contour map of potential for growth and reproduction on a map of North America.

Background:

From its inception our microclimate model was designed to be driven by the local macroclimate variables; shade air temperature, wind speed and relative humidity at 'standard' meteorological height (2 m), solar radiation (calculable from our first principles SOLRAD program) and substrate properties; reflectivity, thermal conductivity, density, specific heat and surface roughness (Porter et al., 1973; Mitchell et al., 1975). For example, the calculations for Fig. 1 used climate data from NOAA (National Oceanic and Atmospheric Administration). The output from NCAR (National Center for Atmospheric Research) supercomputer models has sufficient resolution to provide us with the air temperatures and wind speeds needed for our microclimate model. Prior research on *Sceloporus undulatus*, a widely distributed lizard species, suggests that we can successfully model life history parameters such as survivorship, growth and reproduction based on climate and animal physical and physiological properties (Grant and Porter, 1992; Adolph and Porter, 1993).

Progress Report:

Pat Behling, who does the visualization work at the Climate Research Center (CRC), has helped us obtain and mount on our new HP Apollo 720 workstation the geological, topographic, vegetation and temperature data at 1-degree resolution for the globe. We have also selected and installed imaging software, Ximage and Collage (from NCSA, the national super computer center at Urbana, IL) that allows us to use the new Hierarchical Data File format that is now the international standard for all satellite data files and super computer output files for global simulations. Using this format provides ready portability to any computer platform for visualization using Ximage and Collage, which run on any PC, Mac or UNIX platform.

We have also installed a programming environment, Emacs, developed by the GNU foundation for program development on the Apollo. Additional work has been needed because the Apollo platform is so new, many programs have not been ported to it yet.

We are now ready to extend our simulations from the state of Texas (Fig. 1) to a continental scale for ectotherms and endotherms. Our recent ectotherm results (Grant and Porter, 1992; Adolph and Porter, 1993) and endotherm results showing that we can predict the mouse-to-elephant curve from first principles and the successful model for the semi-aquatic beaver put us in a unique position to forge links between ANY global climate change scenarios and consequences for changes in a broad range of species' growth and reproductive potential across broad spatial scales.

As we develop our user-friendly interfaces, the DOE and the scientific community will be able to do similar calculations on other species. Perhaps most importantly, as the global models mature with the incorporation of better cloud models, estimates of the consequences for biological communities could be quickly re-evaluated.

II.A.2. Models and measurements of water and nutrient flux in a model desert ecosystem on multiple scales. Warren Porter; collaborators: John Norman, Soils Dept., University of Wisconsin, Madison; Clive Jones, Institute for Ecosystem Studies, Millbrook, NY; Moshe Shachak, Ecological Research Unit, Ben Gurion University of the Negev, Israel; and Arnon Karnieli, Head of Israeli Remote Sensing, Ben Gurion University).

Specific Aims. To develop a mechanistic model with dynamic properties including multiple nonlinear feedbacks of a real, yet small model ecosystem that 1) has important climate constraints on its functions at the level of primary and secondary consumers and at the level of nutrient flux through the system, and 2) and is small enough to study and experimentally manipulate in the lab and in the field.

Background and significance. This multinational, collaborative effort has a primary goal of establishing a mechanistic understanding at multiple scales of how climate variation affects nutrient flow and landscape productivity.

The methods of study range from satellite imagery of seasonal spectral changes on the landscape, to hydrologic studies of water and nutrient flow at all scales, to massive landscape manipulations, to studies of photosynthetic activity of lichens growing under the surface of limestone rocks.

Our collaborators in Israel have discovered that by manipulating patches of the landscape, they can convert desert into savannah without adding water or nutrients. They simply redistribute available resources. Literally thousands of acres are being turned into grazing land with shade trees and naturally growing grasses because they have learned how this ecosystem functions at all scales. This understanding involves hypotheses about how nitrogen flows through the ecosystems and watersheds and what controls its flow. Nutrient flows involve the unlikely combination of rocks, endolithic lichens that grow beneath the surface of the rocks, and rock-eating snails that live under the rocks by day and consume the rocks by night when dew covers the rocks.

Our role in this research is biophysical and physiological modeling of these rocks and snails. The first project is to develop and test a heat and mass transfer model describing dew deposition on rocks of different sizes. Such a model is needed because dew deposition brings both a) moisture to activate the endolithic lichens and b) nitrogen in the form of nitrates and ammonia attached to dust particles in the atmosphere.

The central importance of rock size and dew deposition in the control of nutrient flux in this ecosystem is illustrated in Fig. 4. Rocks cover about 75% of the desert surface and act as a 'leaf litter' to minimize evaporative water loss from the soil. Rocks that are too small never condense dew from the moist air that travels inland from the Mediterranean Sea. Small rocks are effectively part of the ground, and stay warm too long at night to condense a significant amount of dew. Similarly, rocks that are too large do not cool off sufficiently to condense dew. Intermediate sized rocks condense dew, have endolithic lichens on top and snails beneath that graze on the lichens when dew forms and retreat beneath the rock at the end of the night. There, they leave nitrogen-rich feces that are leached when the rains come. A significant amount of the desert ecosystem's nitrogen comes from this cycle.

Progress Report. I developed a rock-dew model this year, based on the heat and mass transfer equations (Fig. 3) and the microclimate model. I ran the model for rocks of different sizes using data from the Sde Boker site (100 mm annual rainfall) and a more northerly site near Beer Sheva, where annual rainfall is greater (200 mm) and monthly temperatures are cooler. Figure 5 shows the predicted effect of rock size on dew formation at Sde Boker for 1-14 June, 1991. Figure 6 illustrates when dew might be expected on similar rocks to the north in Beer Sheva, where higher humidity should be increase dewfall significantly.

Experimental field testing of the model has begun at Sde Boker, where macroclimate and microclimate data are being collected along with data on temperature and the timing and amount of dewfall on rocks of different sizes and exposure.

II.A.3. Temperature and Lizard Life Histories: Physiological and Behavioral Optimization Models. Drs. Stephen C. Adolph and Warren Porter

Progress report. We continued to explore the effect of temperature on lizard life histories using mathematical models based on thermal physiology. This research addresses both the proximate and evolutionary effects of temperature. Our first model (Adolph and Porter 1993) addressed the proximate effects of temperature on annual survivorship and fecundity, and is summarized in last year's report. During the past year, this paper was presented at annual meetings of the American Society of Zoologists, Society for the Study of Evolution, and Ecological Society of America; at the Midwestern Population Biology conference; and at a workshop on theoretical ecology.

Work in progress includes mathematical models of (i) digestion and energy uptake and (ii) growth in seasonal environments. The digestion model is similar to the chemical reactor approach of Penry and Jumars (1987). An overview of our model is shown in Fig. 7. Our analysis describes the quantitative relationships between gut processing rate, gut capacity, diet quality, animal size, metabolic needs, and feeding frequency. We are currently writing a manuscript presenting this model.

Our model of growth in seasonal environments builds on experimental data collected in collaboration with Barry Sinervo (now at U.C. Berkeley; see enclosed manuscript by Sinervo and Adolph). Our model combines logistic growth of individuals with seasonal variation in temperature to predict body sizes at different times of year. We are using the model to explore the effect of different thermal environments and different levels of food availability. One prediction is that lizards with long activity seasons should reach reproductive maturity at a younger age, and possibly at a smaller size, as a proximate consequence of temperature. We tested this prediction using published data from the widespread lizard *Sceloporus undulatus* (Fig. 8). We found strong relationships between age and size at maturity and length of activity season for most populations, except for two prairie populations that deviate markedly. This suggests that prairie populations may have diverged genetically in their life history traits.

II.B.1 An evaluation of physiological properties and demographic characteristics of the six-lined racerunner lizard (*Cnemidophorus sexlineatus*) in southern Wisconsin. Joel Stein and Kent Hatch, graduate students

Specific aims. The major goal of this project is to characterize the physiology, life history, and population ecology of *Cnemidophorus sexlineatus* in Wisconsin. The data we are collecting, along with data from parallel studies of *C. sexlineatus* in other parts of the country, will be used to construct computer simulations to model the effects of climate change on individual energy budgets and population dynamics.

Background and significance. Many scenarios of climate change predict differences in global temperature and cloud cover that are similar to present day differences associated with elevation or latitude. By studying how animals are affected by environmental conditions along geographical gradients, one may predict how they will respond to changing climatic conditions. Lizards are ideal organisms for such studies because they are ectothermic, and their activity and energy budgets are sensitive to environmental variation.

Our work addresses the consequences of temperature for energetics, growth and reproduction in the six-lined racerunner *Cnemidophorus sexlineatus*. Although this species has been studied in much of its broad geographic range (Fitch 1958, Carpenter 1959, Hardy 1962, Bellis 1964, Trauth 1980), little is known of its ecology in Wisconsin (Vogt 1981), the northern limit of its distribution. The short growing season in Wisconsin imposes limitations on activity time, which in turn is likely to affect other aspects of their ecology (e.g., growth, reproduction and mortality).

Northern and southern populations of *C. sexlineatus* experience different climates (Fig. 11), and show different activity patterns. The total adult activity season in Wisconsin is only three months long, which restricts their reproduction to one clutch per summer, versus two in the south.

The activity season for hatchlings is several months shorter in Wisconsin, delaying maturity and postponing first reproduction until year 2. In addition, due to direct and indirect effects of temperature, populations in warm and cool environments are likely to have different patterns of energy acquisition and expenditure, resulting in both lower energy acquisition and lower energy expenditure in Wisconsin as compared with southern populations.

Progress report. At the beginning of the summer (1992) we collected southern *C. sexlineatus* in Arkansas. We are maintaining 33 Wisconsin and 42 Arkansas lizards in the lab. We are now in the process of analyzing the following data:

1. Field work. We now have a marked population of 212 individuals in a sand prairie area near Spring Green, Wisconsin. Snout-vent length and mass were recorded for calculation of growth rates. Reproductive condition and amount of food in the gut were also noted. A typical body size distribution over the course of the active season is shown in Fig. 12.

The unusually cool weather this past summer limited the amount of field work we were able to accomplish. The lizards were rarely active during the second half of the summer. Reproduction was largely unsuccessful, since only one hatchling has been observed this season, and that on Sept. 22. A lizard hatching at this late date is unlikely to obtain enough food to amass the energy stores needed to survive the long winter in Wisconsin.

We have constructed hollow-body copper models of *C. sexlineatus* for use next summer. When placed where the lizards perch and forage, these models provide accurate estimates of the environmental temperatures experienced by lizards. This will allow us to quickly and accurately characterize thermal microclimates (Grant, 1990; Grant and Porter, 1992).

2. Critical thermal minimum and maximum. Critical thermal maximum (CT Max) and minimum (CT Min) are standard measurements of thermal physiology in reptiles. We measured the CTMax and CTMin of Wisconsin and Arkansas lizards. We found no significant difference between the two populations in either CT Max (mean = 45.8 ± 0.25 [SE]; ANOVA, P = 0.45) and CT Min (17.6 ±.23; P = 0.54), suggesting that these two populations have not diverged genetically in these traits, despite living in markedly different thermal environments.

3. Temperature effects on egg incubation. Many of the female lizards collected in Arkansas were gravid. We incubated the eggs at different temperatures to examine the effects temperature has on egg development rate, and possibly on hatchling growth rate and survivorship. Although temperature did affect duration of incubation (Fig. 13), it did not affect hatchling size or growth rate (see below).

4. Hatchling growth rate. Arkansas hatchlings were raised in the lab. They were housed in cages with a heat source at one end so they could select from a gradient of temperatures. They were fed ad lib. In the two months since they hatched, the lizards have added approximately 9 mm in snout-vent length (Fig. 14). In contrast, field measurements from Wisconsin lizards (Fig. 12) indicate little growth in hatchling snout-vent length. As we write, Arkansas hatchlings have up to another month to eat and grow, while Wisconsin hatchlings would have begun hibernation. This gives Arkansas hatchlings the opportunity for more growth and greater likelihood of surviving their first winter (Fig. 15).

II.B.2. An analysis of the cost and consequences of habitat fragmentation and climatic change. Charles Curtin.

Specific Aims:

The effects of climatic change and habitat alteration are addressed through:

1) A field comparison of the fecundity, home range size, activity period (daily and seasonal), and preferred temperature range of box turtle (*Terrapene ornata*) populations in habitats with differing amounts of fragmentation.

2) A study of sand-prairies in south-western Wisconsin containing box turtle populations to determine the ecological and biophysical attributes of habitat and how these factors are altered daily, seasonally, and on longer time scales, by fragmentation and climatic change.

3) Laboratory and field comparisons of box turtles from northern and southern populations to determine if physiological differences exist between populations from different climates.

4) Laboratory investigations of the physiological costs of local climatic alteration through habitat fragmentation.

Background and Significance:

The goal of this work is to explore the biophysical costs and consequences of climatic change and habitat alteration. Because reptile behavior and physiology are tightly coupled with climatic constraints, these species are ideally suited for studies of the potential consequences of climatic change and habitat alteration.

Box turtles in remnant sand-prairies represent a model system by which to study the effects of habitat alteration and climatic change. Through these studies the interaction of plant communities, reptile populations, biotic factors, and human social and economic systems are examined. Initial work has focused on the underlying causes of habitat fragmentation in southern Wisconsin. A paper currently in press (Curtin 1993) demonstrates that relatively subtle changes in land use policy and farming practices have led to a rapid conversion of prairie and savanna-like habitats to woods or cropland over the past several decades, radically fragmenting many native habitats in southern Wisconsin. Field studies of disjunct populations of turtles in habitats with differing amounts of fragmentation will yield insights into what happens to populations experiencing fragmentation, while studies of sand prairies, savannas, and associated disturbed and exotic plant communities will determine how the invasion of non-native species of plants and the bisecting of habitats by agriculture alters native communities. Physiological studies determine the thermal preference and other physiological constraints facing box turtles at the northern edge of their range while field and lab comparisons of northern and southern populations determine how evolutionarily static vs. labile these traits are. Finally, biophysical studies will monitor factors such as soil type, wind speed, aspect, and microclimate resulting from changes in vegetative cover, through time, to determine the physical impacts of habitat alteration. This work will provide further insights into how animals experience microclimate and how changes in vegetation type shift habitat availability.

Progress report:

Wisconsin Box Turtle Demography and Biophysical Ecology. Field mark-recapture studies on a population of 14 box turtles (10 with radio transmitters) in predominantly prairie habitat in southern Wisconsin, compared with previous work on Wisconsin box turtles in heavily fragmented habitats (Doroff and Kieth 1990), have yielded valuable insights into the effects of habitat fragmentation on box turtles. Because summer of 1992 studies are not yet completed detailed results are not available. However, initial data indicate that turtles in fragmented sites have larger home ranges and suggest that the lack of optimal nest sites in fragmented areas may lead to longer egg incubation periods. These factors result would directly and indirectly in higher adult mortality and lower recruitment.

Physiological Differences in Populations from Different Climates. Results from laboratory experiments using thermal gradients (Fig. 16) indicate that whereas box turtles in warmer climates and cooler climates show little difference in average or mean body temperature, southern populations can use a significantly warmer range of environmental temperatures (4 - 5 °C), whereas populations from cooler climates can use a significantly cooler range of temperatures (2 - 3 °C). These results support optimality models proposed by Huey and Slatkin (1976) and Porter et al. (1973). While a warmer preferred temperature range should extend potential activity periods in southern climates, a cooler preferred temperature range extends activity periods in cool climates. Initial results from field comparisons of northern and southern animals also support these conclusions. During cool periods 90% percent of northern animals are active (basking or foraging), while 90% percent of southern animals were buried in burrows and inactive.

Biophysical Studies of Habitat. Pilot studies compared different habitats within the box turtle home range to determine the amount of micro-site variation within a given plant communities (Fig. 17). Initial studies found that sand prairie and savanna, the preferred habitats, allowed turtles a much greater range of micro-sites and environmental temperatures than forest or agricultural lands. Sand prairie and savanna, by providing a greater range of micro-climates, can potentially allow turtles longer daily and seasonal activity periods.

Wisconsin Box Turtle Demography and Biophysical Ecology. From spring through the fall of 1992, mark-recapture studies were carried out on remnant dry-prairie and savanna near Mazomanie, Wisconsin. From first emergence on April 3 through hibernation in the fall a population of 14 box turtles has been monitored, 10 with radio transmitters, for the entire active season. Data on population structure, home range size, micro-habitat selection, and thermal preference were collected. Time, depth, duration, and body temperature during hibernation were examined during the fall, winter, and spring to gain an understanding of the effect of climate during the cool season.

Physiological Differences Between Populations from Different Climates. A 'common-garden' experiment comparing northern and southern turtle populations was begun in the summer of 1992. In August 1992, a population of 16 box turtles (8 males and 8 females), 8 from northern populations in western Nebraska and 8 from southern populations in central Kansas were released on a private prairie reserve near Muscoda, Wisconsin. They are being maintained on the site in a one acre enclosure encompassing a diversity of micro-sites for at least one year. Operative environmental temperatures (T_e) and selected body temperatures (T_b) are being measured in the field and lab to determine whether differences exist between northern and southern populations. Maintaining the animals in the field for a year will allow enough time for both populations to acclimate to Wisconsin's climate to determine if animals can adapt to different climates or habitats by shifting their preferred range of body and environmental temperatures. T_e and T_b data from 1992 will be compared to those I will collect in 1993.

II.B.3 Altitudinal and year to year variation in canyon lizard growth and reproductive potential. Dr. Warren Porter. Collaborators: Drs. Art Dunham and Karen Overall, University of Pennsylvania).

Specific Aims.

To determine relevant physical and physiological properties of *Sceloporus merriami*, the canyon lizard.

To evaluate climate effects on activity times, survivorship, growth rates and reproduction by utilizing long term climate data in the region and demographic data collected by Drs. Dunham, Overall and their students at three elevations.

Background and significance.

As Fig. 2 implies, key microclimate and animal properties must be defined for our models to function. Microclimate, physical and physiological variables needed for calculations come from the equations of Fig. 3: (Porter, 1989). Earlier studies of the lizard *Sceloporus undulatus* suggest that biophysical and physiological models of an ectotherm can successfully predict survivorship, and reproduction. Detailed long term demography at single sites is only available for *Sceloporus merriami*, however. This study constitutes a much longer timeframe with detailed physiological data on all aspects of its life history variables. This study also has three study sites at approximately 500, 1000 and 1500 m elevations. A 500 m elevation decrease is approximately equivalent to a 5 °C increase in air temperature. Thus these sites represent gradients that represent possible climate changes that may occur in the next 25 years according to some scenarios.

Progress report.

We have completed all the physical and physiological measurements on the canyon lizard to undertake detailed simulations to compare calculated vs observed reproduction. These measurements include exposed eye surface dimensions and evaporative water loss measurements at different air and radiant temperatures and wind speeds. Dr. Dunham and his student, Steve Beaupre in collaboration with us have measured ad lib food consumption, digestibility and assimilation efficiencies as a function of body temperature (Beaupre et al., 1992). Drs. Overall and Dunham have measured egg temperature and moisture incubation requirements and effects on development time. Measurements of food availability, growth rates and reproductive output for all sites are known (Grant and Dunham, 1990). With these data and the microclimate and lizard biophysical models I have developed, we have been able to run sensitivity analyses of a variety of variables to explore climate variation on patterns of activity (time for feeding, reproduction and growth). Figure 18 illustrates an 8-year sequence of computed activity times for the high site, Maple Canyon, the intermediate elevation site, Grapevine Hills, and the low elevation site (Boquillas). Although Maple Canyon has less activity time in terms of months, diurnal activity is longest (and at lowest temperatures). In contrast, Boquillas has the shortest daily activity time because of the high temperatures near midday. Figures 19 and 20 explore individual growth rates over four-year intervals at all three sites and for males vs females. I assume that once the animals reach minimum reproductive size, all discretionary mass and energy go to egg production (females) or territorial defense (males) until one month before anticipated retreat for the winter. Then discretionary resources go to growth or fat storage. Because territorial defense occupies less time in terms of days of the year than egg production, male growth is greater.

The top half of Fig. 19 compares calculated growth rates for females at the high site vs. Grapevine Hills for 1982-1985 in terms of length and weight. The bottom half of Fig. 19 compares males hatched in 1982 (right) vs hatched in 1986 (left). The final weight of a male hatched from an average sized egg in 1982 is predicted to be greater than one hatched in 1986.

Figure 20 compares growth rates for male vs female canyon lizards in the lowest site, Boquillas. Growth rates for all three sites compare very favorably with observed growth rates for these sites (Dunham and Overall, unpubl. data).

The top half of Fig. 21 is a sensitivity analysis of climate effects on hatchling growth at the low elevation site in Big Bend. There is very little effect. However, the bottom half of Fig. 21 shows that differences in egg size have a very significant effect on size at the end of the first growing season.

The top half of Fig. 22 shows that time of egg laying also has a very important effect on size at the end of the first year. Male lizards hatched in June have a good chance of obtaining a territory in their second year of life because of their size. Hatching in July, however, means almost certain death in the following year, because they will not be large enough to hold territories. Almost 100% of non-territorial male lizards die in a given year. Females are not quite so rigidly constrained, but their time to sexual maturity is delayed if they hatch in July at Boquillas and their offspring appear to be similarly delayed in their sexual maturity (Fig. 20). The bottom half of Fig. 22 illustrates calculated hatchling growth rates for 1982 for each of the three sites. Different food availabilities and environmental temperature differences account for the differences in growth rates. We assumed a food level of 120% for the two upper sites is because the food consumption experiments were not done with ad lib food, but with rations of crickets near the maximum value, so the temperature dependent digestive physiology was not at maximum (Beaupre et al., 1992).

II.C.1 The biophysics of Bergmann's rule.

Progress report:

Bergmann's rule states that animals within a species should get larger at more northerly latitudes and higher elevations to reduce mass specific metabolic rates. This rule has generated considerable controversy in the literature since it was proposed. We (Steudel et al., MS) examined fur properties vs body size effects on metabolic heat requirements needed to maintain a constant core temperature with our latest version of the porous insulation fur model, which incorporates both orthogonal and hexagonal hair packing geometries coupled to an internal heat generation model with heat generation throughout the flesh, rather than only at the center of the body (resistance models of heat transfer). This model is an excellent estimator of metabolic rate, as we show in a new manuscript (Porter et al., MS) that compares the model performance against three simultaneous independent measures: oxygen consumption, doubly labeled water and food consumption mass balance. We found that small mammal fur is so rigidly constrained in length, density, diameter and pelt depth, and changes so little seasonally that the only substantial mechanism for reducing heat loss in colder climates is to increase body size. Large animals can afford to have less dense and longer hair, both of which reduce the need for larger body size to conserve heat in colder climates.

II.C.2. A mechanistic explanation of the mouse-to-elephant curve and optimal endotherm design.

Progress report:

As an outgrowth of my modeling for the Bergmann's rule paper I developed a dimensionless number, the Kowalski number, which describes all four critical fur variables and their effects on heat transfer in a single variable. The larger its value the greater the heat loss. I computed endotherm skin surface area from geometric cylinder and sphere assumptions from an appropriate range of body weights. Calculation of metabolic rates needed to maintain a 37 °C core temperature for mouse to elephant body weights assuming deer mouse fur was compared with similar calculations using red deer fur for insulation. Both cylinder and sphere approximations were used for each body size and fur type. The characteristic dimension for computing convection was the cube root of the volume (Mitchell, 1976). Calculations assumed a common physical environment of no solar radiation, 0.1 m/s wind, air temperature and radiant temperature of 10 °C and a relative humidity of 10%. Evaporative water loss was assumed to occur by respiration only. Thus, metabolic heat production and oxygen consumption could be tied directly to evaporative water loss by a molar balance coupled to a heat balance.

Results are shown in Figs. 23 and 24. The points calculated are shown with solid circles. The regression line through the data gives the slope. The empirically determined mouse to elephant curve has a slope of approximately 0.67. What is immediately apparent from the endotherm model is that posture (sphere vs cylinder) approximations bound the empirical curve. Fur type (dense, short as in deer mouse vs sparser, and longer as in red deer) does not have much bearing on the regression slope for either geometry. The break in the calculations assuming sphere allometry (curled up) is due to a shift in the type of convection between forced and free convection. A second set of results appeared when metabolic rate was computed as a function of body size and the Kowalski number, a nondimensional number incorporating variation in fur density, depth, hair diameter and pelt depth over the range of values found for animal fur. The only constraints for all possible combinations of fur properties were that physically impossible combinations of fur, such as density of hairs with diameters so large that it would be physically impossible to pack large diameter hairs in at ultra high densities. Another constraint was that pelt depth could not exceed hair length.

Figures 25 and 26 show the remarkable response surface that appears when these calculations are done. These are saddle shaped surfaces that mean optimum combinations of fur properties and body size exist. We have found that seasonal changes in fur in deer mice and red deer follow contours on this diagram and occupy restricted regions of the surface (not shown). The results are mirror images of each other, a 'batmobile' surface with fins in the back of a saddle, whether the results are plotted as weight specific metabolism (Fig. 25), or as total metabolism (Fig. 26). This work is being prepared for publication now and I have been invitated to present this work at the International Mammal Society meetings in Australia in July 1993.

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Appendix A. Software Development of User-Friendly Interfaces

Accomplishments to Date

Overview. We are developing an application based on a mathematical model that integrates principles from ecology, physiology, micrometeorology, and heat-transfer engineering. This program, BEASTS (an acronym for Biological Energetics At Simulated Thermal States), allows users to simulate energy requirements of different kinds of animals in different kinds of climatic environments.

BEASTS comprises three interrelated, modular components: a simulation model, a user interface, and a graphic display (Fig. 27). The simulation model, a series of programs written in Microsoft FORTRAN (ver. 5.1), is the core module. The user interface, a Microsoft Windows application written in C with the Microsoft Windows Software Development Kit (ver. 3.1), is the controlling module and allows interactive data input to the model. The graphic display, provided by an existing software package, allows two- and three-dimensional visualizations of model output.

The modular design of BEASTS allows each of its three components to be developed independently of the others. The modules need only to communicate with one another. For example, after the user enters input data, the interface module writes the data to a text file and calls the model module, which reads the file, performs the needed calculations, and writes the output to another text file. Program control then reverts to the interface, which calls the graphics module to display the output. Program control again reverts to the interface module. Through this cyclic process the user can continue to interact with the model by changing input values and output options and displaying results.

Simulation Model. The simulation models rest on the crossed equations of Fig. 3. They are solved numerically by iteration and their solution is used to generate the seven selectable dependent variables.

User Interface. The simulation model is both powerful and flexible--it incorporates numerous animal types, physiological properties, and climate ranges, and will allow users to manipulate many independent variables and examine many dependent variables. We intend that the model serve both as a teaching aid and as a research tool; but to ensure its acceptance, it must be easy to use. Consequently, we are also developing a graphical user interface to make the model accessible to a wide variety of people, ranging from beginning students to experienced researchers.

The creation of the interface is an iterative process comprising three phases: design, implementation, and testing (Fig. 28). Design involves defining specific components of the interface (e.g., how the user enters input variables for the model). Implementation involves writing the program code to effect the design components. Testing involves determining whether the implemented design produces the desired results; if it does not, the design is appropriately altered and further tested (e.g., users are questioned about the effectiveness of the interface, and their suggestions are used to make modifications). The interface includes a series of dialog boxes that allow users to provide input data for the desired simulation. Eventually, BEASTS will let users simulate energetics for a variety of both biological and non-biological systems (see below). We have completed a first version of the interface for ectotherms, which serves here as an example of how the interface functions. Fig. 3 shows the main window of BEASTS. The various dialog boxes (for specifying input) are displayed on the left side of the main window.

Model Dialog Box. With the first dialog box (Fig. 29), the user selects the type of system to be simulated: geometric solid, ectotherm, or endotherm. (Additional options for microclimate and energy balance are not yet implemented and are not discussed here.)

System Dialog Box. Having indicated that an ectotherm is to be modeled, the user selects a specific type of ectotherm (Fig. 30). Built-in options currently include spider, insect, salamander, frog, dinosaur, turtle, lizard, and snake. (In addition to these options, a later enhancement of the program will let users specify various animal characteristics to design animals of their own choosing.) Lizard was selected in this example. Shown in the status bar at the bottom of the main window is the name and a bibliographical reference for the default lizard, the

Desert Iguana in this case. By pressing the animal image button in the dialog box the user can see a picture of the default animal. (Not yet implemented is a scrollable field of textual information about the default animal that will be shown in the rectangular area to the left of the animal picture.)

Variables Dialog Box. After selecting a specific type of ectotherm, the user provides values for input variables (Fig. 31). The user can accept default values for the selected animal or change the values within the indicated bounds. The button to select default values is automatically activated whenever any default value is altered.

Microclimate Dialog Box. The next dialog box (Fig. 32) calls for a quantitative description of the animal's microclimate. Default values are provided for a representative location, as indicated in the status bar at the bottom of the main window--Mojave Desert in this case. Again, users can accept default values or provide their own. And by pressing the range image button users can see a range map for the selected animal; a colored dot on the map (not readily apparent here) marks the location described by the default microclimate values. (Not yet implemented is a scrollable field of textual information about the animal's microclimate and range that will be shown in the rectangular area to the left of the range map.)

Dependency Dialog Box. The final input dialog box (Fig. 33) allows users to select a dependent variable for the model: body temperature, metabolic rate, evaporative water loss, food intake, water intake, discretionary energy, or discretionary water.

Graphic Display. Having entered values for the input variables, the user selects an option for graphically displaying output.

Continuing Development

Simulation Model. The simulation model is really three independent models of heat and mass transfer. One is for inanimate objects with no internal heat generation. The second includes the physiology of respiration with associated. heat generation and respiratory, ocular, and cutaneous water loss. The third adds porous insulation to the second model, and solves for the metabolic rate needed to maintain a specified core temperature. Other associated heat and mass fluxes are determined simultaneously.

User Interface. The simulation model allows users to examine the energetics of three types of systems: geometric solids, ectotherms, and endotherms. The portion of the model dealing with ectotherms is the simplest of the three, and we have therefore developed it first; we have begun, but not yet finished, designing and implementing the portions for geometric solids and endotherms.

Geometric-solid options will include slab, cylinder, ellipsoid, and sphere. Default values will be available for solids made of very different kinds of materials (e.g., polished copper, glass, granite, or limestone). Alternatively, users will be able to provide values for mass, density, specific heat, thermal conductivity, solar transmissivity, thermal emissivity, and to indicate whether or not the surface of the solid is covered by an insulating material. Endotherm options will include quail, chukar, marmot, prairie dog, mouse, wood rat, cotton rat, pig, and cow. Input variables for endotherms will include body mass, body temperature, pelage/plumage characteristics (e.g., hair diameter and length, pelage depth and density), pelage/plumage solar reflectivity and transmissivity, and body posture.

Because users are free to alter many variables, they should be able to save and later retrieve entire sets of these input values. We will incorporate menu options to make this possible. As a means of further tying the program to biology, we will make considerable textual information available to users. For each particular kind of ectotherm and endotherm we will allow the user to learn about energetically relevant aspects of the animal's life history, distribution, range, and habitat. For example, we will discuss how the very large body mass of our default dinosaur (*Maiasaura peeblesorum*) tends to make the animal's body temperature largely independent of short-term (hourly) changes in the thermal environment, but very dependent on seasonal changes in climate. Alternatively, for our default insect (Desert Locust), we will point out how its small body mass, climbing up into vegetation, and orienting relative to incident solar radiation cause the animal's body temperature to be closely coupled to changes in the thermal environment.

Graphic Display. BEASTS's simulations will produce a large amount of output. The raw numbers will be available to interested users in the text file written by the model module (as described above). In addition, users will have the option of seeing simulation results expressed as (i) simple graphs showing a single dependent variable as function of a single independent variable, (ii) two-dimensional contour plots, and (iii) three-dimensional surfaces showing how a dependent variable is related to two independent variables. To circumvent the time and expense of developing the needed software, we will use a commercially available graphics package (e.g., GraphiC for Windows; Scientific Endeavors, Kingston TN).

The complex relationships among the model's independent and dependent variables can be explored through time by animating the output of the model. If the displayed graphs for a series of sets of input values are saved as image files, the resulting series of images can be displayed sequentially to animate model behavior. For example, in a series of 12 images, one might show how an animal's food requirements change as a function of air temperature and solar radiation each month over the course of a year. We will produce these animations using the visualization tool Audible Image for Microsoft Windows developed by NCSA.

Beyond design and implementation, we will continue the development cycle (Fig. 28) for the interface with the help of students and colleagues. Interested undergraduate and graduate students in my classes and research colleagues will test the effectiveness of the interface as a means of exercising the model. We will use their recommendations as the basis for making improvements as BEASTS evolves.

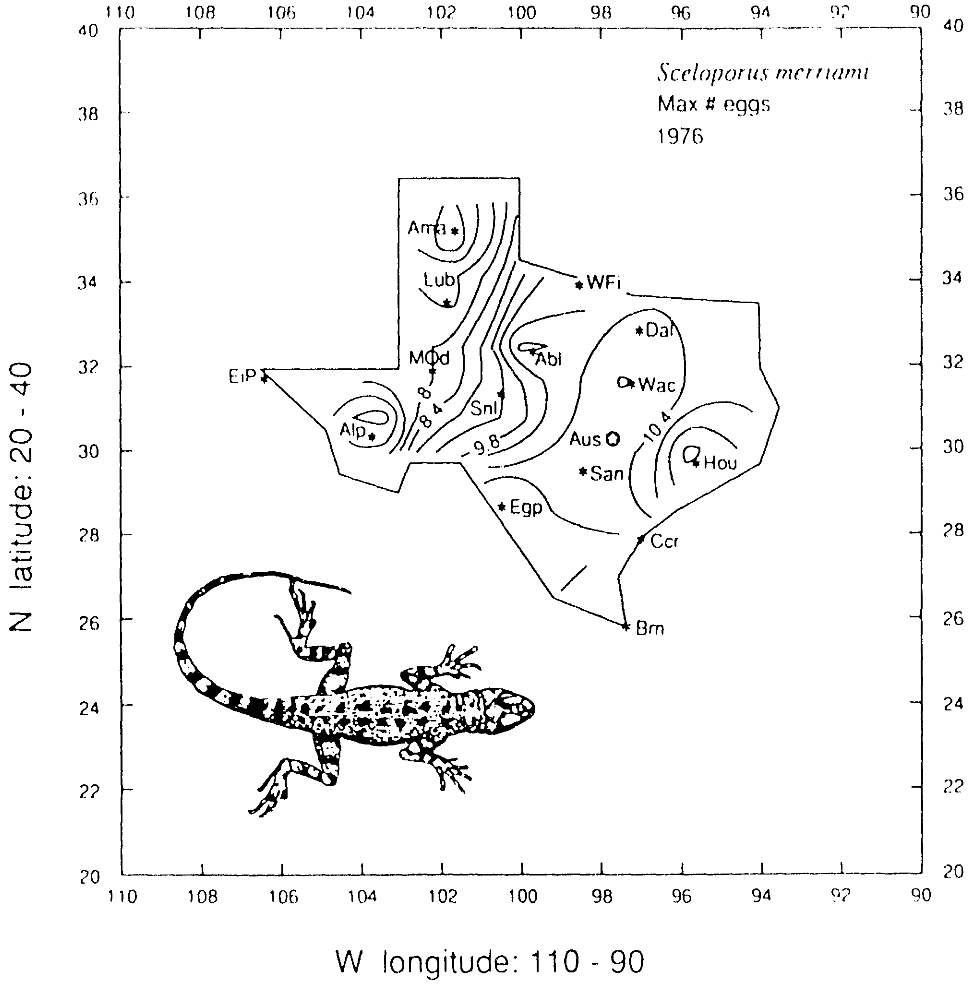


Fig. 1. Map of predicted annual egg output of female canyon lizards (*Sceloporus merriami*) across Texas. Calculations are based on geographic and climate data (1976) from each of the weather stations indicated. These data were used as input to our microclimate and animal energetics computer simulations. During the coming year, we will use this approach to predict growth and reproduction of selected ectotherms and endotherms on a continental scale.

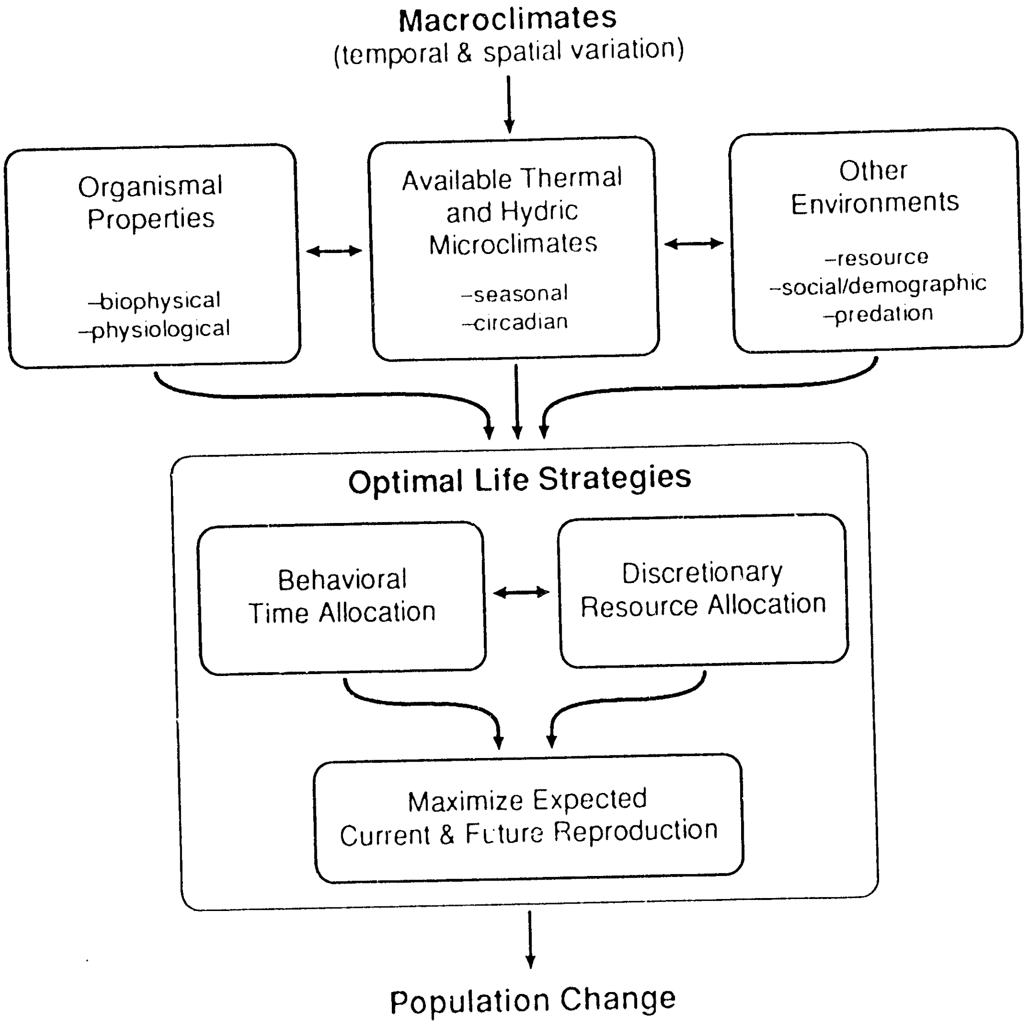


Fig. 2. Conceptual overview of relationships between organisms and their environment. Our research program explores these links using both models and empirical studies.

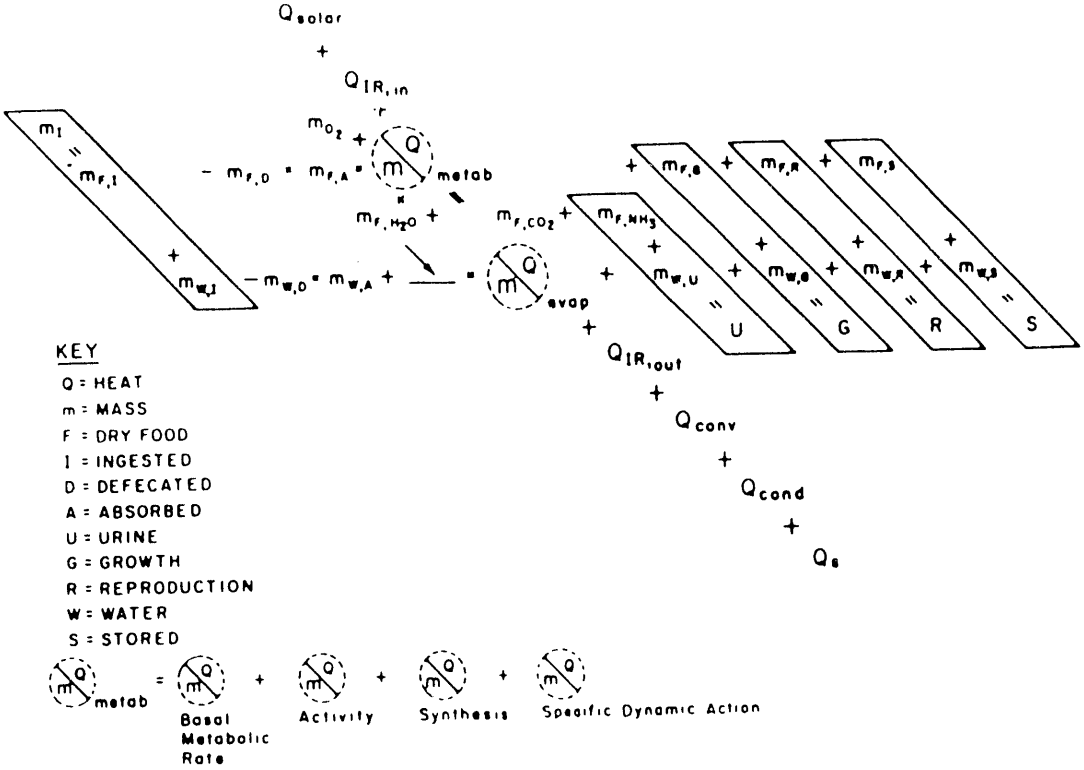
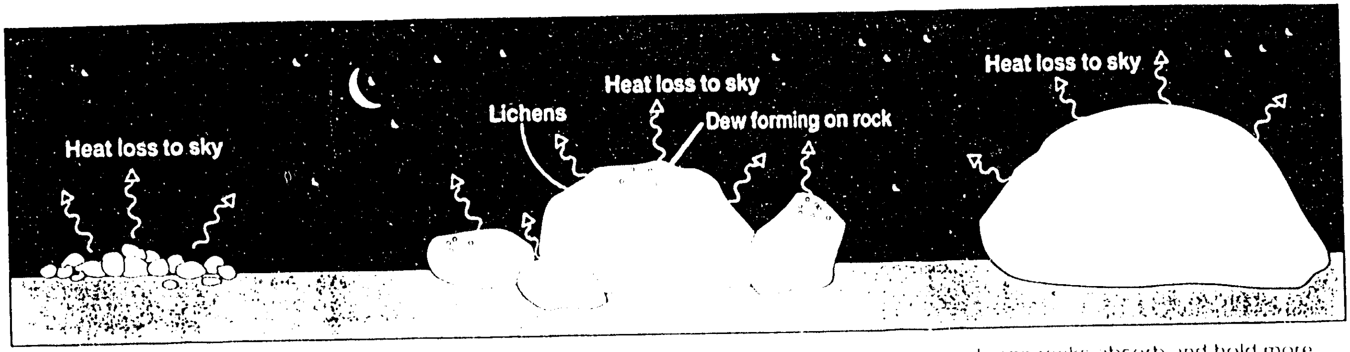


Fig. 3. Coupled equations for heat and mass balance for ectotherms or endotherms. The long center diagonal equation is the heat balance equation. The top and bottom horizontal equations are the dry mass balance and the water mass balance, respectively. Food ingested, which includes dry matter and water, is the left diagonal boxed equation. The masses involved in growth, reproduction, or fat storage are diagonal boxed equations on the right side of the figure.

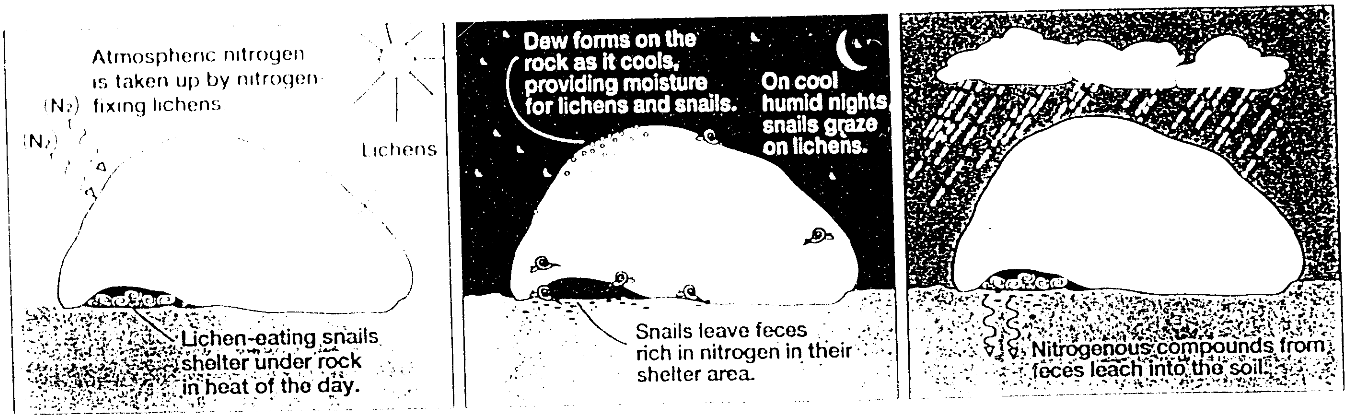
Rock Size and Dew Formation



At night, smaller rocks and pebbles *(less than 1½" in diameter)* remain at soil temperature, which is not cold enough to cause condensation

In mid-size rocks *(1½" to 3" in diameter)*, heat gained during the day is lost at night rapidly enough that the rock becomes cooler than the air, allowing condensation to occur

Large rocks absorb and hold more heat by day and take longer to lose their heat at night Because these large rocks do not cool far enough below air temperature, moisture does not condense on them



The Negev Desert's Snail-Lichen Nitrogen Link

8mm
Snail's actual size

Fig. 4. A cartoon sketch of key events in the rock-lichen-snail small ecosystem. At night rocks of intermediate size condense dew depending on climate (top half of figure). By day, endolithic lichens photosynthsize and take up nitrates and ammonia from dust particles in the dew that settled. Rock-eating snails shelter under the rocks by day (lower half, first cartoon). If there is dew at night, the snails can emerge and feed on lichens by grinding through the rock. By morning the snails retreat to beneath the rock and defecate nitrogen rich feces. When rains come, nitrogen leaches from the feces and is a significant part of the nitrogen in the larger ecosystem. Rains also allow the snails to move from one rock (patch) to another rock. Snail eggs are only deposited when it rains. Thus, climate (dew, dust and rain) controls maintenance, growth, reproduction and dispersal in this small model ecosystem with multiple nonlinear feedbacks between climate primary and secondary producers.

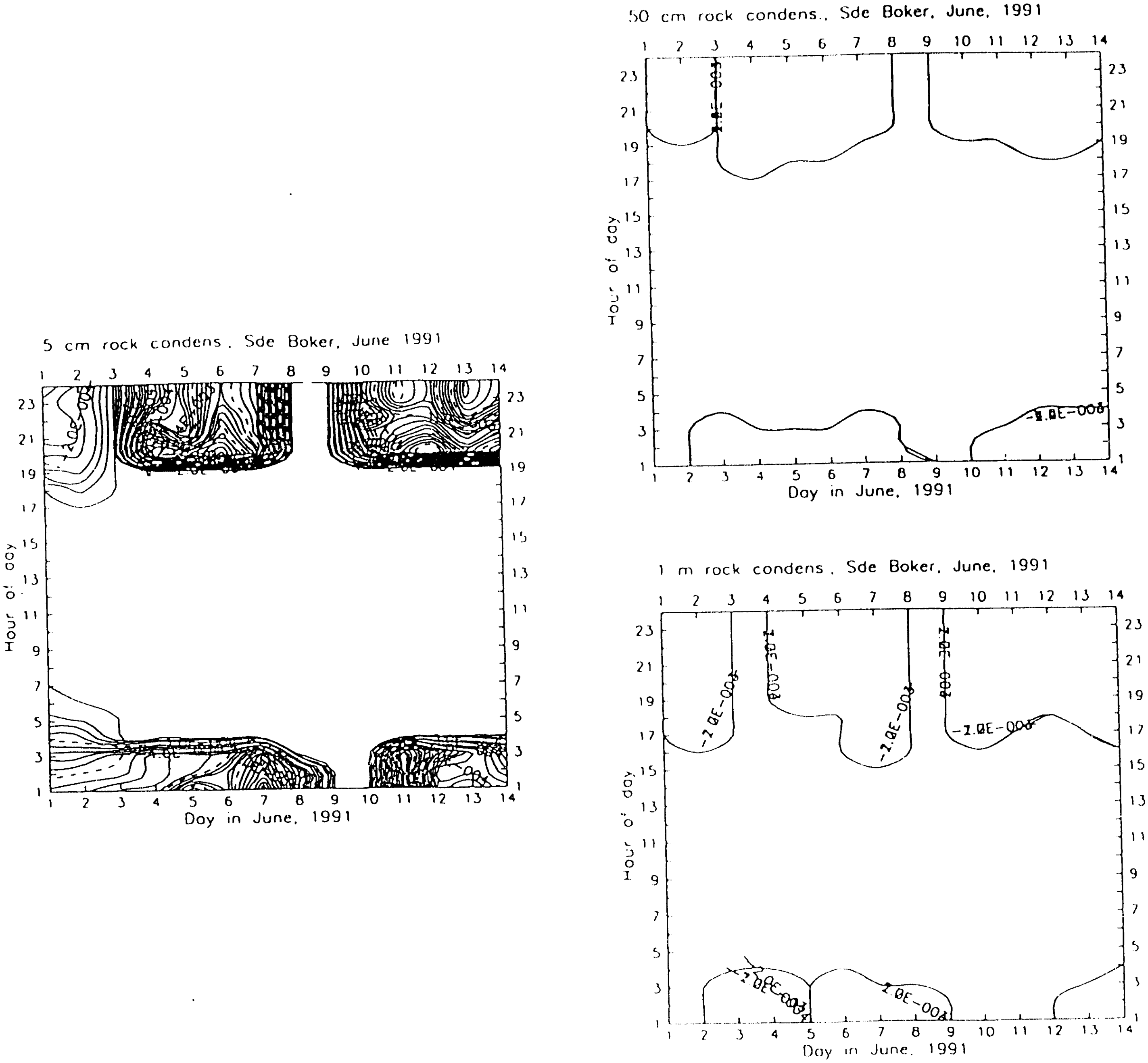
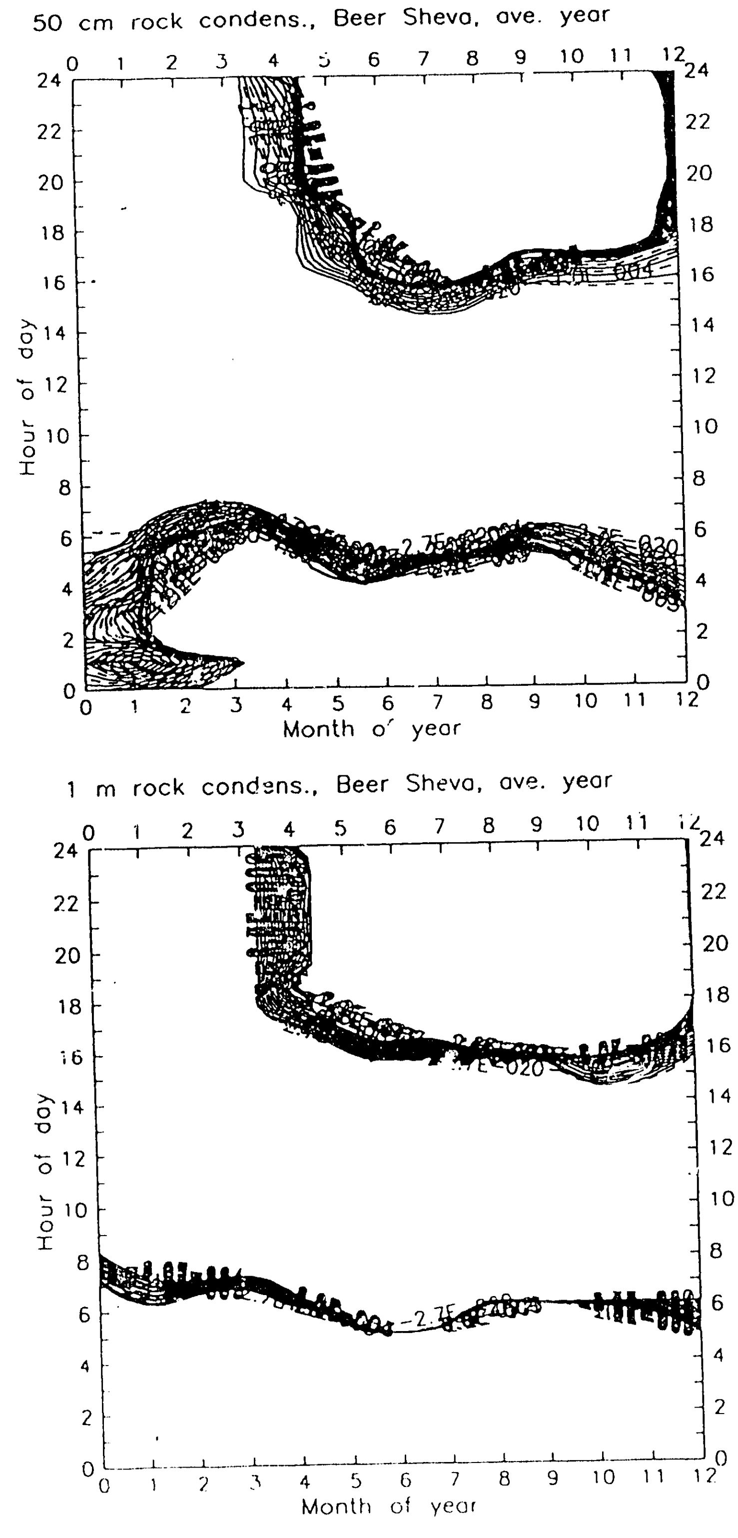
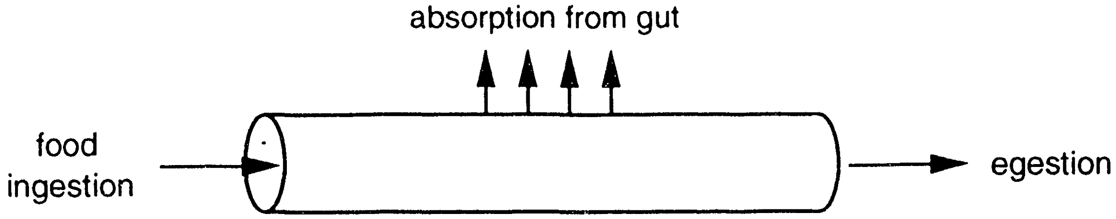


Fig. 5. Calculations of dew duration and amount on rocks of different sizes at the southern (100 mm rainfall per year) site, Sde Boker. The rock heat and mass transfer model is an adaptation of the ectotherm model, modified for inanimate objects by omitting physiology and altering physical properties.


50 cm rock condens., Beer Sheva, ave. year

1 m rock condens., Beer Sheva, ave. year

Fig. 6. Calculations of dew duration and amount on rocks of different sizes at a more northerly site (200 mm rainfall per year) site near Beer Sheva, Israel.



Mass balance equation for digestion: I = A + F

I = ingestion
A = nutrient absorption across lumen of gut
F = egestion (feces)

Maximum rate of food ingestion is set by
(1) Capacity of gut
(2) Rate at which food can be digested and absorbed
(= rate at which space is made available in gut)

Rate of digestion depends on
(1) Volume of food in gut
(2) Type of food (e.g., insects vs. plants)
(3) Temperature, via
    a. Gut motility
    b. Rate of enzyme secretion
    c. Rate of nutrient absorption

Specific Aims:
(1) Determine effects of temperature and food availability on energetics, and hence on potential for growth & reproduction
(2) Use as submodel for integrated model of lizard life history
(3) Provide processing constraint for models of foraging
(4) Provide suggestions for empirical research on digestive physiology

Fig. 7. Overview of digestion model. We have analyzed a general mathematical model, and are writing a model specific to lizards using physiological parameters estimated from published studies.

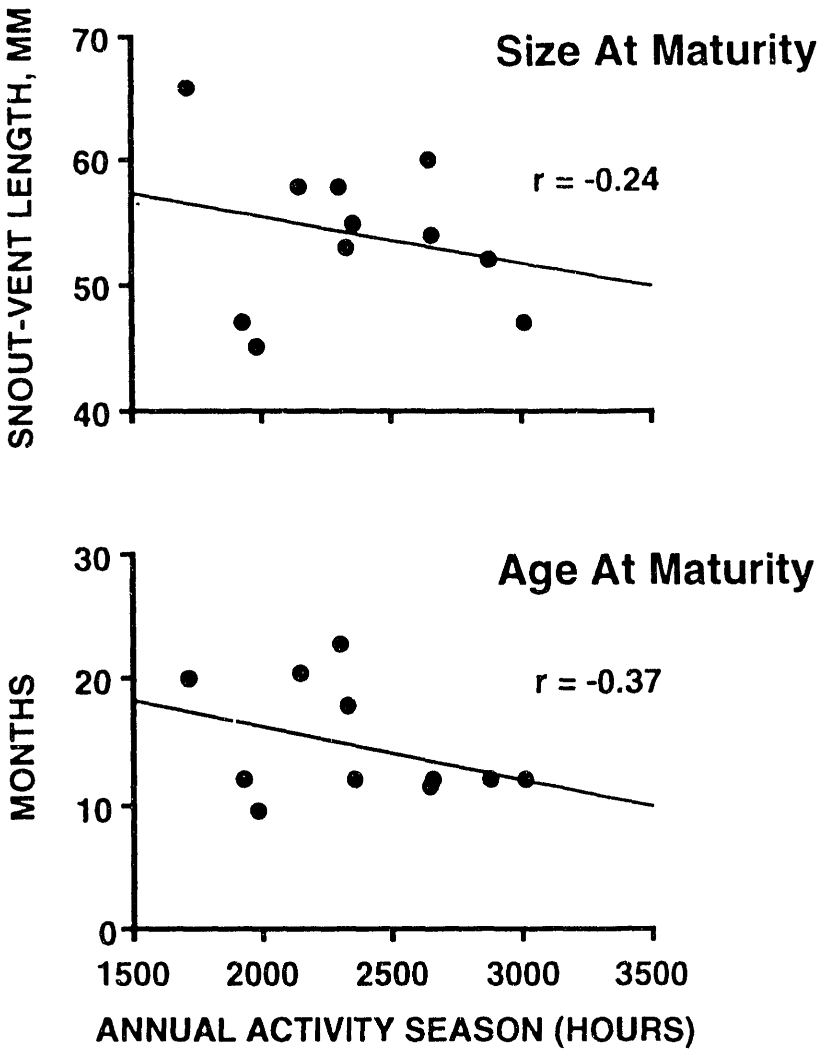


Fig. 8. Size and age at maturity of female eastern fence lizards (*Sceloporus undulatus*) as a function of estimated length of activity season. Life history data are from published studies on 11 field populations. Activity seasons were calculated using climate and geographic data from each site. These data, in combination with lizard thermal properties, were used as input to computer programs that determined the microclimates available to the lizards on daily and seasonal bases, and consequently the times that lizards could be active throughout the year.

Neither size nor age at maturity was significantly correlated with length of the activity season, although both varied in the expected direction, based on our model's predictions. For example, lizards in some populations with short activity seasons mature at an early age despite their small size. This suggests evolved differences in the timing of maturity. Using optimization models, we will explore theoretically the influence of seasonality on reproductive timing.

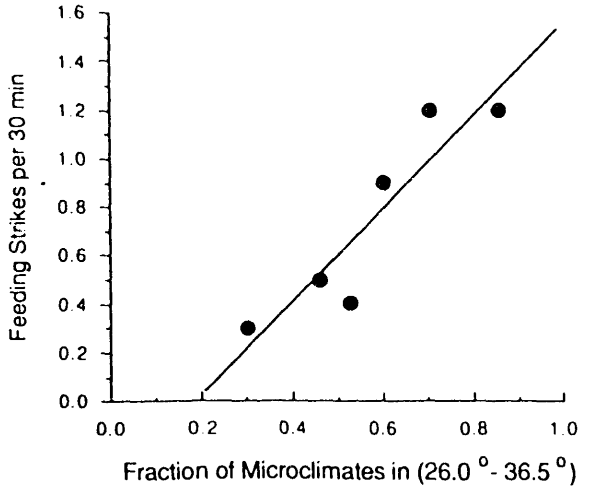


Fig. 9. The number of feeding strikes per 30 min by free-ranging canyon lizards (*Sceloporus merriami*) is linearly correlated with the fraction of available microclimate temperatures within the interval 26.0°-36.5°C, the preferred temperature range of this species. Data from Grant and Dunham (1988).

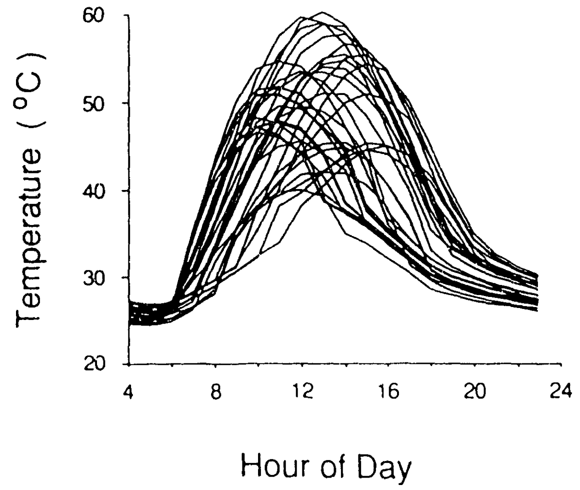


Fig. 10. Simulated microclimate temperatures for 40 randomly oriented substrate surfaces from repeated iterations of the microclimate program. For this example, each orientation was randomly selected from a point on the surface of a fictitious hemispherical rock. However, any distribution of substrate orientations could be used. (from Grant and Porter 1992).

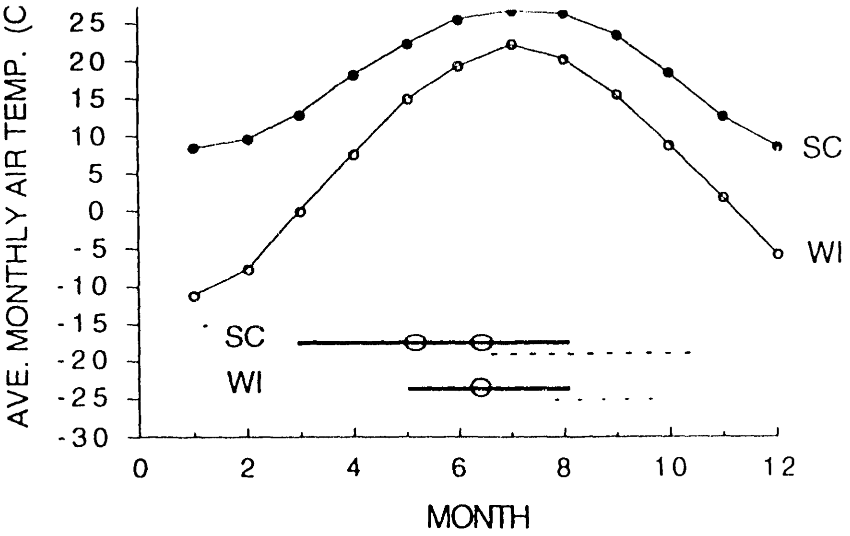


Fig. 11. Average monthly air temperatures (±1 SD) are plotted versus month for Madison, Wisconsin, and Aiken, South Carolina. Beneath these curves, horizontal lines indicate the approximate dates of adult (solid lines) and hatchling (dotted lines) emergence (beginning of each line), initiation of brumation (end of each line), and oviposition (open circles) for Wisconsin and South Carolina populations. This illustrates the variation in environmental temperature and active season length between northern and southern populations.

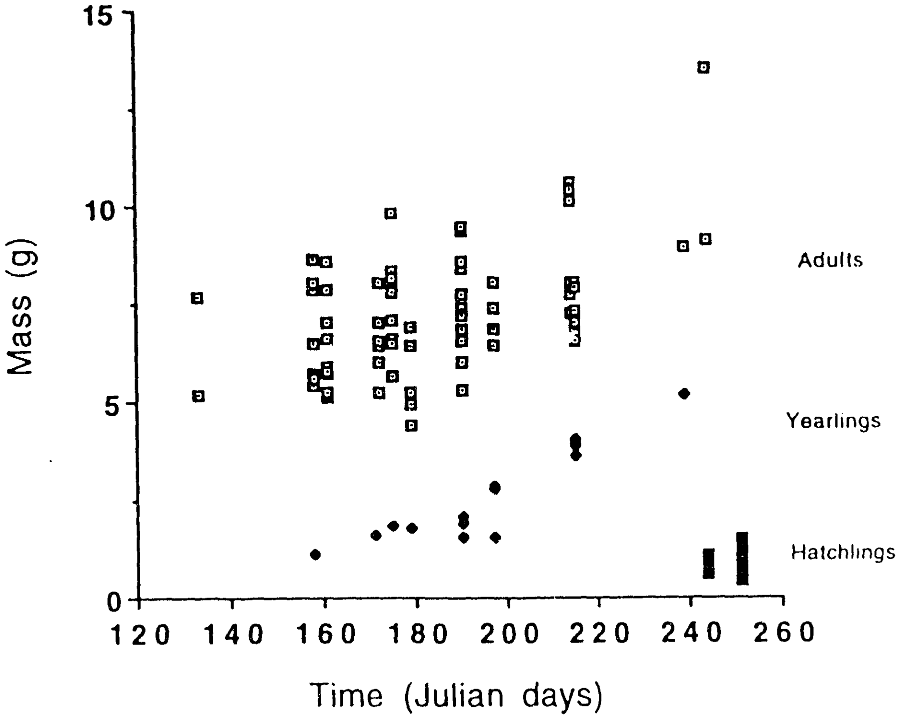


Fig. 12. Typical snout-vent lengths over the course of an active season (1991) for Wisconsin *C. sexlineatus*. Hatchlings are born at the end of the summer and do little growing until the following summer, and do not reproduce until their second year. In southern populations that produce two clutches per summer, first-clutch lizards are able to reproduce as yearlings. For a comparison of Wisconsin adults and Arkansas adults, see Fig. 15.

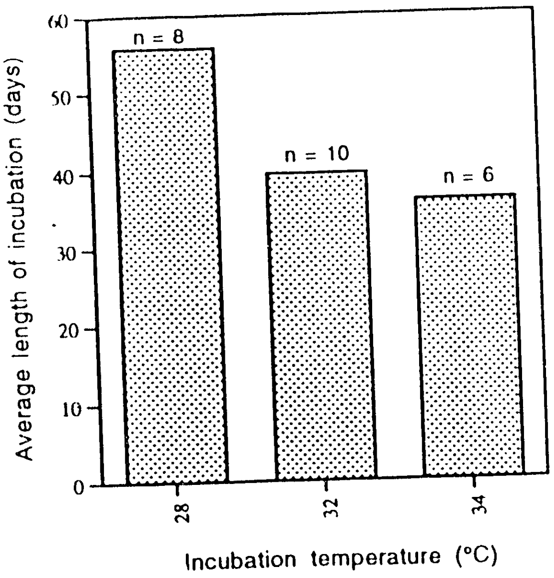


Fig. 13. Temperature dependence of egg incubation. Arkansas eggs were incubated at several temperatures, and all eggs hatched within four days of one another at each temperature. Eggs incubated at 22 °C did not hatch.

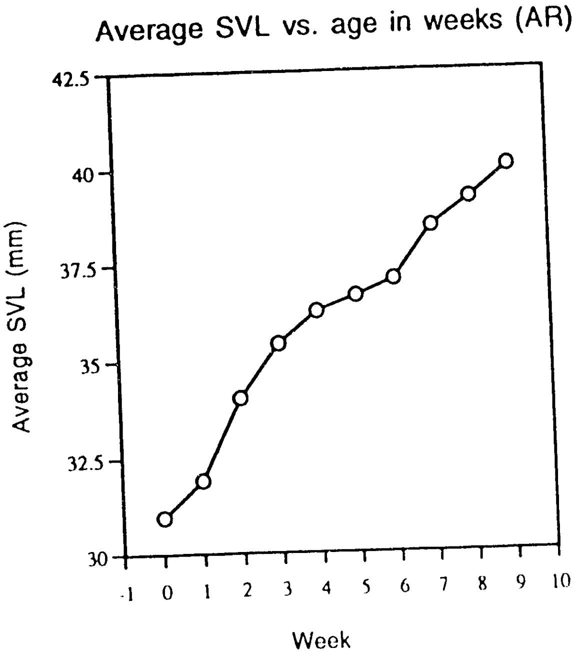


Fig. 14. Average increase in snout-vent length in Arkansas hatchlings raised in the lab. The lizards were fed ad libitum and could select from a gradient of temperatures.

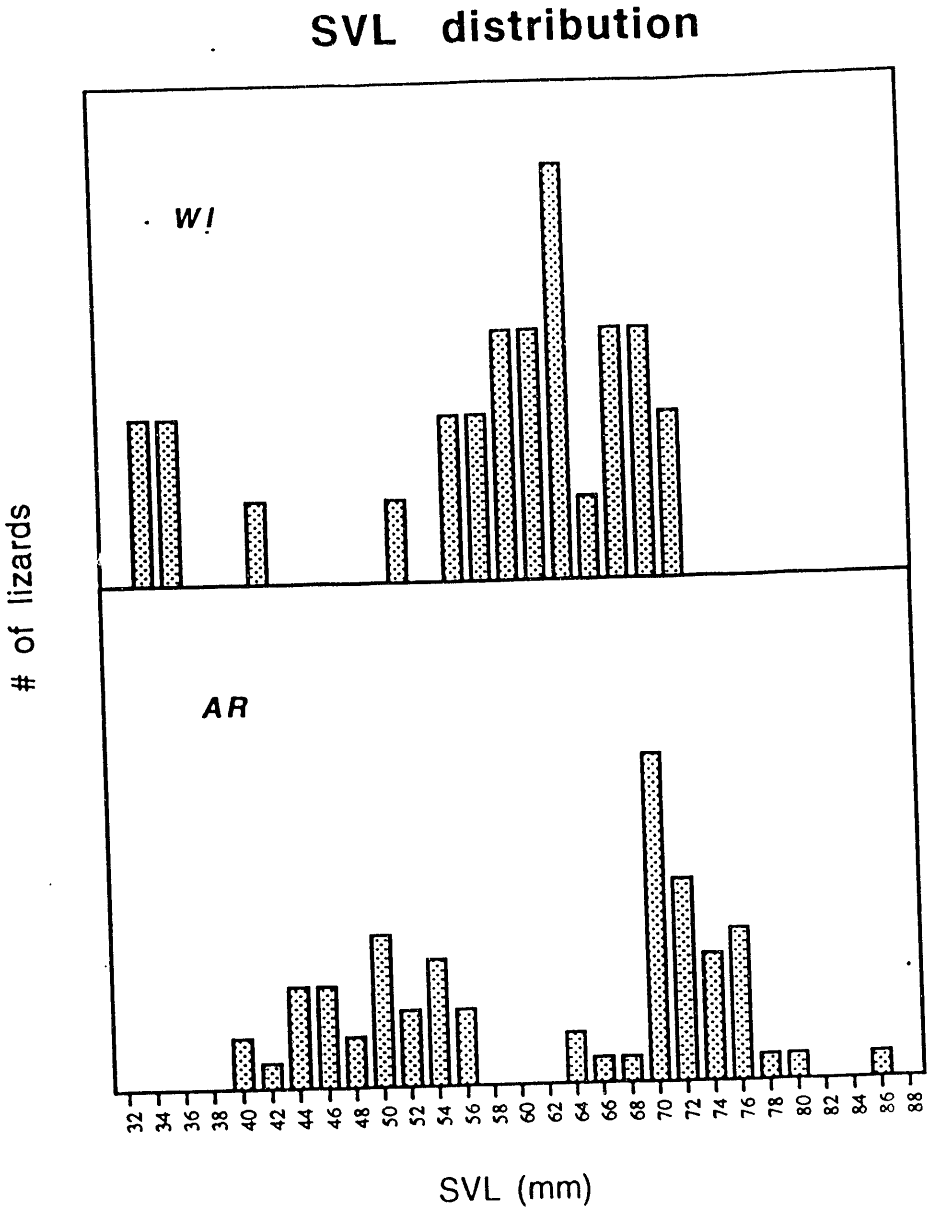


Fig. 15. Typical distributions of lizard snout-vent lengths from Wisconsin and Arkansas at the same time of the summer (late May-early June). The pulses on the right illustrate the difference in adult size between the two populations. The pulses on the left are yearlings. Unlike Wisconsin juveniles, Arkansas lizards have more months to eat and grow both at the end of their hatchling year and at the beginning of their yearling year. Some Arkansas lizards attain large enough size to reproduce as yearlings.

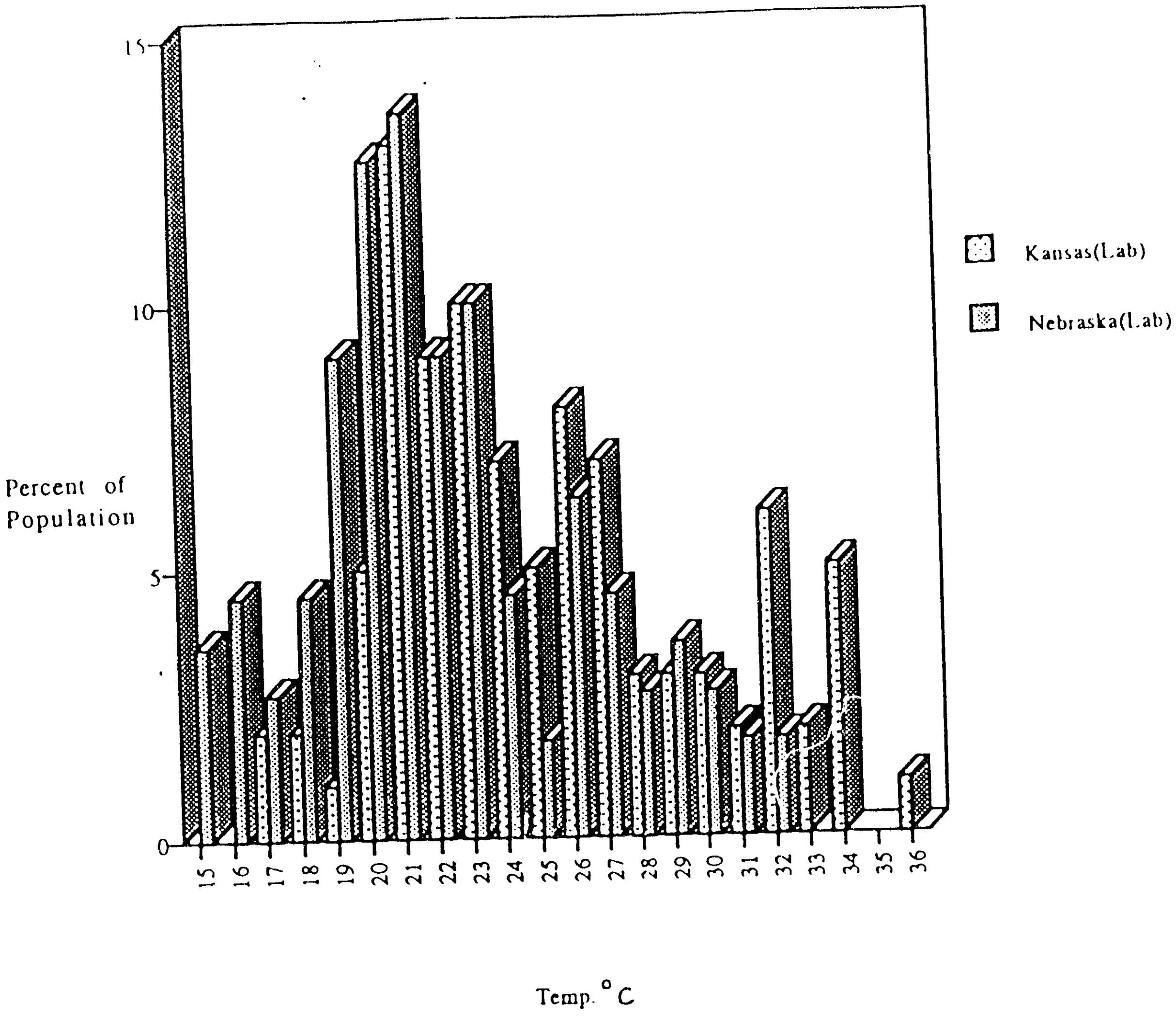


Fig. 16. Body temperatures (T_b) chosen by northern and southern ornate box turtles (*Terrepene ornata*) in laboratory thermal gradients (data from Gatten 1974). Box turtles from Kansas (the latitudinal center of their range) chose T_b 4°C warmer than box turtles from Nebraska. These data suggest that box turtles can extend their activity periods by tolerating lower T_b in cooler environments and higher T_b in warmer environments. Such a pattern of flexible thermoregulatory behavior is suggested by optimal models (Huey and Slatkin 1976; Porter et al. 1973).

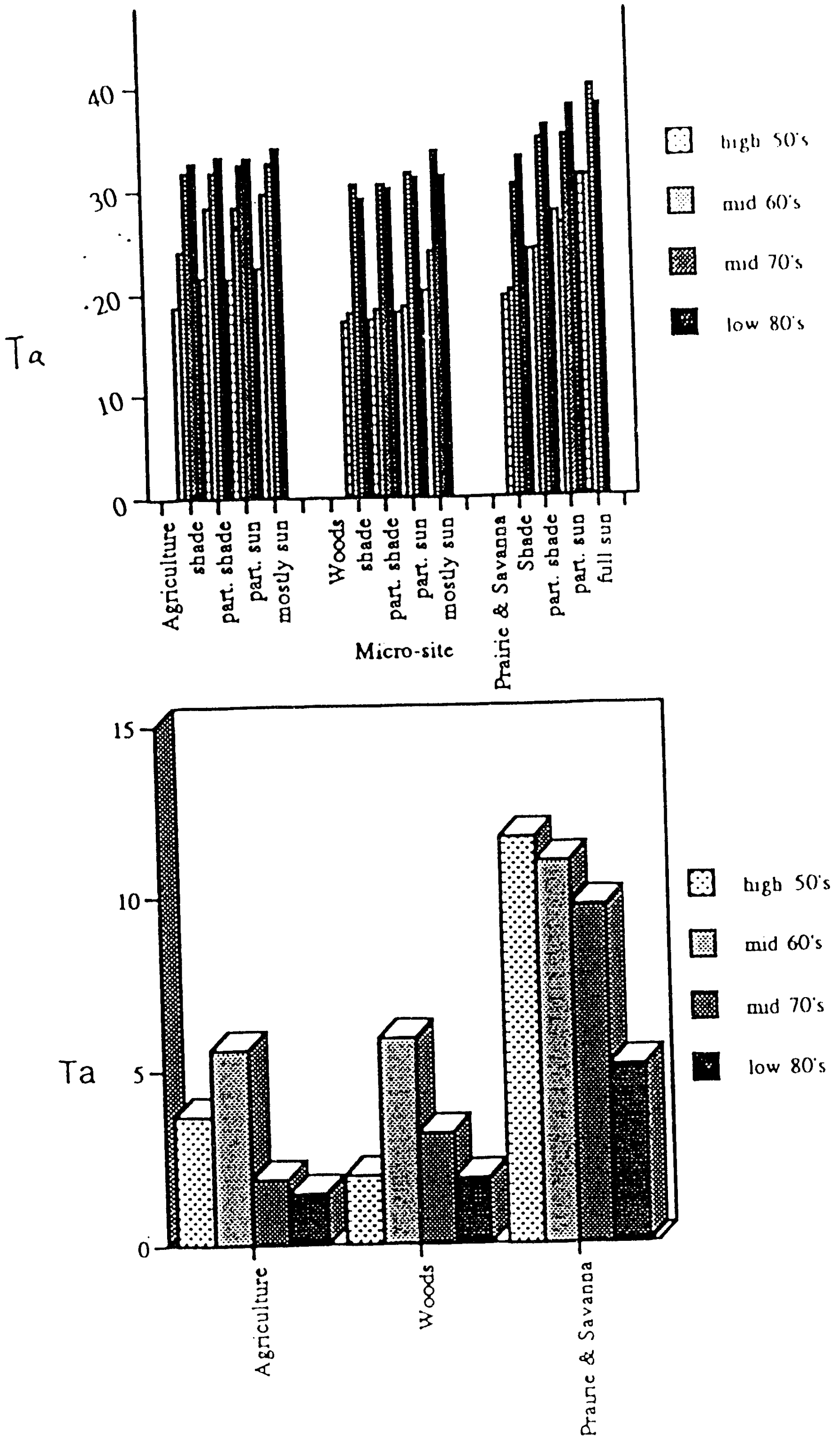


Fig. 17. Availability of microclimate temperatures in different habitats. The upper figure shows the distribution of available temperatures within each habitat. The lower figure illustrates the range of microclimate temperatures (a measure of thermal heterogeneity) available within each habitat. These data indicate that native savanna and prairie habitats (the preferred habitats of box turtles) offer a wider range of available temperatures, thus allowing longer daily and seasonal activity periods.

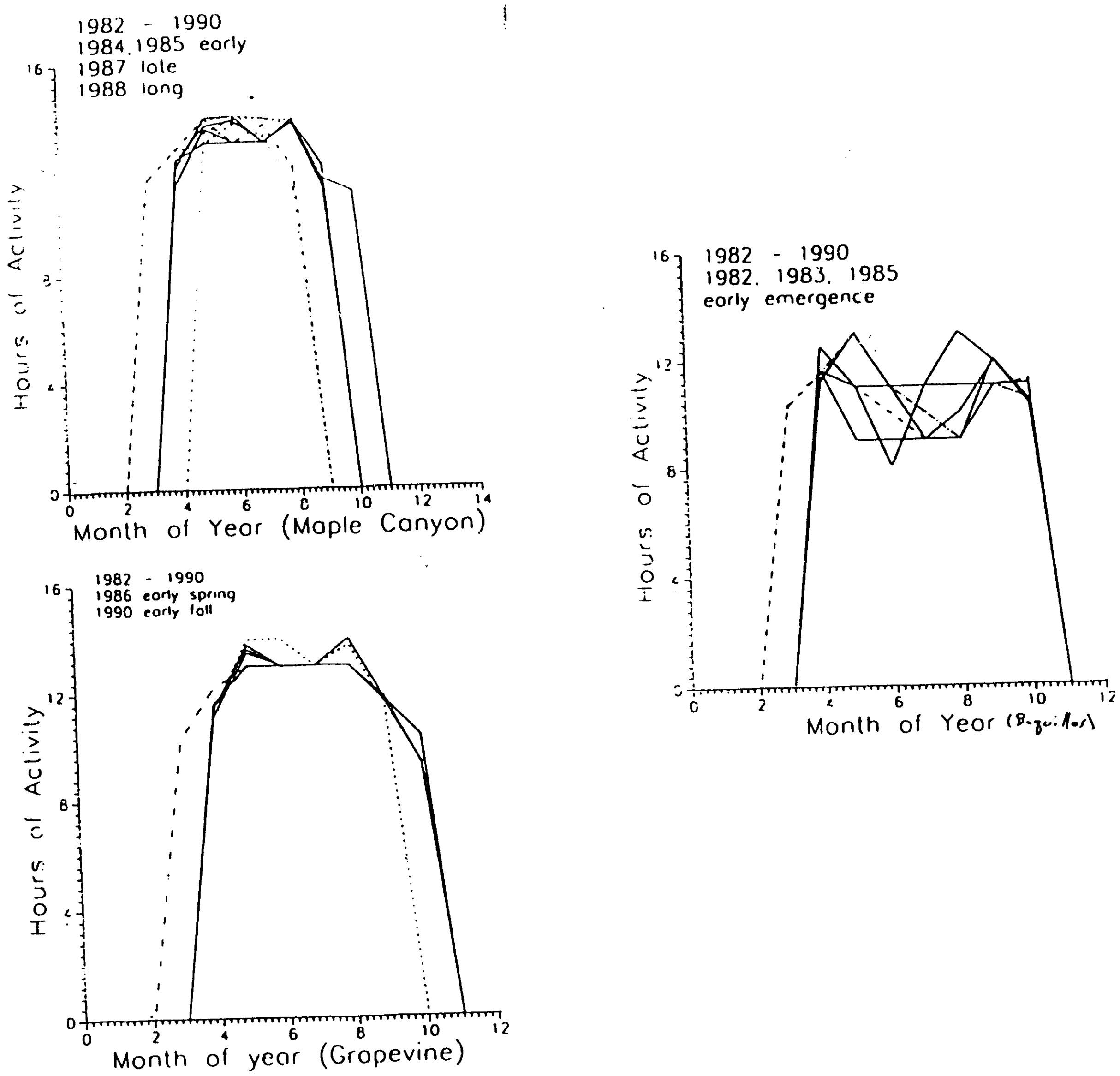


Fig. 18. Calculations of daily activity time as a function of time of year for *Sceloporus merriami* for all three elevation sites in Big Bend National Park, Texas for the years 1982 - 1990. The calculations are based on macroclimate data that drive a microclimate model for each site. The microclimate model output specifies all available habitats every hour, which the lizard model uses to determine whether activity is possible for that hour. Behavioral constraints, such as no nighttime activity, are also included. Year-to-year variation in temperature causes variation in predicted activity seasons.

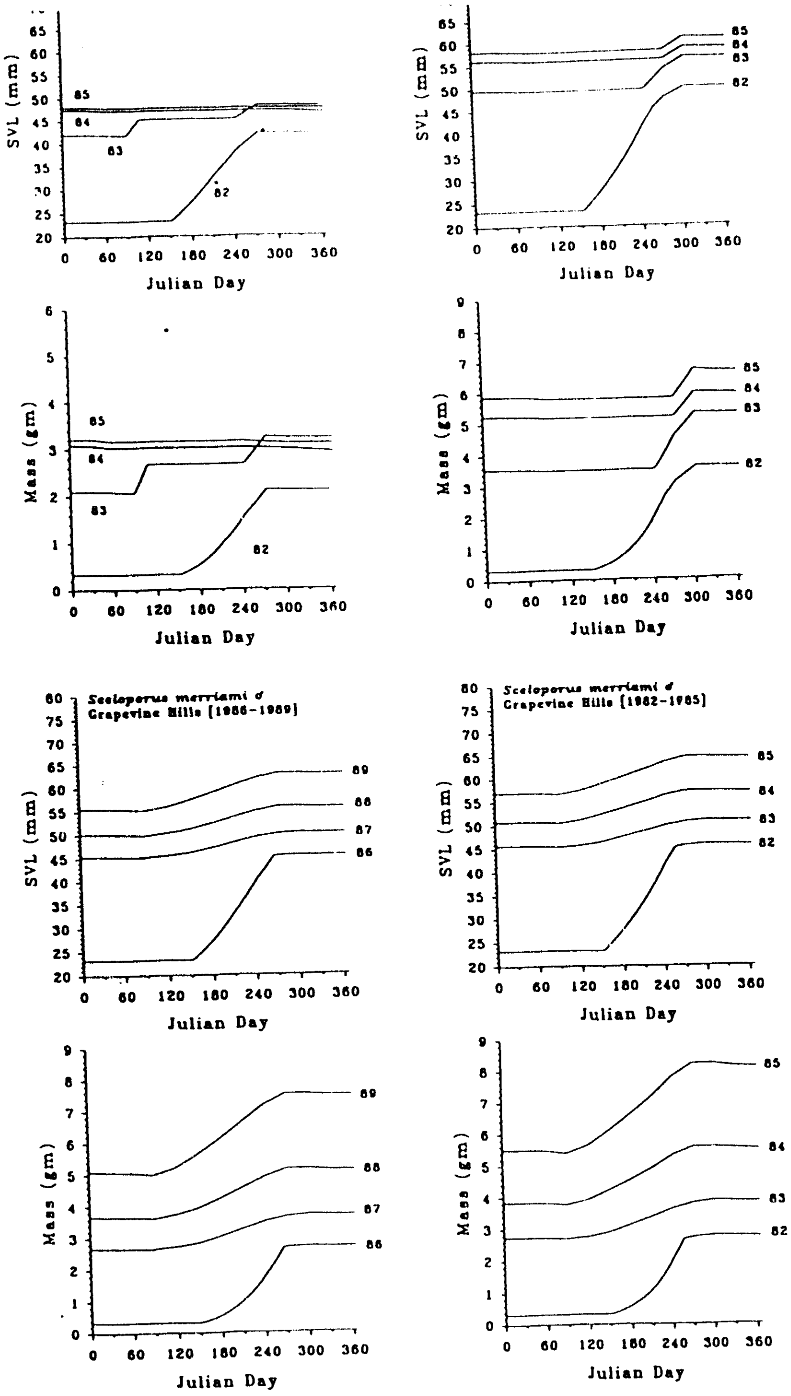


Fig. 19. Calculated growth rates for *Sceloporus merriami* at the high elevation site, Maple Canyon and the intermediate site, Grapevine Hills in Big Bend National Park. Based on climate data from the years 1982 - 1989. Calculated growths are for animals hatching in July in 1982 or 1986. Calculations are based on a macroclimate-driven microclimate model for the sites and the physical, physiological and behavioral properties of the lizards. Females at the two sites (upper four graphs) differ in body size primarily because of temperature differences that impose different activity times and time above minimum digestion temperatures. Males at the same site, but hatched in different years from average sized eggs are projected to reach different weights by the end of their fourth year due to slight differences in year to year climate variation. Results for all are consistent with long term demographic data collected by Drs. Art Dunham and Karen Overall.

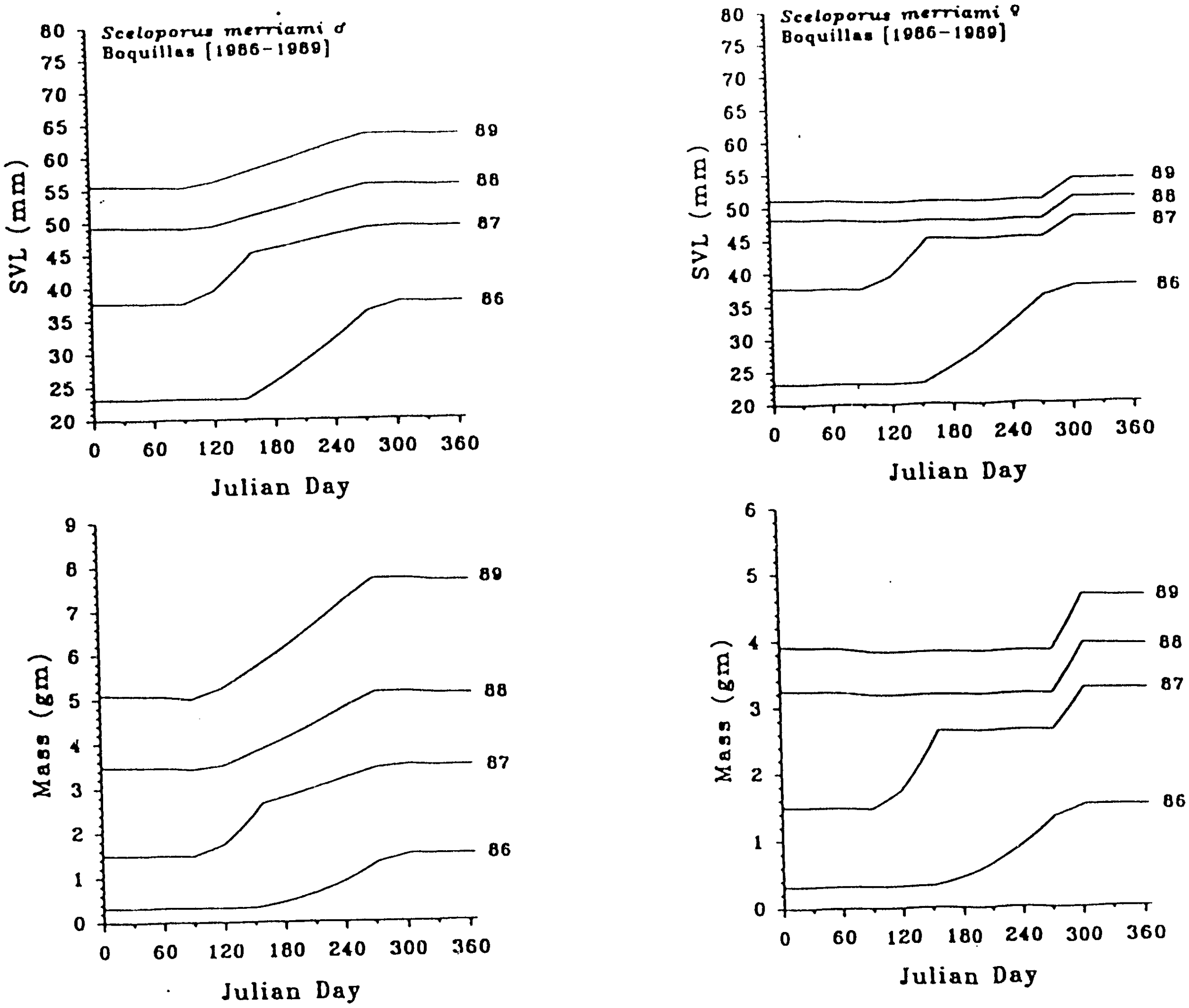
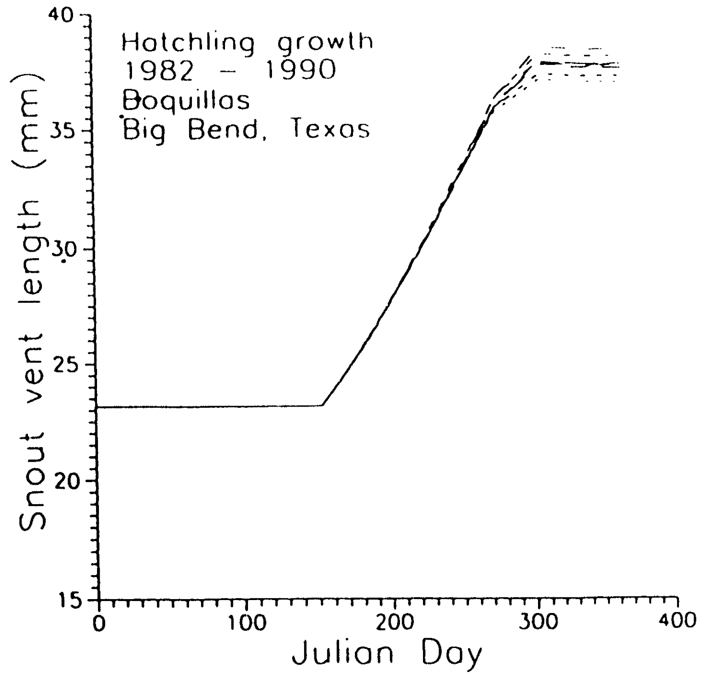


Fig. 20. Calculations of growth rate for male and female *Sceloporus merriami* at the low site, Boquillas, near the Rio Grande River in Big Bend National Park. Differences in weight between males and females can be attributed to differences in time involved in allocating discretionary resources to territorial defense vs. egg production. All simulations presume cessation of allocation to reproductive activities one month before expected initiation of hibernation at each elevation. All simulations closely mimic actual growth rates and body sizes see in long term demographic data collected by Drs. Dunham and Overall at these sites.



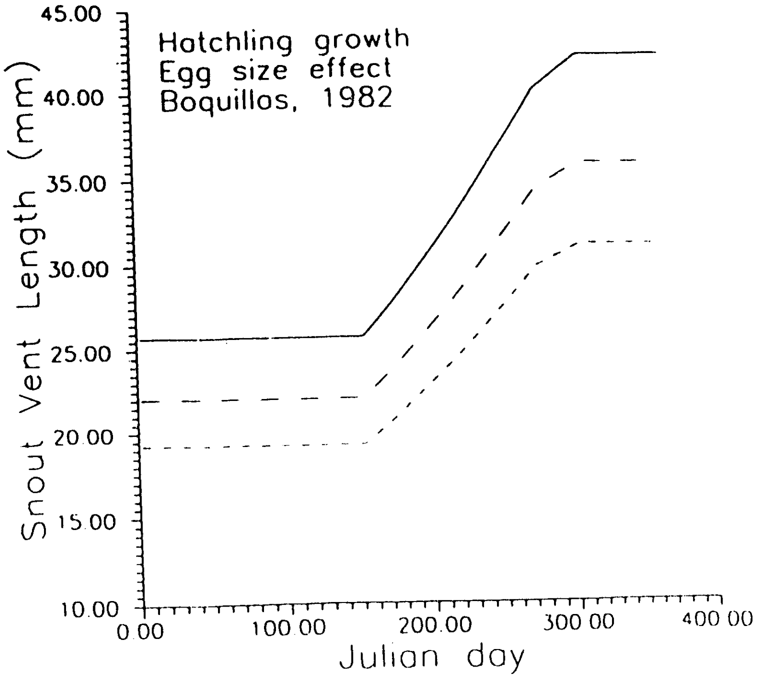


Fig. 21. Sensitivity analyses of calculated hatchling growth in *Sceloporus merriami* due to year to year variation in climate (top) and size of egg from which they hatch (bottom).

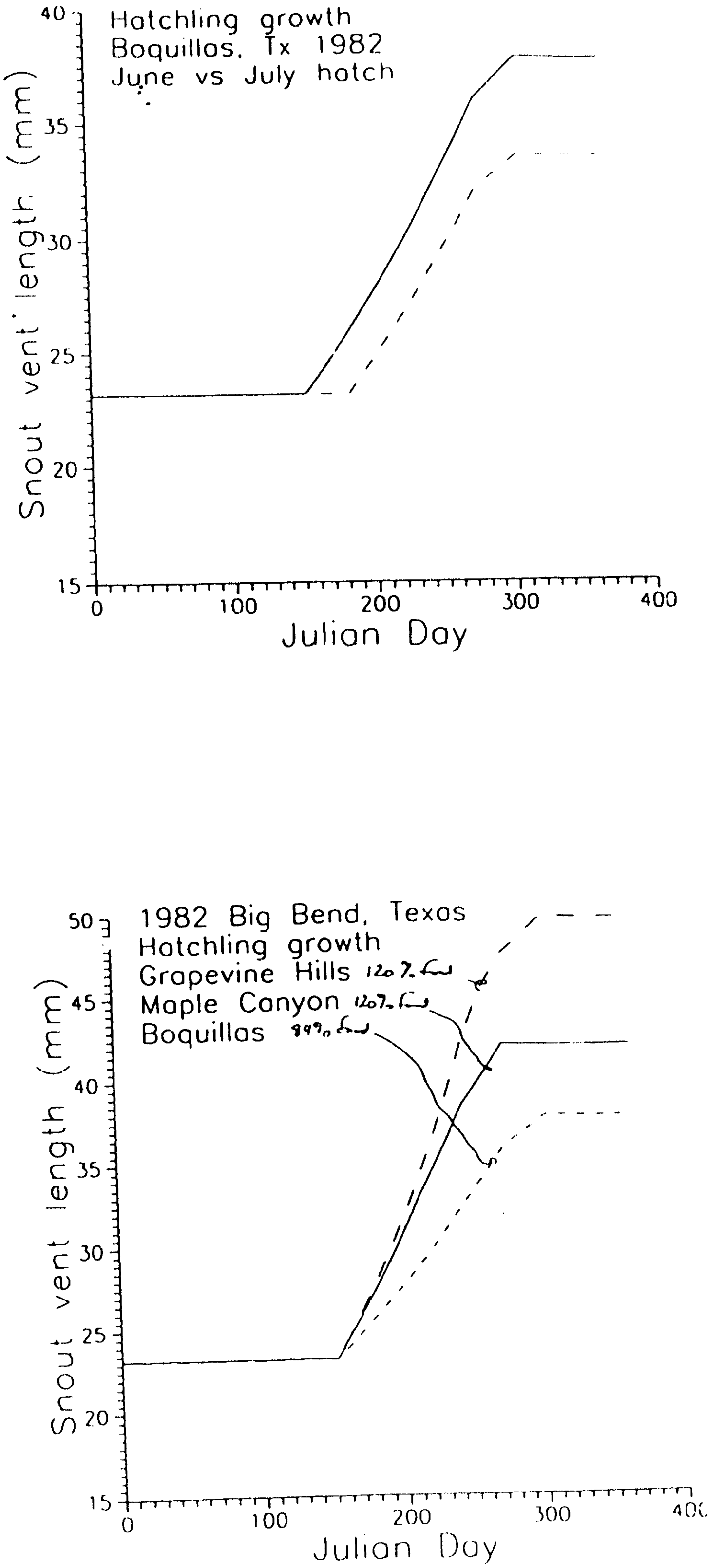


Fig. 22. Sensitivity analyses of *Sceloporus merriami* hatchling growth at Boquillas, the low elevation site, due to time of hatching (top) and due to site and its covarying food supply (bottom). The 120% food is our best estimate of maximum food consumption, since the digestive physiology used in the calculations was not done with ad lib feeding.

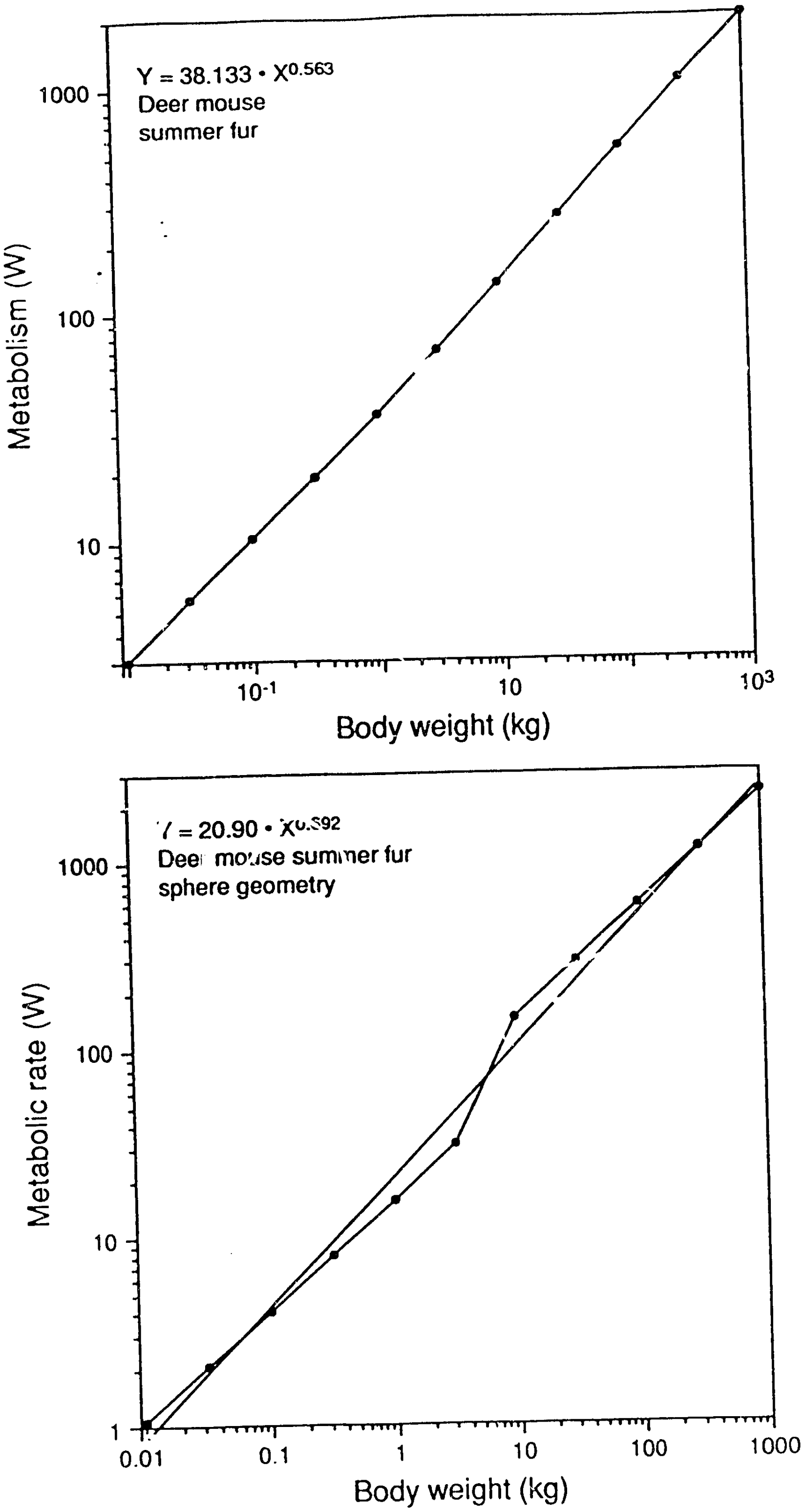


Fig. 23. Calculated mouse-to-elephant curve expressing metabolic rate as a function of body size, assuming deer mouse fur on all animals. Cylindrical geometry (top) vs. sphere geometry (bottom) gives slopes that bound the empirical data with its slope of approximately 0.67. Calculation points are marked with solid circles. A regression line is fitted to the calculated points.

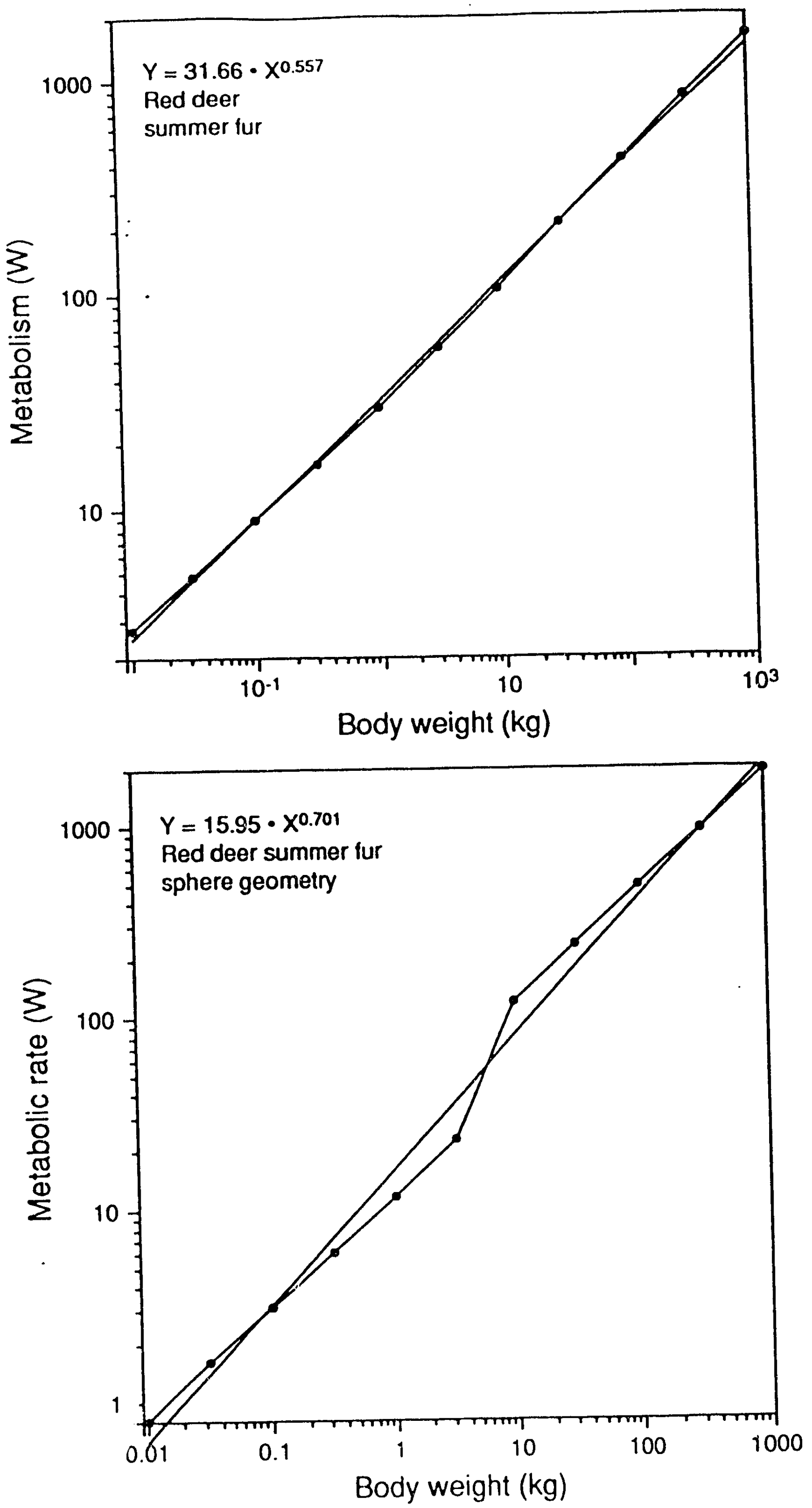


Fig. 24. Calculated mouse-to-elephant curve expressing metabolic rate as a function of body size using red deer fur (longer and more sparse) on all animals. Cylindrical geometry (top) vs. sphere geometry (bottom) gives slopes that bound the empirical data, with its slope of approximately 0.67.

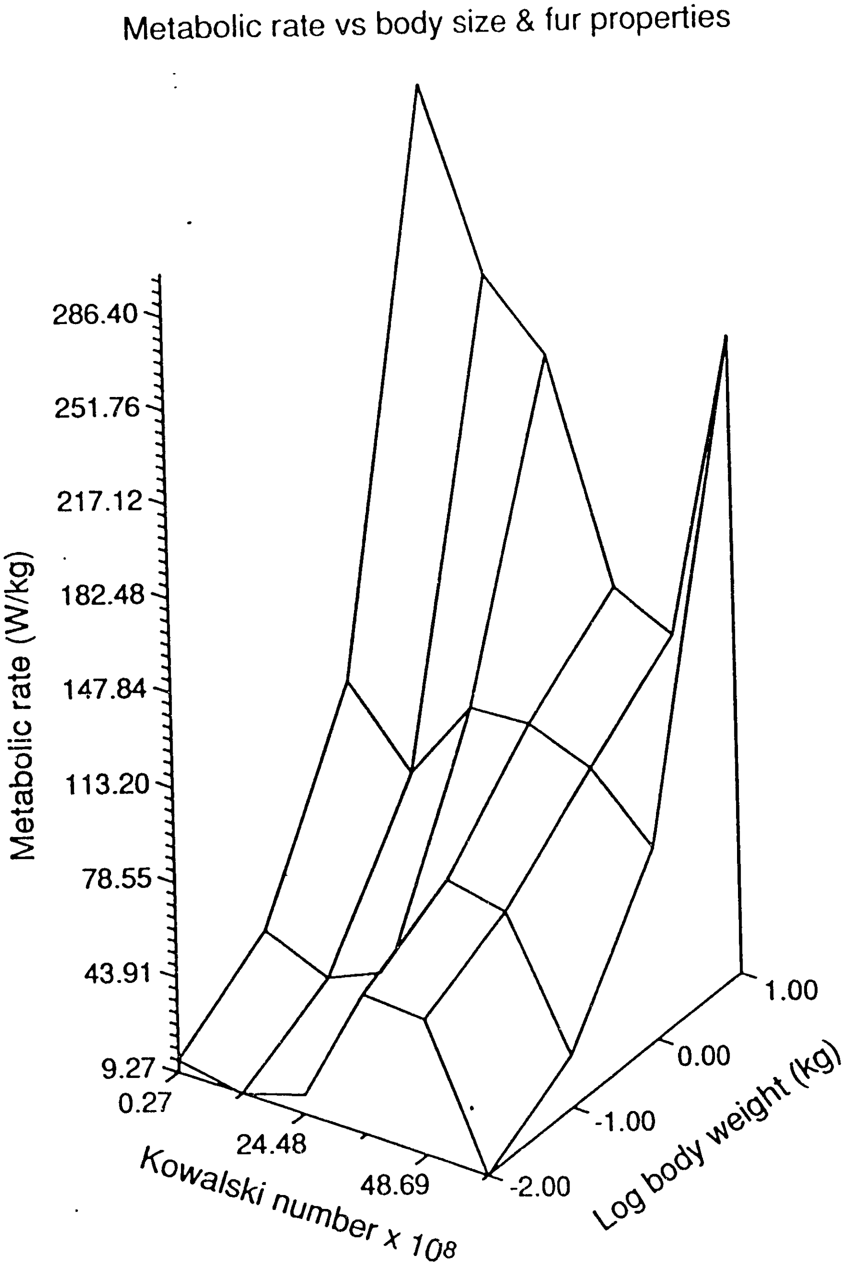


Fig. 25. Calculated mass-specific metabolic rate vs. log body weight and a new nondimensional number for all fur properties, the Kowalski number. The Kowalski number includes hair length, diameter and density and pelt depth. The range of variation includes the maximum range for all known fur properties, including many unpublished data from our laboratory. Constraints are that hair diameters must be consistent with density (hairs may not be packed more tightly than physically possible) and pelt depth cannot exceed hair length.The 'Batmobile' response surface clearly shows a saddle-shaped optimality surface with optimal fur properties clearly dependent on body size.

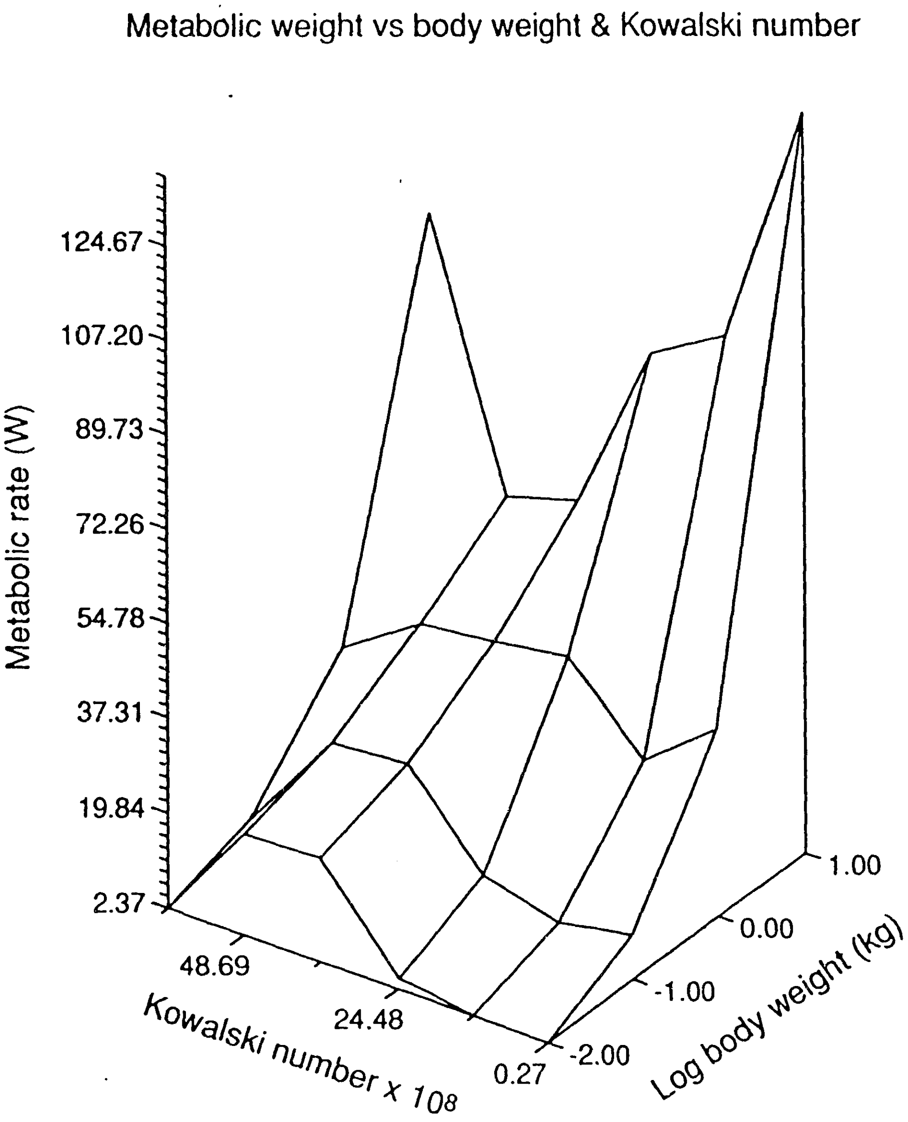


Fig. 26. The same calculations as Fig. 25, except the results are expressed as total metabolism rather than mass-specific metabolism.

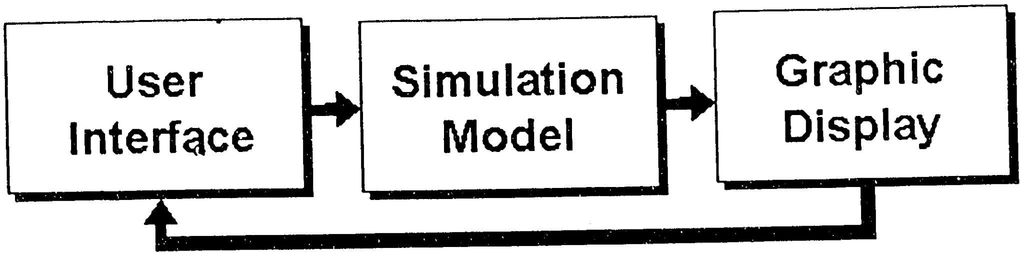


Fig. 27. Modular components of the BEASTS computer program.

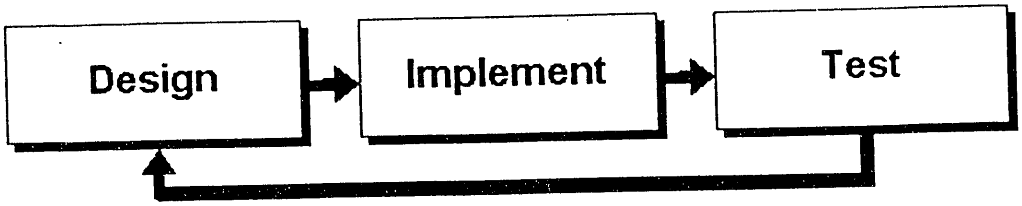


Fig. 28. Steps involved in creating the user-friendly interface for BEASTS software.

I. A. Summary

This report summarizes our research and publications during the past year of support from DOE. The common goal of these diverse projects is to understand the mechanisms of how animal populations respond to the continual changes in their environment in both time and space. Our models are mechanistic (rather than descriptive); this has allowed us to explore how a wide array of environmental variables may determine individual performance. For example, Fig. 1 shows a map of the maximum number of eggs that could be produced by the lizard *Sceloporus merriami* in the climatic range found in Texas in 1976. Weather and geological data were collected from 19 sites, and maximum possible egg production was calculated with the microclimate and lizard heat and mass balance models. These calculations illustrate which populations will be affected most strongly by specific changes in climate. In a check of the model's accuracy, our calculations for one site (Big Bend) compared favorably with field data collected at Big Bend by our collaborators, Drs. Art Dunham and Karen Overall, for ten successive years (summarized in last year's report).

The basic research and model development that DOE has supported in our laboratory is directly applicable to climate change. Large scale climate change and its effect on animal populations can be seen as quantitative extensions of biological responses to smaller scales of environmental variability. Changes in developmental rates or reproductive levels of individuals, extension or contraction of geographic ranges, and modification of community organization have all been documented in response to previous changes in habitats. We know from our biophysical work that some changes in function are driven by microclimate conditions directly, and some are mediated indirectly through ecological parameters such as the food supply.

Our research is guided by a comprehensive conceptual scheme of the interaction of an animal with its environment (Fig. 2). Animals live in a set of microclimates whose thermal and hydric properties are determined in part by the influence of the macroclimate, in part by behavioral modifications by the animal itself. The physical and physiological properties of the organism, and the range of available microclimates, set bounds on the performance of organismal function, such as growth, reproduction, storage, and behavior. To leave the most offspring over a lifetime, animals must perform those functions in a way that maximizes the amount of resources devoted to reproduction. Maximizing the total size of the budget and minimizing those budget items not devoted to reproduction (i.e. maintenance) are both crucial. Animals can also trade off among expenditures for current and future reproduction. Both water and energy are important, potentially limiting resources (Fig. 3).

Projects described here include empirical studies, theoretical models, and combinations.

B. Key papers published during the past year (with synopses)

Adolph, S. C. and W. P. Porter. 1993. Temperature, activity, and lizard life histories. American Naturalist (in press). We found that geographic variation in lizard survivorship and reproduction can be explained in terms of climate and physiology, rather than invoking evolutionary arguments.

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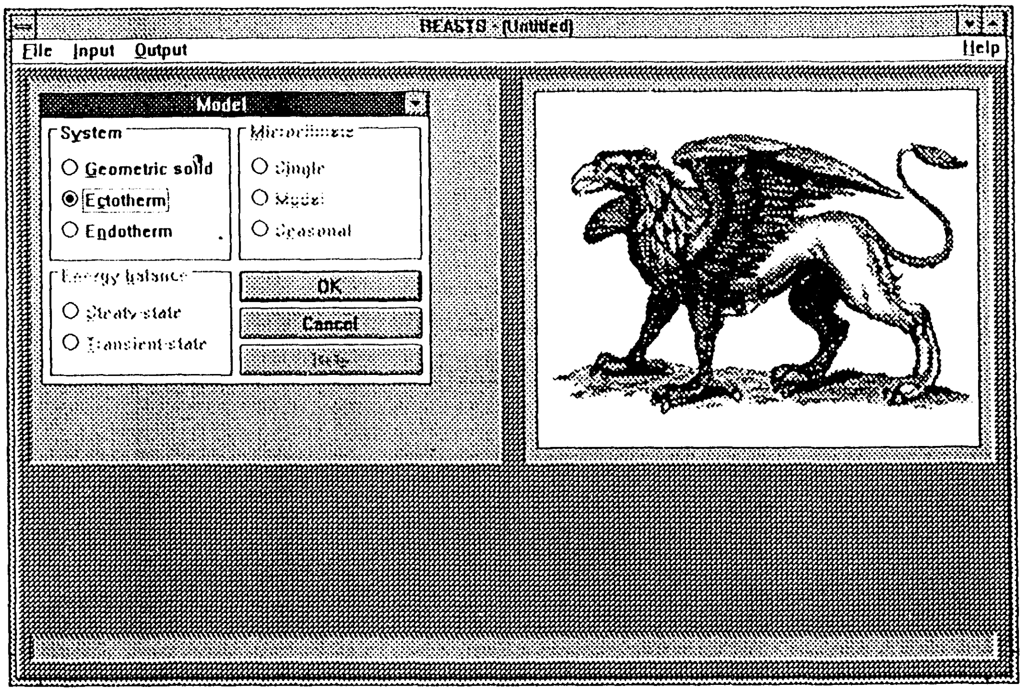
Grant, B. W. and W. P. Porter. 1992. Modeling global climatic constraints on animal energy budgets. American Zoologist 32: 154-178. We found that optimal foraging behavior is different in the two sexes of *Sceloporus merriami*, apparently because of different criteria for optimality in males than females. We also showed that environmental constraints on optimal behavior are more applicable when energy reserves are high. On a daily basis, the availability of suitable microclimates is far more important than food availability or predation levels in affecting optimal behavior.

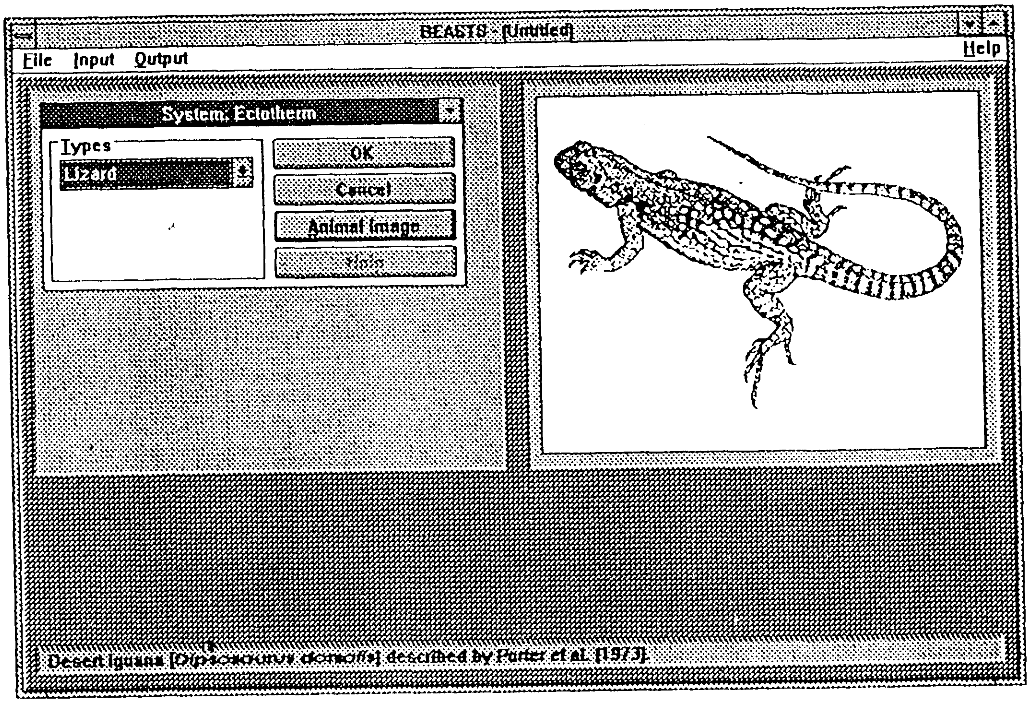
Reynolds, P. S. 1992. Behavioral and biophysical ecology of beaver (*Castor canadensis*) in North-Central Wisconsin. Dissertation, University of Wisconsin. showed that climate



System
○ Geometric solid
● Ectotherm
○ Endotherm

Microclimate
○ Single
○ Model
○ Seasonal

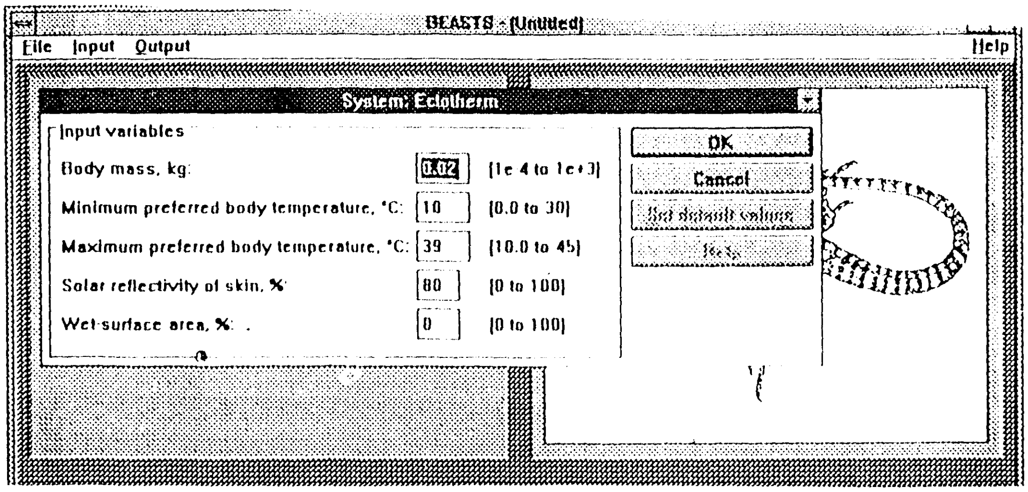
Energy balance
○ Steady-state
○ Transient-state



Types
Lizard

Desert Iguana [Dipsosaurus dorsalis] described by Porter et al. [1973].

Figs. 29 (top) & 30 (bottom). Sample dialog boxes from BEASTS user interface.



Input variables

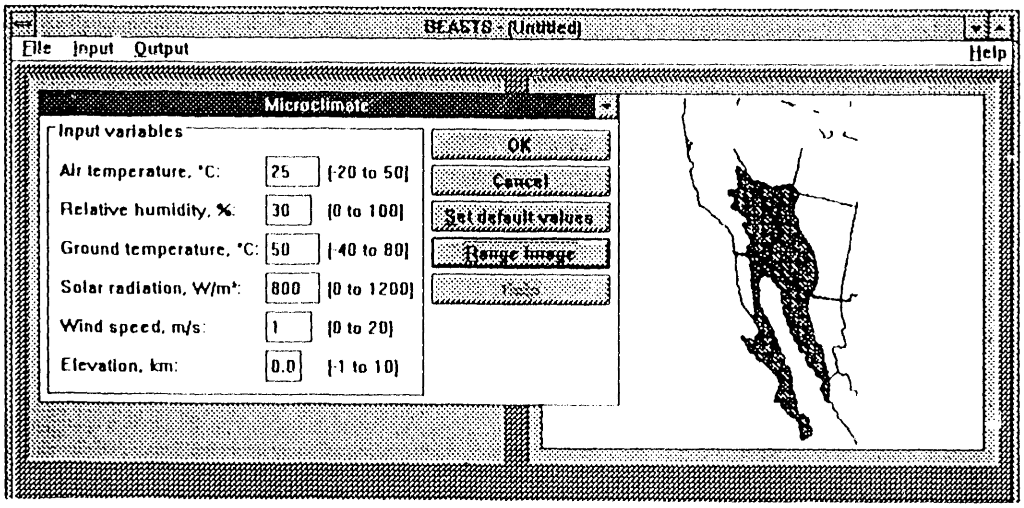
Body mass, kg: 0.02 [1e-4 to 1e+3]

Minimum preferred body temperature, °C: 10 [0.0 to 30]

Maximum preferred body temperature, °C: 39 [10.0 to 45]

Solar reflectivity of skin, %: 80 [0 to 100]

Wet surface area, %: 0 [0 to 100]



Input variables

Air temperature, °C: 25 [-20 to 50]

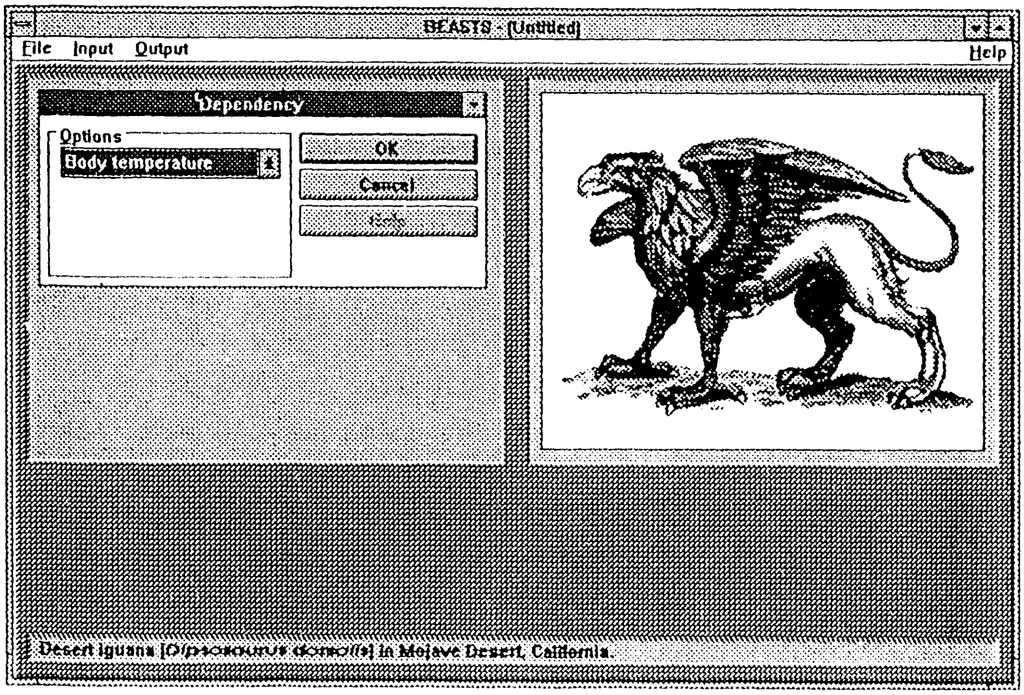
Relative humidity, %: 30 [0 to 100]

Ground temperature, °C: 50 [-40 to 80]

Solar radiation, W/m²: 800 [0 to 1200]

Wind speed, m/s: 1 [0 to 20]

Elevation, km: 0.0 [-1 to 10]



Options

Body temperature

Desert iguana [*Dipsosaurus dorsalis*] in Mojave Desert, California.

Figs. 31, 32, & 33 (top to bottom). Sample dialog boxes from BEASTS user interface.

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END