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Latitudinal gradients in biophysical constraints:
implications for species response to shifting land-use and climate

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by

Charles G. Curtin

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Latitudinal gradients in biophysical constraints: implications for species response to shifting land-use and climate

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Latitudinal Gradients in Biophyiscal Constraints:

Implications for Species Response to shifting land-use and Climate

Charles G. Curtin

Under the supervision of Warren P. Porter

At the University of Wisconsin-Madison

To examine latitudinal variation in ectotherm response to microclimate, this work integrates laboratory and field studies of latitudinal variation in thermal preference, field studies of life history in response to shifts in land-use and microclimate, with computer simulations of activity of ornate box turtles (Terrapene ornata). My laboratory gradient and field studies indicate that latitudinal variation in thermal preference, while somewhat labile, remain significantly different between northern and southern turtles. My field studies of life history variation across habitats experiencing different land uses indicate that a cooling of microclimates, resulting from alteration of plant association structure, can lead to decreased time for incubation, growth, activity, and reproduction and declining turtle populations. This suggests that relatively subtle shifts in land-use and/or microclimate can have profound, and varying effects on the distribution and abundance of species.

This thesis also examines the generality of patterns of ectotherm response to climate noted in Wisconsin at the north-eastern edge of the Great Plains. My data on latitudinal variation in box turtle thermal constraints, life history, and microclimate, are input into computer climate and ectotherm activity simulations to assess latitudinal variation in box turtle response to environmental variation across the plains. Simulation calculations, supported by field data, indicate this cooling of microclimate has pronounced effects on box turtle activity periods and reproductive potential not just at the northern edge of their range, but across the Great Plains.

The results suggest that a cooling of the microclimate, resulting from changes in land-use can have impacts greater than those predicted for climate change resulting from global warming. Results highlight the importance of managing both preserves and the surrounding landscape matrix for a diversity of thermal environments and demonstrate the value of a biophysical approach in predicting population viability under conditions of shifting land-use and climate.

Warren Porter
Prof. of Zoology - Chair

Introduction

This study integrates biogeography, landscape ecology, and biophysical ecology to examine the interaction between land-use, landscape, and climate, and its implications for grassland herptofauna. I use studies of Wisconsin sand-prairie sites with disjunct populations of ornate box turtles (Terrapene ornata) as a model system to explore how habitat modification, resulting from changing land-use, affects the life history of ectotherms not only in Wisconsin, but throughout the Great Plains. In doing so I address four fundamental questions: 1) Is there latitudinal variation in box turtle response to the thermal environment, 2) if differences exist, are they fixed or phenotypically plastic, 3) what are the biophysical implications of shifting land-use for box turtle populations in Wisconsin, and 4) if shifts in life history resulting from changes in land-use occur, are they an isolated event occurring in disjunct populations at the northern edge of the species' geographical range or indicative of processes occurring across the species range? Simulations of activity potential under current climate and microclimate cooling result from shifting land-use are contrasted with those computed in response to climatic warming scenarios (Rosenzweig 1989, as presented in Gates 1993).

To estimate species response to environmental variation one needs to determine if latitudinal variation in environmental response exists. Studies on latitudinal variation such those by Bevan et al. (1979) on green frogs, Levinton (1983) and Levinton and Monhan (1983) on marine invertebrates, Conover and Present (1990) on fish, and St. Clair et al. (1994) on aquatic turtles support the 'Countergradient' or 'Latitudinal Gradient' hypothesis that predicts local evolution should maximize metabolic efficiency and thus favor maximum growth under local conditions (Levinton 1983). Yet, these studies have not examined the implications of latitudinal variation in physiology, for species life history, under conditions of climatic change. A goal of this work is to determine how latitudinal gradients in thermal preference affect species response to land-use and climate.

The formal link between thermal preference, habitat use, and behavior in essence quantifies the fundamental niche (Hutchinson 1957) in a thermodynamic framework (Magnuson et al. 1979). Work by Adolph and Porter (1993) illustrate how latitudinal variation in the activity potential of the lizard Sceloporus undulatus affects time for growth, activity, and reproduction. Their work demonstrates tradeoffs in increasing activity time with activity periods negatively correlated with annual survival rate and positively correlated with annual fecundity. This suggests that species, through their thermal niche, should adjust local activity periods (thermal niche) to maximize growth and reproduction and minimize mortality. Rapid climate change, or shifts in microclimate resulting from changes in land-use, in altering activity potential is expected to disrupt this balance between reproductive potential and mortality risk leading to declines in some populations and increases in others. Thus an understanding of latitudinal variation in the physiological constraints on species can provide insight into how shifts in land-use and climate will affect species range and distribution.

Methods

The ornate box turtle (Terrapene ornata) is a small terrestrial turtle (±300 g) which in Wisconsin is at the Northeastern edge of a broad geographic range spanning much of the Great Plains (Stebbins 1966). Ornate box turtles are dry prairie and savanna specialists relegated to disjunct patches of prairie and savanna (Vogt 1981). They have been listed as endangered in Wisconsin since 1972 (Vogt 1981). Though considered common throughout the rest of their range there is increasing evidence that collecting and road mortality are leading to population declines (Anderson 1965, New York Times 1994).

The close relationship between microclimate (the thermal environment) and ectotherm growth, activity, and reproduction (Congdon 1989, Grant and Porter 1992, Spotilia et al. 1989, Porter and Tracy 1983) allows one to estimate climatic constraints of population activity, growth, and reproduction (Porter et al. 1973, Porter 1989, Adolph and Porter 1993). Because of their long life span, low adult mortality, and relatively cool thermal preference (Legler 1960, Blair 1976, Gatten 1974, Ellner and Karasov 1992), box turtles are likely to be more resistant to climatic fluctuation making them a relatively conservative indicator of ectotherm response to climate.

In southwestern Wisconsin soils, topography, and even the specific individuals within a population have remained relatively constant over the past forty years, while air photos (Wisconsin Department of Transportation) and my plant community surveys indicate that landscape structure has shifted significantly from open prairie and savanna-like habitats to what I will term degraded habitats dominated by agricultural fields and closed woodlots (Figure 1)(Nuzzo 1985, McCune and Cottam 1985, Curtin In preparation). I define these habitats as degraded because they have ceased to have the structure of native prairie and savanna communities (Curtis 1959). The small size of these habitat remnants, dense undergrowth, and exotic species compositions result lower diversities than existed in native plant associations (Curtis 1959, McCune and Cottam 1985). I hypothesize that these degraded habitats are cooler and less thermally diverse than native plant associations. The relatively rapid shifts in landscape structure and microclimate, besides posing a threat to native species, provide a natural experiment of species response to changes in landscape and microclimate. The examination of disjunct box turtle populations at the northern edge of their range, where they are up against climatic constraints, provides a model system for studying patterns and processes that may be acting on box turtle populations throughout their range.

In addressing the impact of shifting land-use and climate, I have taken a four tiered approach across a hierarchy of scales ranging from laboratory studies of latitudinal variation of thermal constraints, to field studies of the effect of microclimate and habitat alteration on life history, to computer simulations of latitudinal variation in species response to land-use and climate (Table 1).

For laboratory and translocation studies 24 box turtles were collected during road surveys in northern, central, and southern portions of the box turtles' range. To reduce sampling bias which might result from the turtles being habituated to the area, northern animals where not taken from Wisconsin, but where collected in Cherry county in north-western Nebraska, 900 km to the west (latitude 42.17n, longitude 100 37w, elevation 852 m). Turtles from central populations where collected in Chase county in eastern Kansas (latitude 38.22n, longitude 96.33w, elevation 375m). Southern animals where collected south of Norman (latitude 35 13n, longitude 89.23w, elevation 360m) in south-central Oklahoma by Robert St. Clair of the University of Oklahoma, while Texas populations where collected from Witchita and Denton counties in north-central Texas (latitude 33.35n, longitude 98.38n, elevation 310m). All collection locations contained a combination of tall and short-grass prairie. Field studies were conducted in Dane, Iowa, and Sauk counties in south-western Wisconsin 50 to 100 km southwest of Madison (latitude 43.04n, longitude 89.23w, elevation 315m).

Differences in habitat structure (contrasted between plant association types), thermal environment, and body temperature (between the box turtles from different latitudes), were calculated using Superanova^{tm} on a Apple MacIntosh computer. In both single and two-factor ANOVA's the Tukey-Kramer test was used. Turtle habitat preference was estimated using Chi square analysis procedures outlined by White and Garrott (1990). Survival rates for each population were calculated following techniques presented in Heisey and Fuller (1985). From telemetry data, mean daily survival rates were calculated and then expanded by the total number of days in the study (L.B. Keith, pers. comm.). Critical assumptions of the Heisey and Fuller technique is that telemetered animals are assumed to be a random, representative sample of the population, and survival rates are constant among sites and over time.

Turtles were marked by notching marginal scutes of the carapace with a file used the Cagle system (Cagle 1939 as reported in Legler 1960). In this system from a dorsal perspective marginal scutes on the left side are numbered 10 through 10, while those the right are 1 through 10.

In all study populations age structures were determined by counting rings on scutes on the animals' carapace. Long-term studies by Blair (1976) and Legler (1960) verify that this method is reasonably accurate (within 2-3 years) at determining an animals' age during the first 15 to 20 years of life when the animal is still growing. Above age 20, the degree of wear on the shell gives only a general indication of the animals age.

Fecundity was determined by measurement of clutch size prior to laying using X-ray photography (following procedures outlined by Gibbons and Greene 1979) at the University of Wisconsin Veterinary School. In June 1993, a total of 40 box turtles were x-rayed from the eight different habitats sampled. In captivity almost 100% of eggs are viable (Robert Hay, pers.comm.), suggesting that clutch size is a reasonable indicator of fecundity.

When a box turtle was encountered in the field the habitat type and location , individual's identity, activity (moving, eating, basking, inactive, or burrowed-in), were recorded. Air temperature was measured at 5 cm (turtle height), and soil temperature was measured at 1 to 2 cm below the soil surface. The turtle's body temperature was measured cloacally with a quick reading cloacal thermometer (Miller & Weber, Inc. Queens, NY). Thermometers were checked against calibrated digital thermometers (Omega Engineering, Inc. Stamford, Ct.) several times during the field season to ensure consistent measurements (no difference was noted). The use of hand-held thermometers, while perhaps not as accurate as implanted temperature sensitive transmitters, allowed me to sample larger numbers of individuals and enabled direct comparison between my data with those from other studies on ornate box turtles (Blair 1976, Doroff and Keith 1990, Legler 1960). Sampling periods began in the spring a week to ten days before the anticipated emergence of turtles in early April and for ten days to two weeks after the animals went into hibernation in mid-October. During the turtles active season field sites were visited three to five times a week during daylight hours (box turtles are diurnal - Legler 1960).

A) Laboratory studies

I used laboratory studies to determine whether latitudinal differences exist in box turtle response to thermal climate. I asked: 1) do differences in thermal preference exist between populations, and 2) if thermal differences do exist, do they persist after the populations are subjected to the same climate for more than one year in the field. Persistent differences in thermal preference are considered evidence that box turtle behaviors and thermal preferences were fixed and not phenotypically plastic.

After acclimating in the lab for ten days (25° C with 10 hrs. of light) the laboratory thermal preferences of the different turtle populations were determined following procedures used by Gatten (1974) and Ellner and Karasov (1992). Plywood gradient boxes 2m x 0.5 m x 0.5 m, with floors covered with sand (2 cm deep) were placed in a cold room with an ambient temperature of 10° C. Two heating lamps (Sylvania 250 watts) were placed at one end of the gradient box. To ensure consistent illumination, two lights with standard 60 watt bulbs were placed at the opposite end of the box. A thermal gradient from 60 to 10° C was established in the box. Fed animals were placed in the box 90 minutes before measurement. Body temperature (T_b) measurements were taken with a quick measuring cloacal thermometer (Miller & Weber Inc., Queens, NY) at half-hour intervals over a five hour period. The box turtles were large enough that brief handling for temperature readings did not change their T_b, nor were any behavioral changes noticed as a consequence of periodic handling. Body temperature did not differ from previous studies with implanted transmitters by Ellner and Karasov (1992).

Body temperatures were measured in a thermal gradient during mid-day in August 1992 (eight individuals from Nebraska and eight individuals from Kansas populations - equal proportions of males and females), June 1993 (Four adults from Texas populations - two males and two females), and July 1993 (Six adults from Oklahoma populations - three males and three females). A second set of gradient box experiments was conducted in September 1994 with surviving individuals. By this time sample sizes had dropped to six Nebraska, two Kansas, four Oklahoma, and two Texas turtles. Due to these small sample sizes statistical comparisons where only made pair-wise between the six northern turtles from Nebraska and the six southern turtles from Oklahoma and Texas.

The effect of temperature on box turtle growth and thermal preference was also examined in the lab with hatchling box turtles. Starting in September 1993, nine juvenile box turtles (sex could not be accurately determined at this age) hatched from two clutches from the same population of Wisconsin box turtles (from a degraded site in Columbia county 45 km northwest of Madison), were subjected to warm and cool daytime temperatures. The September 1994 the experiment was repeated, in collaboration with Maggie Raczek, with eight hatchlings from the same population. Protocols were the same for both studies.

The hatchling turtles were placed in a 2m x 1m x .25m box divided into eight identical sections. The bottom of each section was covered with five cm of Sphagnum moss which was moistened daily to maintain an environment with close to 100% humidity and cover. Five turtles were kept at one end with a Sylvania heat lamp producing an ambient day-time air temperature similar to that experienced by populations in dry prairie and savanna habitats (28 to 30° C). The other half of the enclosure, with four turtles, was kept at a day-time temperature similar to that of degraded (containing primarily exotic vegetation) habitats (21-22° C). In 1994 four turtles were placed in each treatment. A timer maintained 10 hrs. of daylight in both sections and a divider maintained the thermal difference between the sections. Night time temperatures where 20 to 22° C for animals in both treatments. The animals were fed ad labium a mixture of crickets, red worms, and canned dog food. The turtles were kept in the different microclimates for four months (the equivalent of one growing season) and after the first month weighed every two weeks.

B) Translocation studies

Field enclosures were used to examine how box turtles respond to environmental variation. Specific questions addressed were: 1) is there latitudinal variation in body temperature and behavior between northern, central, and southern box turtles, and 2) do these differences persist after more than one year. If behavioral differences persist for more than one year, this suggests that the differences are fixed and not phenotypically plastic.

The field enclosure was designed to be large enough to allow the turtles to thermoregulate, yet small enough that animals could be easily located without telemetry. In August 1992 a 0.33 ha enclosure was erected out of 60 cm flashing on an east-facing slope on Wisconsin Power and Light Corporation lands near Muscoda, Wisconsin (90 km south-west of Madison). The enclosure was sunk approximately 20 to 35cm into the ground with approximately 10 to 20cm above ground. In April 1993 the enclosure was enlarged by 40% to 0.52 ha to encompass more woods and mesic prairie habitat.

The enclosure was designed to include a diversity of plant assemblages representative of the Great Plains including: oak woods comprised of black oaks (Quercus velutina), sand blows composed of a small dune-like sand area with dry grasses such as needlegrass (Stipa spartea), mesic prairie with dominant grasses big blue stem (Andropogon gerardi) and indian grass (Sorghastrum nutans), and sand prairie comprised of mostly little blue stem (A. scoparius), needlegrass (Stipa spartea), and june grass (Koeleria cristata). Between the sand prairie and mesic prairie was a transitional/dry prairie plant association containing representative species from the other two prairie types. Plant association designations were made following Curtis (1959).

During the growing season (May - October), aspects of plant community structure were measured monthly. During each monthly sample, five measurements were taken at random within each of the five plant communities. Vegetation height was measured with a meter stick. Percentage of open ground was estimated with a 0.25 m^2 gridded square (a 0.25 m^2 square is considered optimal for sampling prairie habitats - Curtis and MacIntosh 1950). Density (stems per 0.25 m^2), and species richness (number of species per 0.25 m^2), were also recorded. General trends in phenology in species composition were recorded during the growing season. During the same monthly sample, ten air and ground temperatures were taken in rapid succession within each plant community to compare thermal differences between plant associations.

In August 1992 16 adult box turtles, eight from Kansas and eight from Nebraska were placed in the enclosure. In the summer of 1993 eight additional animals (four male/four female) from north Texas and southern Oklahoma were placed within the enclosure. To minimize potential behavioral differences in the turtles which might result from recent local weather patterns, turtles were collected during cool periods when there was relatively little temperature variation across the box turtles' range. To ensure that all the populations experienced the same climate before release, turtles where held in the lab (25° C with 10 hours of light) for 10 days prior to being placed in the field.

To make direct comparisons between the behaviors of the box turtles from different latitudes, it is important that the animals be sampled as closely together in time as possible. To assist in rapid identification during field sampling color coded number tags were attached to the rear of the animals. These tags, constructed out of small fishing spoons (Little Cleo^{tm}) with the treble hook removed, were attached with a small snap-swivel to a hole drilled in the turtles' anterior marginal scute. Green spoons were attached to northern animals, orange spoons to central animals, and yellow spoons to southern animals. In addition to speeding up identification the different colored spoons aided in locating animals in the pen.

To ensure equal coverage of all habitat types I sampled the site by walking transects across the enclosure. Transects were walked in different directions so that cover-types were not always sampled in the same order. Examinations of body temperature, behavior, and habitat preference were carried out in consecutive seasons to determine if changes in behavior and thermal preference shifted through time in response to environmental factors. In addition to the late summer and fall of 1992, work was carried out from emergence in April until hibernation in October in both 1993 and 1994. I varied sampling periods to measure turtle behavior at different times of day and under a variety of weather conditions.

C) Field Studies

Field studies were used to examine the thermal preference, behavior, and life history of Wisconsin box turtle populations under a variety of environmental constraints. These studies investigated how shifts in microclimate resulting from changes in land-use affect the life history of ectotherms. Physical models and telemetry studies were used to quantify environmental variation in habitats, and box turtle response, to the changes in plant association structure.

Physical models

The use of replicas of box turtles provided a means to measure the thermal environment as experienced by the turtles (Porter et al. 1973, Bakken 1992). A Beckman DK-2A Spectroreflectometer was used to measure the solar absorptivies of an ornate box turtle shell. The reflectance of 0.812 to 0.816 was similar to measurements by Ellner and Karasov (1992). This absorptivity was compared with those of grey primers (also measured in the Spectroreflectometer), and Krylon^{tm} Dove Grey was found to be within 2% of the reflectivity of an ornate box turtle shell. Absorptivity was calculated based on spectral reflectivity;

absorptivity - reflectivity. Hollow clay replicas of turtles were painted with Krylon^{tm} Dove Grey to match this reflectivity. While metal castings are customarily used for this type of modeling (Porter et al. 1973, Bakken 1992), work by Ellner and Karasov (1992) suggested that hollow copper models warmed and cooled too quickly compared to warming and cooling rates exhibited in adult box turtles. The clay models are not only simpler and cheaper to produce, but appear to accurately approximate box turtle body temperatures. In comparing the temperatures of my clay models with the body temperatures of turtles in the field (N=50), I found the models to be within ±2° C of a live animal. The models were attached by a thermocouple to a digital thermometer (Omega Engineering, Inc. Stamford, Ct.) to get temperatures experienced by the model. The digital thermometer attached to the box turtle models in shade, part-shade (60% shade), part-sun (60% sun), and full sun at ambient temperatures typical of spring and fall (13 to 23° C), and summer (20 to 29° C) (N=50 measurements at each temperature range), were used to measure environmental temperatures (T_e) in old field, woods, and prairie-savanna plant associations. Using two digital thermometers (with four model), I simultaneously measured temperatures in four different micro-habitats (sun, part sun, part shade, and shade) within each plant association. After allowing five minutes for the temperature of the models to equilibrate, temperature measurements where recorded and the models were moved to a new location. These physical models, by providing a lumped index of environmental factors, allow one to make predictions of environmental constraints on animals within different habitat types.

Telemetry

My telemetry studies contrast Wisconsin box turtles in four habitats with differing land-use histories. Maps of presettlement vegetation derived from 1840s surveyor's notes (Finlay 1976), indicate that the study sites were primarily composed of prairie and savanna. The amount of habitat alteration was determined by looking at aerial photos and estimating the amount of cover by woodland, old field, and prairie and savanna-like plant communities.

My study sites were located within 45 km of each other in the Wisconsin river valley in Dane, Iowa, and Sauk counties in south-central Wisconsin. The four areas I studied were roughly four ha in size. The Nature Conservancies' Spring Green preserve contains 90% open dry prairie habitat and is an intensively managed prairie restoration (i.e., frequent burning and clear to maintain the openness of the site). Spring Green east is located at the east end of the Nature Conservancy's Spring Green site and has undergone minimal restoration and is roughly 70% open old field and savanna-like habitat. The Mazomanie Wildlife Area, owned by the Wisconsin Department of Natural Resources, is 40% open dry prairie. In collaboration with Doris Rouche, a land manager for the Wisconsin Department of Natural Resources, in the winter of 1992-1993 this site was burned and cleared leading to 70% cover by open habitats in the second and third years of study. The American Players Theater (APT) study area is under development pressure and has been invaded by woody cover over the past 20 years, leaving roughly 10% of the site as open dry prairie. Plant association identifications where determined according to Curtis (1959).

In addition, Doroff and Keith (1990) studied a population of ornate box turtles on a 8 ha site containing a woodland, agricultural, wetland, and prairie habitat (>10% open), five km south-east of my Mazomanie research site. Starting in 1977 mark-recapture studies were carried out and from 1986-1987 53 radio-marked individuals were intensively monitored during the summer. The severe habitat fragmentation and the degree to which the habitat is closed-in by exotic vegetation make it a useful contrast to my study populations in less degraded habitats. Note that Doroff and Keith's study was done during some of the warmest years on record (1986-1988), while my studies (1992-1994), were done during some of the coolest years on record (U.S. Weather Service). This resulted in monthly average temperatures which were 3 to 5° C cooler in 1993-1994 than in 1986-1988. Because activity periods appear to be linked to ambient temperatures (Curtin in press) the activity periods listed in my studies probably underestimate typical lengths of activity seasons, while those recorded in Doroff and Keith's work may overestimate typical activity season length. Other studies of box turtles at Dunlap Hollow cited in this paper are an examination of the edge effects on box turtle recruitment by Temple (1987), and studies of thermal preference by Ellner and Karasov (1993).

Telemetry allowed me to recapture greater numbers of local animals, and attain a less biased sample of habitat use (White and Garrott 1990). In the summer of 1992, I studied a population of 14 box turtles at the Mazomanie Wildlife Area. Eight turtles carried Wildlife Materials (Carbondale, Ill.) 2160 LD transmitters (150-152 MHz) attached by a snap swivel to a hole in the rear of the carapace and dragged behind the animal. A Telonics TR-2 receiver and TS-1 scanner (Telonics, Inc., Mesa, Az.) with hand-held antenna was used to pick-up the signal.

In the summer of 1993 I monitored a total of 25 turtles at all four sites with radio telemetry (Wildlife Materials transmitters were again used but with most transmitters glued to the carapace to reduce the chance of the transmitters being tangled in vegetation or dropped). This included a total of 10 turtles at Spring Green, four at Spring Green East, eight at Mazomanie, and three at American Players Theater (APT). These telemetry studies were continued in 1994 on 18 turtles: five in the Mazomanie Wildlife Area, ten at Spring Green, and three at Spring Green east. Because of difficulty getting adequate sample sizes in 1993, the American Players Theater was dropped from 1994 studies.

Sites were sampled three to five times a week beginning ten days before anticipated emergence in the spring (early April) and extending ten days after the animals went into hibernation in the fall (mid October). I sampled the sites at different times of the day and under different weather conditions. I did not sample during heavy rain or electrical storms due to risk of damaging the telemetry receiver or personal injury.

Air (T_a) and ground (T_g) temperatures taken when locating a box turtle in sand prairie, tall grass prairie, oak savanna, mixed hardwood, and European grass plant communities resulted in 100^+ measurements per season over three field seasons. These measurements provided a second means of quantifying the box turtles' thermal environment.

Home range sizes were calculated by techniques similar to the minimum convex polygon method (Mohr 1947 as discussed in White and Garrott 1990). Siting locations where plotted on a 1"-400' scale air photo (Wisconsin Department of Transportation 1978). A polygon was drawn around the points and the size of the area was estimated visually from the known scale of the map. Because box turtles tend to have distinct home ranges with little variation year to year (Legler 1960, Blair 1976), this simple approach produced adequate results for estimating box turtle home range.

Census Studies

To determine if demographic patterns, evident in telemetry populations, were widespread I conducted surveys of four additional areas with box turtles in Columbia county (50 km north-east of the telemetry study sites). This work was done in collaboration with Robert Hay and William Moore of the Wisconsin Department of Natural Resource-Bureau of Endangered Resources. Sites were visited at least four times during late April and May and transects were walked across the site. Located animals were marked and released or captured as part of a translocation study (Curtin, Hay, Moore In review).

D) Computer simulations

Using computer simulations of ecotherm response to microclimate developed by Warren Porter and the University of Wisconsin Biophysical Ecology Group (Porter et al. 1973, Porter and Tracy 1983, Porter 1989) I asked the following questions: 1) are patterns of box turtle response to changes in microclimate indicative of ornate box turtles in general or only a reflection of individuals at the northern edge of their range, and 2) are microclimate changes resulting from shifts in land-use, or climate change predicted in Global Circulation Models (Rosenzweig 1989, as presented in Gates 1993), potentially more important in determining the range and distribution of ornate box turtles?

Potential activity seasons were calculated for each geographic area using computer simulations that estimate microclimate and animal body temperature based on heat transfer principals (Adolph and Porter 1993, Porter et al. 1973, Porter and Tracy 1983). These simulations have been validated by field studies over the past 25 years (Porter et al. 1973, Porter and Tracy 1983, Porter 1989), and have been demonstrated to be effective predictors of ectotherm activity.

Simulation locations were Cherry County located in north-central Nebraska (latitude 42.17n, longitude 100 37w, elevation 852 m), Chase County located in east-central Kansas (longitude 38.22n, longitude 96.33w, elevation 375m), and Witchita County located in north-central Texas (latitude 33.35n, longitude 98.38n, elevation 310m). These areas were chosen because: 1) the turtle populations examined in the transplant study had come from these locations, 2) there were nearby weather stations with extensive long-term climatic data, and, 3) the land-use history can be easily determined for these sites.

Three microclimate simulations were run for each location: 1) under current climate 1970 - 1990 Av.(National Weather Service Records), 2) with a 4° C decrease in air temperature as I hypothesize results from shifts in plant community structure resulting from changes in land-use (as suggested by my field studies), and 3) under conditions of global warming (3 - 5° C) using General Circulation Model output (Rosenzwieg 1989 as presented in Gates 1993). Rosenzwieg's model of Great Plains climate indicates climatic change will not lead to consistent climatic warming but instead leads to latitudinal and seasonal variation in climate

(Gates 1993, p. 211-212). This spatial and temporal variation was integrated into my computer simulations.

Monthly average minimum and maximum temperatures were obtained from the United States Weather Service records for the nearest monitoring site to the simulation location. Weather records indicate roughly a 4° C difference between northern and central, and central and southern locations (U.S. Weather Service records 1970 - 1990). The temperature data were adjusted for differences in altitude between simulation locations using the theoretical adiabatic cooling rate of 9.9° C per km altitude (Sutton 1977). Porter (1973) presents a detailed discussion of this model. Solar radiation calculations were based on McCullough and Porter (1971; software program SOLRAD [Porter 1989] available through WISCWARE, University of Wisconsin Academic Computer Center, 1210 W. Dayton St., Madison, Wi. 53706). Except for temperatures, altitudes, and latitudes, all meteorological characteristics (including cloud cover, wind speed, soil thermal properties) were assumed to be equivalent. Parameter values for the simulations are listed in Table 2.

The microclimate simulations estimated soil and air temperature profiles, and radiation, at 1 hour intervals for the 15th day of each month. These data were then used as input to the computer simulations that calculated steady state equilibrium body temperatures (T_b) which could be attained by the box turtles under climatic conditions specified by the microclimate model (Table 2). Data on absorptivity (0.808-0.816) were determined by my measurements and those of Ellner and Karasov (1992) using a Beckman DK-2A Spectroreflectometer (discussed in previous paragraphs). Body sizes, determined from my measurements of Wisconsin, Nebraska, Kansas, Oklahoma, and Texas box turtles, were assumed to be typical of adults throughout the box turtles' range. All physiological parameters remained constant across latitudinal range except thermal preference. Thermal preference, adjusted to correspond to the latitude of simulation location, used thermal gradient temperature data from my gradient box laboratory studies. The computer simulations determined how much time the turtles could have been active on an average day of each month. Daily activity profiles were generated for comparison with existing data and cross-latitude comparisons. Predictions stemming from simulations were compared to my field data presented in this paper and data from Wisconsin (Ellner and Karasov 1992), Kansas (Legler 1960), and Texas (Blair 1976) box turtles.

Egg incubation periods (i.e. reproductive potential) under different climatic and land-use regimes where estimated by: 1) integrating soil temperature profile output from the microclimate portion of the computer simulation, and 2) combining activity season predictions from the ectotherm activity portion of the computer simulation, with 3) laboratory data on the effects of temperature on box turtle egg incubation times (Legler 1960, Packard et al.1985, Hay pers. comm.). The predicted incubation periods where compared against field data by Legler (1960), Doroff and Keith (1990), and my field data (Curtin In press).

Results

A) Laboratory studies

Thermal niche breath (mean thermal preference plus and minus one standard deviation - May and MacArthur 1972, Magnuson et al. 1979), varied between northern and southern turtle populations. Prior to placement in the field a single factor ANOVA indicated significant differences (*P* =<0.01) existed between northern (22.3 C ± 0.4 C SE, N = 8), and southern (25.9 C ± 0.4 C SE, N = 8) populations. Thermal preference of central populations (24.9 C ± 0.5 C SE, N = 8) was also significantly different (*P* = <0.05) from northern, but not southern populations (Figure 2).

After a year in the field a second comparison of thermal preference of turtles from different latitudes was made with a two factor ANOVA. This was done to test if significant differences persisted between turtles from different latitudes and to examine if significant shifts in thermal preference occurred within turtle groups. In 1994, due to small sample sizes resulting from mortality, comparisons where only made between northern and southern populations with significant differences (*P* = <0.01) still existing between northern (23.6 C ± 0.3 C SE, N = 6), and southern turtles (26.4 C ± 0.3 SE, N = 6)(Figure 2). Yet a convergence in thermal preference occurred between northern and southern turtles. While not significant southern thermal preference was 0.4° C cooler in 1994 (*P* = <.07, 25.9° C in 1993 vs. 25.5° C in 1994). The thermal preference of northern turtles was significantly warmer in 1994 (*P* = <.05, 24.0° C in 1993 vs. 22.5° C in 1994).

Comparisons of hatchling turtle thermal preference indicated that after four months of different thermal treatments, the thermal preference of warm treatment animals (20.0 C ± 0.7 SE, N = 30) did not differ significantly from animals in the cool treatment (18.9 C ± 0.5 SE, N = 24) (*P*=<0.7). In 1994, significant differences existed between the warm treatment (21.1° C± 0.5 SE, N = 52) and cool treatment (23.2° C ± 0.5 SE, N = 65) (*P*=<0.5) (note that sample sizes of gradient box measurements were greater in 1994). Growth rates in 1993 varied significantly between populations with animals in the warm treatment attaining almost twice the size of the cool treatment animals (Figure 3). In 1994 growth rates were lower in both treatments and no difference in growth existed between the animals in warm and cool treatments (the turtle food was lower in protein to reduce shell deformities resulting from excessive growth rates).

B) Translocation studies

A single factor ANOVA was used to contrast body temperatures of box turtle populations. Field body temperatures were not significantly different (*P*=<0.07), between northern (28.1° C ± 0.4 SE, N = 6), central (26.7° C ± 0.3 SE, N = 6), and southern (26.5° C ± 0.3 SE, N = 4) populations in 1993. In 1994 significant differences (*P* = ≤0.01) existed between northern (27.0° C ± 0.5 SE, N = 6) and southern (25.3° C ± 0.5 C SE, N = 6) box turtles (Figure 4).

Nebraska animals from roughly the same latitude as Wisconsin had much higher survivorship than transplanted animals from other latitudes. Northern turtles (N=8) ended with 6 individuals remaining after 2.5 years in the field. In the same time period central turtles (N = 8) ended with 2 individuals remaining with heavy mortality in the spring of 1994. Southern turtles (N=6) after two years in the field also ended with two individuals in the field at the end of the study in the fall of 1994. As with central turtles, mortalities were also concentrated in the spring of 1994. There appears to be no age trend in mortalities with all deceased animals middle aged (15 to 25 ±). Two animals in 1993 (one from Nb. and one from Ks.) died from predation, the causes of death of the others is unknown. The increased mortality rates appeared in the spring of 1994 after the animals were in the field more than one season, suggesting the impact of climatic constraints may take time to appear.

In the fall of 1992 both northern and central turtles went into hibernation between October 17 and October 27th. In 1993 and 1994 seasonal activity periods of northern and central animals in extended from mid April through late October (186 days, ± 9). Southern animals were active from late March (N = 6) through early October (189 days, ± 10).

Differences in plant assemblage structure (Table 3) resulted in significant differences in the thermal environments (two factor ANOVA, Tukey-Kramer test *P*=<0.05) between oak woods and grassland habitats and between the sand blows and mesic and transitional prairie (Figure 5). No significant interaction existed between sampling period and temperature of the plant association type indicating differences in thermal environment persist during the entire growing season. Standard deviation of temperature (i.e. variability) differed between the plant associations. Oak woods were the least thermally diverse with a standard temperature variation of 2.5° C. Prairie habitats temperature variation ranged between 3° and 4.5° C and sand blows thermal variation was 6° C. This thermal variation was anticipated to be important for box turtles (and other ectotherms) by allowing the turtles to expend their activity periods increasing time for activity, growth, and reproduction. Turtles are expected to select more diverse thermal environments, especially in the spring when the availability of suitable microclimates is limited.

During the cool season the warm mesic prairie and sand blow habitats saw disproportional use by box turtles, while transitional/dry prairie and cooler woods habitats were avoided. In the warm season the more thermally diverse mesic prairie and cooler woods saw disproportional use while hot dry and sand prairie and sand blow habitats were avoided. In the summer the activity areas shifted to greater use of the cooler woods and mesic prairie habitats (figure 6a). Chi-square analysis indicated significant differences (<0.05) between observed and expected habitat use in all but sand prairie communities (Figure 6b) (a arcsine transformation was not conducted because these values represent both percentages and actual numbers).

The proportion of northern animals active was significantly greater in northern than central or southern box turtles (single factor ANOVA $P = <0.01$) (a transformation was not conducted because these values represent both percentages and actual numbers, N = 100). While the proportion of each group of turtles active followed a latitudinal gradient in both 1993 and 1994 (Figure 7), the total length of active season did not differ between populations. In 1992 Nebraska and Kansas animals went into hibernation in mid to late October and both emerged in the spring of 1993 during the third week of April. All populations went into hibernation during the third week of October 1993, emerged during the first week of April 1994, and went into hibernation in mid October 1994 .

In 1993 and 1994 the morning air temperatures from 7:00 to 10:00 HRS averaged 21.0° C (20.9° C ± .3 SE, N=10), late morning/early afternoon air temperatures from 10:00 to 13:00 hrs averaged 23.0° C (22.9° C ± .4 SE, N=10), while afternoon air temperatures were 25.0° C (24.7° C ± .4 SE, N=10). A two factor ANOVA indicated that significant interaction effects existed in the proportion of southern and northern animals active in the morning (*P* = <0.05), but not mid day or late afternoon (Figure 8). These differences persisted over the box turtles entire active season in both 1993 and 1994 .

C) Field Studies

The structure of the plant communities varied between native and exotic plant associations (Table 4), affecting the temperatures of these habitats. Native plant associations were warmer than exotic plant associations (single factor ANOVA, *P*=<0.01)(figure 9).

Measurements taken with clay models of box turtles in agricultural, woods, and prairie and savanna habitats illustrate that native plant associations are not only warmer, but are more thermally diverse than exotic plant associations. These differences were particularly evident in the spring and fall. Exotic plant associations can limit cool season activity while not conferring any advantages during the warm season. In contrast, native plant associations' temperature allows for sustained activity during the spring, summer, and fall (Figure 10).

Telemetry data from the Mazomanie Wildlife Area indicate that box turtles differentially select warmer sites, particularly during the cool season (Figure 11a). Similar results exist for studies from Dunlap Hollow (Doroff and Keith 1990). At the Mazomanie site almost all cool season activity is concentrated in the 0.5 ha area of south-east facing sand prairie. Summer activity was spread across a variety of habitat types still primarily concentrated in native plant associations (Figure 11a). After clearing in the winter of 1992-1993 animals shifted their habitat usage to increased activity in the warmer prairie-like burned old-field area (Figure 11b), suggesting that box turtles are capable of responding to shifts in their thermal environment.

Turtles at the Mazomanie site were active from early April through early October (1992 - 1994 Ave. 177, ± 7 days). At Spring Green and Spring Green East animals were also active from early April through early October (1993-1994 Ave. 179, ± 10 days). Reliable activity estimates do not exist for the APT site. In 1992 survivorship at Mazomanie was 0.91 (N=8). In 1993 survivorship was 0.91 at all sites including Mazomanie (N = 8), Spring Green (N = 8), Spring Green East (N=4), and APT (N = 3). In 1994 survivorship was 1.0 at all sites including Mazomanie (N = 5), Spring Green (N = 8), and Spring Green East (N = 3).

My measurements of a south-facing nest in sand had a mid-day temperature of 29° C (N=8) which resulted in a 61 day incubation period (Curtin, In press). This is corroborated by laboratory studies. Legler (1960) found at a temperature of 33° C a mean incubation period was 59 days; at 28° C, 70 days; and at 24° C, 125 days. Work by Packard et al. (1985) had a similar result with laboratory incubation times at 29.0° C lasting 51 to 55 days (N=28). While work by Robert Hay (per. comm.) indicated that the incubation times of eggs held at 26° C (N=14) averaged 63 days (± 3 days). Though a trend exists in clutch size with decreasing number in cooler habitats (i.e. number of eggs), there was no significant difference between sites (Curtin, In press). The age structure of turtles in degraded sites indicates little or no recruitment is occurring in these habitats (Table 5). Home range sizes in my study sites averaged 2.4 ha and ranged between .8 and 4 ha.

D) Computer simulations

Contrasts of simulation predictions with my field observations from the Wisconsin enclosure study, and contrasts with field data from studies in Kansas (Legler 1960), and Texas (Blair 1976) indicate a high degree of similarity between calculated and recorded activity season lengths(Figure 12). The relatively lower percentages of central and southern animals recorded as active is probably a reflection of these studies having not been done with telemetry and should not be considered indicative of biological differences between turtles from different latitudes.

I compared observed and calculated activity patterns predicted from simulations, with data from 1992 - 1994 of Nebraska box turtle activity periods in the Wisconsin field enclosure. In figure 13a the calculated time available for activity (contour plot), and recorded activity periods (represented by dots) are contrasted demonstrating that the computer simulation is able to estimate daily activity periods with reasonable effectiveness. In figure 13b predicted and recorded daily hours of activity are contrasted across the active season again showing a close relationship between predicted and observed values. Because the simulations are derived from 1970 - 1990 weather averages one would not expect an exact correspondence between observed and estimated activity for any given year. In addition, because the simulations are set to estimate the maximum time available for activity they will overestimate actual activity times recorded in the field. For example, the simulations recorded that the average weather conditions in March could potentially allow turtle activity, even though none was recorded during that time period.

Comparisons of total hours of activity time under current climate verses microclimate cooling, indicate a moderate loss of activity time for northern and central populations and a net gain in activity periods for southern populations (Figure 14a). Comparisons of simulation output from current climate and warmer climates resulting from predicted global warming (Rosenzweig 1989 as presented in Gates 1993), indicate a moderate loss of activity time for northern and central populations, and a large drop in activity potential for southern populations (Figure 14b). In contrasting activity potential under both scenarios of climate change northern and central populations are demonstrated to have identical losses of overall activity time under either scenario. Southern animals are calculated to have either a large net gain, or large net loss in potential activity time (Figure 14c).

Simulation output indicates that a cooling in microclimate, which I demonstrated can result from shifts in plant association structure, results in a loss of: March and October activity periods in northern populations; March, October, and November activity periods in central populations; and no reduction in the length of activity periods in southern populations (Figure 15). Northern and central populations experienced a net loss in time for activity, growth, and reproduction with large losses in cool season activity offset slightly by increases in mid-summer activity potential (Figure 15a and 15b). Egg incubation periods are expected to be pushed later in the summer and are estimated to increase from 65 to 80 days as a result of changes in microclimate (as discussed in previous section). This would result in the almost complete cessation of successful reproduction in degraded sites as indicated by Wisconsin field studies (Doroff and Keith 1990). In Kansas, there is expected to be a 7 to 10 day delay of nesting. There would also be an increase in incubation period that is expected result in a loss of the second clutch and may often reduce the success of the first clutch (Figure 15b). Southern populations experience a net gain in time for activity with no losses during the cool season and gain in potential activity periods during the summer months (Figure 15c). The reproductive potential of the southern animals appears to be unaffected (Figure 15c). This shift in reproductive success is expected to lead to declines in northern and central populations, with no change in the reproductive success of southern populations.

Under conditions of climatic warming predicted by Global Circulation Models (Rosenzweig 1989 as presented in Gates 1993) the winners and losers shift (Figure 16). Northern populations appear to experience climates, activity periods, and reproductive potentials similar to those reported for Kansas populations (Legler 1960)(Figure 16a). This could lead to net gains in northern population sizes. While central populations loose some late-summer activity potential, this does not lead to a predictable lose of reproductive potential (Figure 16b). Southern populations show a large drop in late summer activity potential (Figure 16c).

Discussion

Since Darwin's time biologists have addressed the problem of what limits species' range and distribution (Wallace 1876). Early in this century studies of geographic variation in species response to the environment laid the foundations of modern ecology, leading to the development of the niche concept (Grinnell 1917). The past 20 years have seen a renewed interest in biogeography (MacArthur 1972, Brown and Gibson 1983, Hengeveld 1990), with recent studies examining the physiological constraints climate places on growth, activity, and reproduction (Porter and Tracy 1983, Adolph and Porter 1993), and how climatological variables limit species distribution (Root 1988a, 1988b). My work applies the n-dimensional niche concept (Hutchinson 1957) to species thermal preferences (Magnuson et al. 1979) to integrate physiological and behavioral constraints on box turtles with landscape, climate and microclimate variables to examine how ectotherms are effected by changes in land-use and climate (Table 6).

Latitudinal variation in ornate box turtle response to microclimate

Gould and Johnson (1972) state: "The foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the verification of predictions made about it." Yet few studies have directly addressed the implications of geographic variation in species response to the environment (See Garland and Adolph 1991 for a recent literature review).

Ellner and Karasov (1993) in contrasting data from box turtles at Dunlop Hollow (five km south of my Mazomanie study site), with gradient box data collected on Kansas box turtles (Gatten 1974), found significant differences in the thermal preferences of the two groups which they attributed to latitudinal variation. What was not know was whether these differences in thermal preference were genetically predetermined or phynotypically plastic. My studies were designed to determine, through direct comparison of animals from different geographic areas, if latitudinal differences occurred in the box turtles' thermal preference, and if differences occurred were they labile or fixed.

Physiological adaptation to latitudinal variation in climate has been classified into three distinct types: 1) Labile compensation where individuals differ physiologically due to local acclimatization with physiological differences reversible after a period in the laboratory or when populations are subjected to similar climate treatments, 2) irreversible non-genetic compensation where field conditions induce irreversible physiological changes in the organisms, and 3) genetically-based physiological differences (Levinton 1983). While without multigeneration common garden experiments it not possible to determine if physiological differences are genetic or phynotypically plastic, my multi-season contrasts of the box turtles do provide insight into the nature of ornate box turtle thermal preference. The convergence in thermal preference of northern and southern animals suggests that these are somewhat labile. The divergent thermal preferences of hatchling box turtles after being exposed to different thermal environments is further evidence that thermal preferences are labile. Thus the convergence of the thermal preference of adult turtles experiencing the same climate and divergence of the hatchling turtles experiencing different climate demonstrates that ornate box turtles can adjust their thermal preference.

The ability of reptiles to adjust their thermal biology is not an uncommon phenomena. Christian and Bedford (1995) measured seasonal differences in thermal preferences in Australia Frillneck lizards and found a shift in thermal preference, apparently in response to seasonal temperature fluctuations. In reviewing the literature Christian and Bedford found 17 examples of seasonal shifts in field thermal preference for a range of different lizard species. The problem with field data (Hertz et. al 1993), as elegantly demonstrated by Heath (1964), it is hard to determine what is active thermoregulation and what is a reflection of the thermal environment. Of the 20 studies reviewed by Christian and Bedford only seven reviewed thermal preference in the laboratory (McGinnis 1966, Mayhew 1963, Mayhew and Weintruab

1971, Case 1976, Huey and Pianka 1977, and Peterson and Davies 1978, Van Damme et al. 1987). Three of the seven did not exhibit a seasonal laboratory shift in thermal preference suggesting that while this pattern is common, it is not pervasive.

At the same time because significant differences in thermal preference persisted after a year in the field these differences are not completely labile. Differences in thermal niche and activity indicate that significant, non-reversible differences exist between box turtles from different latitudes. Van Damme et al. (1989) recorded similar altitudinal variation in the thermal preference of the lizard Podarcis tiliguerta in Belgium. As had Hertz and Huey (1981) who found compensation for altitudinal changes by Anolis lizards on Hispiola. Tsuji (1988) recorded seasonal adjustments in metabolic rates of Sceloporus occidentalis in the western United States in response to latitudinal gradients. Yet, Sinervo (1990) conducted perhaps the only common garden, muti-generational study which demonstrated genetic differences in thermal physiology of reptiles in studies of the lizard Sceloporus occidentalis. Thus while differences in thermal physiology have been recorded between reptile populations, the extent to which these patterns are fixed or labile has rarely been completely determined.

The significantly cooler fundamental thermal niche (Huchinson 1957, Magnuson et al. 1979) displayed in the laboratory thermal gradient by northern box turtles as compared with central and southern populations (Figure 2), apparently lead to the opposite response to the thermal environment in the field with northern animals realized thermal niche (Hutchinson 1957, Magnuson 1979) actually resulting in these animals having higher average body temperatures (Figure 4). The contrast of field and lab thermal preferences suggest that the fundamental thermal niche (observed in the lab), rather than extending activity periods and increasing body temperatures (in the field), can actually reduce activity potential. This counter-intuitive result can be understood by looking at the distribution of activity of the different groups of turtles in relation to temperature (Figures 7 and 8). Northern turtles, because of their lower thermal preference are able to be out and active earlier in the morning than their more southerly counterparts. This results in northern populations being active longer and remaining warmer on average. Due to their dark shell coloration and relatively low thermal preference, all the box turtles reach the upper end of their preferred temperature range relatively quickly during the heat of the day and have to retreat to cover. This means that a warmer thermal preference exhibited by southern populations does not extend activity during the mid-day, or warm season, yet reduces cool season opportunities. This suggests a divergence in thermal strategy between northern and southern box turtles.

The thermal preference of northern animals apparently maximizes activity throughout their relatively short growing season. Because of the longer growing season and warmer temperatures the marginal benefit of extending cool period (both daily and seasonal) activity periods is minimal in southern populations. Particularly important is the maximization of time for activity and reproduction in the spring. Studies of ornate box turtles at the northern edge of their range indicate that because it takes 60 to 70 days for the eggs to hatch (Doroff and Keith 1990, Curtin In press), a delay in spring nesting will compromise the ability of the eggs to hatch prior to fall. Southern box turtles may be under different selective pressures because time for reproduction does not appear to be a limiting factor (one-third of southern populations hatch two clutches during the active season - Legler 1960).

Increases in activity time represent a trade-off in cost and benefits: increases in time for feeding, growth, activity, and reproduction are achieved at the expense of increased predation risk (Adolph and Porter 1993). If one assumes predation pressure is consistent across latitude, then box turtle thermal preference should have evolved to produce consistent optimal yearly activity periods across latitude which maximize feeding, activity, growth, and reproduction and minimize mortality. Evidence for this would be different daily activity periods which, adjusted for varying season lengths at different latitudes, result in a similar total hours of activity per season by populations at different latitudes. Using average daily activity estimates by Ellner and Karasov (1993)(9.7 hours a day in northern population vs. 7.6 hours a day in southern populations), the calculated total yearly hours of activity for the five month activity period typical in Kansas (Legler 1960), and the four month activity period typically experienced in Wisconsin (Curtin, In press), show remarkably similar yearly activity hour totals (1,169 in Wi. vs. 1140 in Ks.). This suggests that thermal niches, in addition to expanding or contracting daily activity, may serve to adjust yearly activity to optimize life history characters under different climatic constraints. Under this scenario populations at the northern edge of the species ranges should have evolved a thermal preference which maximizes activity relative to populations from the southern and central regions. Because central and southern turtles with relatively longer growing seasons already have enough time for one and often two clutches of eggs (Legler 1960), these populations thermal preferences may actually serve to reduce activity times, and the associated mortality risks, beyond that necessary for reproduction.

Other studies provide evidence for counter gradient variation in thermal preference in turtles. Work on painted turtles (Chrysemys picta) and false map turtles (Graptemys phseudogeographica) (Bull 1983), indicated that southern populations have a lower thermal threshold. Studies by Ellner and Karasov (1993) on ornate box turtles, indicated a broader thermal preference in Wisconsin compared to Kansas box turtles, suggesting different thermal constraints in northern populations which can potentially expand activity periods. Work by St. Clair et al. (1994) in contrasts of northern and southern painted turtles recorded faster annual growth in northern than southern populations (potentially a result of longer activity periods). Northern turtles also showed delayed maturity so that adult northern turtles were older and larger than their southern counterparts. Because northern painted turtles (like the box turtles I studied), are restricted to one clutch per season compared with several in the south the delayed maturity and larger size at adult-hood was thought to promote relatively larger clutch sizes which the authors hypothesized were necessary to compensate for fewer clutches. My studies of box turtles (Curtin, In press) show no such increase in clutch size at northern latitudes.

The divergence in thermal strategy exhibited by the box turtles, as predicted by the latitudinal compensation hypothesis, has primarily been studied with marine or aquatic organisms (Bervan et al. 1979, Levinton 1983, Levinton and Monahan 1983, and Conover and Present 1990, St. Clair et al. 1994). My studies of the box turtles are one of the first records of latitudinal compensation in terrestrial vertebrates. Hertz and Huey (1981) recorded compensation in habitat use and basking behavior of Anolis lizards, across and elevational gradient, on Hispaniola. Yet these studies did not control for environmental factors by conducting both field and laboratory measurements of thermal preference (Hertz et al. 1993). My studies suggest that populations balance tradeoffs associated with increases in activity. Indicating that an understanding of latitudinal compensation is crucial to interpreting how populations at different latitudes will response to variation in land-use and climate.

Impacts of shifting land-use on landscape structure and microclimate

There is a well developed literature discussing the impacts of habitat fragmentation on native species (Wilcox 1980, Ambuel and Temple 1983, Soule et al. 1988, Bolger et al. 1991, Robinson et al. 1992). What has received little attention are changes in landscape structure operating at a scale between hectares and square meters (within patch changes in structure and composition). This is surprising when one consideres that the impact of the physical environment on landscape and community structure was recognized at the turn of the century (Cowles 1899). Grinnell (1917) in developing the niche concept states: "The California Thrasher is unquestionably delimited in its range in ultimate analysis by temperature conditions." Illustrating that the niche concept was originally a measure of the physiological and environmental limitations on a species and only later did Gause and Elton link the niche concept with competition and interspecific interactions (Real and Levin 1991).

In 1920s microclimate and the physical environment continued to be cited as a major factor structure ecological communities (Cooper 1923). Later, in studies using direct gradient analysis, Whitaker (1956, 1960) correlated plant community structure with local climatic and environmental factors. While recent botanical studies have examined species response to environmental gradients (Austin 1987). These studies have predominately focused on tropical systems (Bazzaz and Pickett 1980, Kaspari 1994, Belsky and Canham 1994). Studies examining changes in microclimate resulting from changes in land-use have primarily focused on the edge effects of forestry (Chen et al. 1993, Harrington at al. 1994, Valigura and Messina 1994, Chen et al. 1995), and have not linked landscape pattern with microclimate to assess population viability and community structure.

The heterogeneous structure of native plant communities illustrated in tables 3 and 4 lead to greater thermal diversity allowing box turtles greater activity times (Figure 10). The warm microclimates of the sandy areas and dry prairie apparently are critical habitat during the cooler months while mesic prairie and woods appear to provide thermal cover during summer months (Figures 5, 6, 9, 10, 11). This suggests that prairie and savanna thermal structure are critical in providing the landscape diversity necessary for allowing the box turtles to carryout their life history.

The land-use history of Wisconsin illustrates how relatively subtle shifts in land-use can profoundly alter landscape structure and species habitat availability. After European settlement, fire was eliminated by plowing, grazing, and the construction of roads and railroads, all of which formed functional firebreaks (Dix 1959, Curtis 1959). In the 1830s, with the cessation of the natural fire regime, pine barrens, bush prairies, and oak savanna attained closed canopies, eliminating light-dependent prairie species from the ground layer. Many of southern Wisconsin's present forests date from this period (Cottam 1949, Curtis 1959). These initial changes in vegetation were relatively temporary, as farming radically altered the landscape. After the failure of wheat crops in the 1880's, southern Wisconsin's agriculture shifted to a livestock economy (Dix 1959), which continues until the present.

In the absence of historical disturbance such as fire, surrogate disturbances like grazing appear to have replaced presettlement disturbance patterns in maintaining many grassland and savanna communities (Dix 1959, Nuzzo 1985, Milchunas et al. 1988, Milchunas and Lauenroth 1993). Following the loss of disturbances, such as grazing, open prairie and savanna-like habitats can quickly become choked with weeds or exotic grasses or forests with dense understories (Curtis 1959, Dix 1959, McCune and Cottam 1985, Potvin and Harrison 1984). Since a decrease of large-scale grazing starting in the 1940s, a dramatic closing of the forest has occurred in Wisconsin with open, savanna-like habitats attaining dense understories dominated by exotics like buckthorn (Ramnus Spp), honeysuckle (Lonicera tatarica and L. morrowi), barberry (Berberis vulgaris), and native blackberries and saplings (Curtis 1959, McCune and Cottam 1985). By comparing a map of long-term changes in land-use in Cadiz Township in Green county, Wisconsin (Curtis 1956) , with current air photos and surveys on the ground, I found that while the extent of remaining forest area has changed little since the 1950s, the characteristics of the forest cover had been significantly altered (Curtin, In preparation). In the early 1950s, Curtis (1956) recorded grazing in 77 percent of the woodlots, indicating that the majority of the woodlots had open savanna-like qualities. My observations in the fall of 1991 indicated only 11 percent of all woodlots were grazed resulting in an almost 70 percent decrease in the amount of open, savanna-like habitat within the township. This is not an isolated example; in Vermont township in Dane County, Wisconsin, almost all forests have attained dense understories since the late 1960s as woodlot grazing has been eliminated (Authors observations, air photos, photographs). Open meadows and savanna-like open oak forests, until twenty-five years ago the prevalent plant association type, are now almost nonexistent.

This extreme shift in within patch landscape structure should have a dramatic affect on landscape microclimates. My studies illustrate that a loss of disturbance factors can result in a 3 - 5° C cooling in the landscape as cooler and less heterogeneous exotic plant associations replace prairie and savanna-like plant assemblages (Figures 1, 5, 9, 10). These affects of shifts in grazing regime are not limited to the eastern edge of the plains. In Arapaho Prairie in Arthur County, Nebraska (900 km west of Wisconsin) significant, widespread shifts in vegetation composition were recorded since cattle were removed from the site in 1976 (Potvin and Harrison 1984). Dense grass areas gradually increased and open sandy areas were revegetated. My measurements of Arapoho Prairie microclimate in August 1994 using the clay replicas of box turtles used in the Wisconsin studies, and copper models of racerunner lizards (Cnemidophorus sexlineatus), attached to a Campbell 21x data logger for 10 days also recorded a 3 to 5° C difference in microclimate between dense grass and open sand-prairie habitats (Curtin, unpublished). Fahnestock and Knapp (1993) found similar differences in tallgrass prairie in Kansas grazed by bison suggesting that presettlement grazing by native species had similar affects on landscape microclimate. The results of these studies indicate that the structural and thermal differences between Great Plains habitats experiencing different land-uses are widespread and pervasive.

Biophysical implications of shifting land-use

A cooling in microclimate is shown to effect box turtle life history in three ways: 1) a reduction in time for activity and growth, 2) reproduction through delay in spring emergence and a shortening of fall activity periods, and 3) a lengthening of egg incubation periods.

In the previous section I illustrated how changes in plant community structure can result in cooler, more homogeneous microclimates. Spring emergence was correlated with an inversion in soil temperature profile and a 7° C + deep soil temperature (Curtin in press). This is comparable to results of studies in Missouri by Grobman (1990) in which spring emergence over seven years was correlated with five days of subsoil (10-20 cm) temperatures of 7° C or higher. Fall hibernation was less directly correlated with air temperature and appearing to also be associated with insect prey availability (Curtin in press). This indicates that cooler thermal environments should reduce activity periods.

Comparisons of seasonal activity periods from Doroff and Keith's (1990) studies in the severely degraded Dunlap Hollow (1986 and 1987 average 155, ± 8 days) and my study site at Mazomanie (1992 through 1994 average 177, ± 7 days) suggest a three week difference in minimum yearly activity between the two sites. Studies by Legler (1960) indicate populations at the center of the species range in Kansas had yearly activity periods of 186 days, suggesting that total yearly activity periods available to turtles at Mazomanie has more in common with populations in Kansas (600 km to the south), than to Dunlap Hollow (5 km to the southeast).

A delay in spring emergence appears to affect the timing of egg laying and incubation periods. The cooler microclimates resulting from changes in landscape structure (Table 4) lead to cooler, less thermally diverse microclimates (Figures 1, 9, 10). A cooling in the microclimate results in reduced growth rates (Figure 3), which presumably delays adulthood and reduces overall reproductive output.

Turtles in degraded habitats in Wisconsin typically emerged in late April or early May and laid clutches later in June than turtles in less degraded sites (Doroff and Keith 1990). Field studies in Wisconsin (Doroff and Keith 1990) in degraded habitats indicate a 22.3° C (N=3) June, 26.3° C July (N=11), and 27.6° C August (N=5) mid-day temperature in the nests which resulted in a 79 - 81 day incubation period (N=4) for box turtle clutches in degraded habitats. Nest temperatures in Doroff and Keith's study did not differ significantly ($t = 1.02$, $p = 0.32$) from air temperatures recorded concomitantly at ground level. This indicates that a knowledge of habitat air temperatures is sufficient to make reasonably accurate estimates of incubation times in different habitats.

A delay in nesting combined with longer incubation times apparently can compromise reproduction by not allowing developing animals to hatch before fall. Laboratory studies by Legler (1960) Packard et al. (1985), Hay (pers. comm.), and field studies by Doroff and Keith (1990), and my own observations from the Mazomanie study site, demonstrate that a cooling in microclimate can delay laying and increase incubation times by ± 20 days. Turtles in the severely disturbed sites in Dunlap Hollow, even in warm years, did not hatch before fall and often suffered winter-kill (Doroff and Keith 1990). This, combined with increased nest predation in these fragmented sites (Temple 1987), appears to lead to skewed age structure indicative of low levels of recruitment (Table 5).

Habitat degradation appears to increase adult mortality as turtles shuttle increasingly larger distances between habitat remnants. In the degraded Dunlap Hollow site (Doroff and Keith 1990) home range sizes (8.7 ha) were almost four times those typically recorded for ornate box turtles (2.5 ha)(Legler 1960, Blair 1976). Larger home range sizes should increase the likelihood of encounters with people which are a major cause of mortality for adult box turtles (Anderson 1965, Blair 1976, Doroff and Keith 1990, Legler 1960). Estimates by Doroff and Keith (1990), and work on Blandings turtles by Congdon et al. (1993), suggest that an adult survivorship of at least 0.91 is necessary for populations of long-lived, slow reproducing animals, such as box turtles, to persist. Telemetry studies of my four research sites suggest adult survivorship in populations experiencing only moderate degradation was adequate to sustain the populations. Yet as was pointed out by Congdon et al. (1993), a monitoring period of more than three years is necessary to get a complete picture of adult survival. In contrast, Doroff and Keith (1990) estimate, from 10 years of census data, that the populations at Dunlap Hollow where not viable with adult survival rates of 0.81. The predicted loss of Dunlap Hollow's box turtles has become a reality. The large populations (over 50 individuals), which existed in Dunlap Hollow in the mid-1980s, appear to be all but gone (Keith pers. comm.).

The preceding studies demonstrate that changes in microclimate resulting from shifts in and-use, in reducing recruitment and adult survivorship, can lead to a redistribution of source and sink populations across the landscape. In Wisconsin, changes in within patch microclimate resulting from reduction in widespread grazing, which apparently mimicked fire in these disturbance adapted systems, apparently is leading to the decline of ornate box turtles and probably affects other plains ectotherms.As with microclimate and landscape structure, the patterns and process noted in my Wisconsin box turtle studies have also been recorded in other parts of the Great Plains.Studies of the three species of lizard on Arapaho Prairie in Arthur County, Nebraska, *Sceloporus undulatus*, *Holbrookia maculata*, and *Cnemidophorus sexlineatus* (Ballinger and Jones 1985) indicated the lizards prefer more sparsely vegetated, disturbed areas. As illustrated by my Wisconsin box turtle studies (and my own measurements discussed in the previous section), these areas with a warmer, more heterogeneous microclimate should expand the lizards time available for growth, activity, and reproduction. A decrease in these disturbed habitats resulted in corresponding declines in lizard density and diversity from 1978 to 1983 with populations of *Sceloporus* and *Holbrookia maculata* steadily decreasing in ungrazed mark-recapture areas (Ballinger and Jones 1985).Trends in species composition in disturbed areas also held for invertebrate species. Thirty-eight species of grasshoppers grouped into four subfamilies were collected at Arapaho Prairie with clear differences existing between the disturbed (grazed) and undisturbed (ungrazed) sites (Joern 1982). With the loss of the grazing regime, there was an increase in the relative abundance of *Melsanoplines* and decrease in *Gomphocerines*. *Trimerotropis citrina* which inhabit disturbed sand blow areas and was common the prairie prior to cessation of grazing, disappeared from the site. In general, much higher densities of grasshoppers existed in disturbed than undisturbed vegetation areas with grasshopper densities overall falling following the cessation of grazing (Joern 1982). The study suggests that as with vertebrates, invertebrates also are affected by shifts in microclimate resulting from loss or modification of surrogate disturbance regimes.

Affects of climate and microclimate change on box turtle range and distribution

Studies of the effects of macro scale climate change on species have been a major research priority over the last decade (Peters and Lovejoy 1992, Gates 1993, Kareiva et al. 1993). Yet large-scale climatic models are rarely directly linked with ecological studies. This has resulted in a gap between large scale climate simulations and an understanding of the ramifications of climatic shifts for local species populations (Root and Schneider 1993). Biophysical models of ectotherm response to the thermal environment (Porter et al. 1973, Porter and Tracy 1983, Porter 1989) can serve an important role in linking large scale climatic patterns to local climate and species life history (Porter and Tracy 1983, Grant and Porter 1992, Adolph and Porter 1993).

My computer simulations of box turtle response to shifting land-use and climate address how changes in microclimate affect yearly activity periods, survivorship, reproduction, and egg incubation time (Porter and Tracy 1983, Adolph and Porter 1993). These life history parameters, estimated with the output of the computer simulations, are used to predict how ornate box turtles respond to changes in land-use and climate across their latitudinal range.

Simulation output was compared with my field data from the Wisconsin enclosure study, and field data from Kansas (Legler 1960), and Texas (Blair 1976)(Figure 12). The estimates of activity potential based on assumptions of clear weather overestimated spring and fall activity periods, however they still succeeded in characterizing the general patterns of seasonal activity exhibited by northern, central, and southern turtles. At a finer resolution, I compared observed and calculated daily activity patterns predicted from simulations, with data from 1992 - 1994 of Nebraska box turtle activity periods in the Wisconsin field enclosure (Figure 13). The simulations bound the problem by predicting the maximum potential activity time. They thus overestimate actual activity periods seen by Nebraska box turtles in Wisconsin. Yet the model succeeded in capturing the general activity patterns of box turtles in northern latitudes. These results: 1) reaffirm the usefulness of the model as a tool for predicting ectotherm activity periods, and 2) provide additional support for the premise that thermal constraints can affect species life history.

The redistribution in microclimate can have implications for the reproductive potential and population viability of ectotherms (Adolph and Porter 1993). For example, the climatic shift experienced by central and southern box turtles when relocated to the enclosure in Wisconsin (4 - 5° C - U. S. Weather Service Records 1970 - 1990), is comparable to that which can result from changes in land-use (Figure 10). Field studies within the Wisconsin enclosure indicate that mortality rates where higher in southern and central than northern populations. While two of the individuals where lost by predation. Most of the mortality occurred from unknown causes during the cool season after hibernation in the spring. This suggests that central and southern animals experience greater stress from cool climates than northern turtles. Indicating that turtles from central and southern locations may be more sensitive to microclimate alteration than their northern counterparts. That microclimate cooling alone, in addition to reducing time for activity, growth, and reproduction, may lead to increased mortality rates and eventually population decline in central and southern populations.

Work by Root (1988a, 1988b) illustrates how climate can shape the distribution and abundance of species, with the northern limits of North American bird species often coinciding with isoclines in mean January temperatures, duration of frost free period, and vegetation composition, while western and eastern range limits were correlated with annual precipitation and vegetation. This suggests that the core of species range is composed of populations which are evolutionary stable in relation to climate (Weins 1989, p. 243). Around this core area climatic variation should lead to instability in populations. Dry periods may contract western distributions while wet periods contract eastern distributions. Northern populations contract during cool and expand during warm periods while southern populations decline during warm periods and expand during cool periods. This approach is in essence a biophysical extension of the 'general biogeographical rule' (Hengeveld and Haeck 1982), that species densities should be highest in the central portion of a species range and decrease toward the periphery as has been generally accepted since proposed by Grinnell (1922). This is a basic prediction of Brown's (1984) 'general theory' of species distributions comprising the 'Central Limit Theorem' which predicts that ecological conditions should be most favorable for species (and that they would have the highest densities) in one area, and that densities should decrease with increasing distance in any direction from that location. This suggests that climatic change will result in a shift with the entire range moving in response to climatic variation. The computer simulations verify the assumption that climate change predicted from Global Circulation Models will result in a unified shift in species distribution.

The impacts of microclimate cooling, as I have demonstrated can result from within patch changes in plant association structure (Figure 15), do not appear result in the shift in species range suggested by simulations of climatic warming (Figure 16). Instead, they impose costs on northern and central populations in the form of additional constraints on activity and reproductive output, while not conferring any advantages to southern populations. This indicates that microclimate cooling resulting from shifts in land-use, in addition to affecting peripheral populations at the fringe of the species range, could potentially threaten the entire species by reducing populations in the core of their range.

In summary, while this study has not studied actual land-use patterns which exist in the Great Plains and thus cannot make estimates of box turtle viability beyond study populations in Wisconsin. The results strongly suggest that conservationists and land managers need to look beyond the intensive management of isolated remnants of native habitat and work to establish land-uses that are more compatible with the historical disturbance regimes of the landscape. While not necessarily protecting the community composition and diversity of native habitats in the landscape matrix between intensively managed preserve areas, the maintenance of surrogate disturbances, which maintain the thermal integrity of the landscape, may be critical to the long-term protection of biotic systems.

Conclusions

This study illustrates that when assessing species response to climatic variation, one cannot assume species are a homologous entity. If species' thermal preference is adaptive and leads to an optimal number of hours for activity, growth, and reproduction balanced against increased predation pressures, then shifts in climate, that alter daily and seasonal activity periods (i.e. cost-benefit tradeoffs), are expected to affect metapopulation dynamics by redistributing source and sink populations across the landscape.

The results indicate that microclimate cooling resulting from shifts in land-use can have widespread, profound impacts on species life history and the viability of species throughout their range in ways not anticipated by currently accepted theory (Table 6). In contrast to climatic shifts from global warming which are predicted to lead to a shift in species range and distribution, the impacts of microclimate cooling are estimated to be more profound with the decline of populations in the core of the box turtles' range.

This work illustrates that shifts in microclimate can affect the life history of native species leading to decline of populations not only at the northern fringes of a species range, but across much of its' distribution. Finally, the explicit link between landscape and physiological ecology is demonstrated to provide an important synthesis of spatial pattern and physical process. In addition to being an effective means of addressing classical evolutionary questions of what limits species range and distribution. This approach, by quantifying some of the biophysical consequence of land-use change, provides a valuable tool for conservationist and land managers. The results of this study suggest that to predict population viability, in addition to macro scale investigation of landscape fragmentation, biologists need to address consequences of within patch shifts in microclimate within habitat remnants.

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Table 1 - My studies of ornate box turtle response to land-use and climate represents a synthesis of laboratory studies of thermal preference, field studies of the proximate affects of microclimate on species life history, and computer modeling of activity potential under different scenarios of microclimate and climate change. These approaches, in integrating laboratory and field studies from the same populations with computer simulations of latitudinal variation in these population's response to climate, allows me to link predictions and experiments across a range of spatial and temporal scales.

Scale	Process	Environmental variables	Response variables
< 5 m^2 10 days to 4 months	Laboratory studies of thermal preference and the effect of temperature on growth	Air temperature	Body temperature, body weight
< 1 Ha 2 years	Field studies of temperature preference of geographically distinct populations in the same habitat	Air and ground temperature, plant association	Body temperature, activity reproduction
1 to 10 Ha 3 years	Field studies of temperature preference of five Wi populations in different habitats	Air and ground temperature, plant association	Body temperature, activity, habitat preference, mortality, reproduction
> 100 Ha Years +	Computer simulations estimate activity times, and air and soil temperature profiles at different latitudes under varying climate and habitat regimes	Microclimate under current climates, global warming, and shifting land use	Activity times, temperature profiles, egg incubation time

Table 2 - Parameter values used in microclimate and animal activity potential simulations.

Parameter	Values
Environment:	
Soil solar absorptance	0.70
Soil density x specific heat	2.096 x 10^6 m^{-3} K^{-1}
Soil thermal conductivity	2.5 W m^{-1} K^{-1}
Substrate roughness height	0.001 m
Cloud cover	None (Clear skies)
Wind Speed @ 2.0 m	Varies daily from 0.5 to 2.5 m s-1
Humidity	Varies daily from 20 to 50%
Slope	10° north-facing
Box Turtle:	
Body mass	300 g
Carapace length	11.5 cm
Height	5 cm
Solar absorptivity	0.812
Infared emissivity	1.0
Surface area, silhouette areas, and shape factors	See Porter and Tracy (1983)
Preferred T_b range:	
Northern populations (Wi. & Nb.)	20 - 26° C
Central populations (Ks.)	21 - 29° C
Southern populations (Ok. and Tx.)	23 - 29° C

* Simulations and parameters are described in detail in Porter et al. (1973) and Porter and Tracy (1983). Except T_b all values were assumed to be equal for all study sites (microclimate simulation inputs adjust habitat to account for latitude and elevational differences).

Table 3 - Measurements of plant assemblages taken monthly during the growing season (May - September), five measurements per sample, are averaged across the growing season to illustrate structural differences in plant association. In sampling an effort was made to measure taller, denser areas (for example big blue stem clones), in addition to shorter less dense micro habitats. The greater variation is mesic prairie should provide greater thermal diversity allowing turtles to use the habitat during both the warm and cool season. These structural difference are expected to lead to significant differences in microclimate and box turtle habitat use.

Plant Community Structure
(Field Enclosure)

Community Type	Ht. (cm)	% Cover	Density (.25m^2)	Richness
Mesic Prairie	68.5 (SE = 6.7)	52.8 (SE = 3.4)	63.5 (SE = 6.7)	5 (SE = 1.1)
Dry prairie	32.6 (SE = 4.2)	25.5 (SE = 2.3)	25.8 (SE = 3.2)	3 (SE = 0.1)
Oak Woods	25.7 (SE = 4.0)	7.8 (SE = 0.9)	14.0 (SE = 2.4)	2 (SE = 0.1)
Sand Blow	21.3 (SE = 2.7)	12.8 (SE = 2.0)	15.8 (SE = 2.8)	2 (SE = 0.1)
Trans. Prairie	46.2 (SE = 3.3)	39.2 (SE = 3.0)	45.8 (SE = 4.5)	4 (SE = 0.1)

Table 4 - Measurements of plant assemblages taken during June, July, and August 1993, five measurements per sample, illustrate the structural differences in native and exotic (degraded) plant assemblages. These structural difference are expected to lead to significant differences in microclimate and box turtle habitat use.

Plant Community Structure
(Mazomanie Wildlife Area)

Community Type	Ht. (cm)	% Cover	Density (.25m^2)	Richness
Burned Old Field	55 7 (SE = 6 7)	49 3 (SE = 6 9)	39 5 (SE = 3 1)	3 (SE = 0 4)
Old Field	91 8 (SE = 4 2)	84 3 (SE = 2 5)	92 5 (SE = 6 1)	2 (SE = 0 4)
Woods	57 3 (SE = 7 9)	54 3 (SE = 5 4)	42 1 (SE = 6 8)	4 (SE = 0 2)
Dry Prairie	36 6 (SE = 4 5)	40 0 (SE = 6 4)	46 8 (SE = 7 0)	6 (SE = 0 4)
Savanna	33 6 (SE = 6 2)	50 0 (SE = 5 0)	50 0 (SE = 5 0)	4 (SE = 0 3)

Table 5 - By counting rings on the turtles scutes ages where estimated for eight populations in habitats experiencing different land-uses and microclimate. Included are my four telemetry populations in Sauk, Dane, and Iowa Counties and four additional populations in Columbia County, Wisconsin.

	Age Structure	
Age	Moderate Habitat (>70%) (N = 5)	Degraded Habitat (<70%) (N = 3)
Hatchling (< 1 year)	-	-
Juvenile (1 to <7 years)	4	-
Subadult (7 to <10 years)	2	-
Young Adult (11 to <15 years)	7	1
Adult (16 to <20 years)	7	2
Old Adult (<20 years)	7	7

Table 8 - Outline of the studies conclusions illustrate how a biophysical approach, across a hierarchy of scales, can be used to asses the impacts of shifting climate and land-use

Hypothesis	Experiment	Conclusions
Box turtle are differentially constrained by the thermal environment. Differences in thermal preference and behavior are genetically predetermined and not phenotypically plastic	Laboratory gradient box experiments of thermal preference before and after a year in the field and laboratory studies of hatching response to different thermal environments Multiple year field studies of northern, central, and southern box turtles in a Wisconsin field enclosure	Box turtle thermal preference and behavior did not vary suggesting the differences are genetically predetermined and not phynotically plastic Southern and central turtles had lower field survivorship
Changes in plant association structure can result in changes in microclimate Changes in microclimate can alter the life history of ectotherms leading to population decline	Five box turtle populations in Wisconsin in habitats with differing plant association structures and microclimates are contrasted with chronosequence studies of Nebraska lizard and grasshopper populations	Shifts in land use can alter plant association structure and microclimate resulting in declines of ectotherm populations in the northern plains following the cessation of grazing.
Patterns of ectotherm response to micromicroclimate cooling affect northern, central, and southern box turtle populations across the plains Microclimate changes resulting from shifts in land use affecting plant community distribution and global climate change will equally impact northern, central, and southern box turtle populations	Computer simulations of northern, central, and southern box turtle populations under current climate, microclimate cooling, and climatic warming examine latitudinal varination in box turtle response to land use and climate	Changes in microclimate can have a greater impact on box turtles than global climate change While climate change shifts species range, microclimate alteration can potentially impact turtles across the northern two-thirds of the species range potentially threatening the survival of the entire species

Figure 1 - Map of Mazomanie study area, scanned from Wisconsin Department of Transportation air photos, illustrates landscape changes typical of southern Wisconsin. On this site box turtle habitat (savanna and prairie) have declined from 83% of the landscape in 1937, to 73% in 1962 (pine plantations were planted this year but are not yet visible in the air photo), 70% in 1977, and 23% in 1992. The radical changes in landscape cover in the last 15 to 25 years is typical of southern Wisconsin. In addition to increased fragmentation of the landscape, the increase in exotic plant communities may cool the landscape. Allowing for a 5° C difference in the microclimates of native (prairie and savanna) verses exotic (old-field and woods) plants communities (Curtin in press), the average microclimate of the landscape has dropped by 3° to 4° C. These shifts in microclimate are expected to lead to declines in time for activity, growth, and reproduction which may have great impacts on the species within these habitat remnants.

Figure 2 - Significant differences (< 0.05) exist between laboratory gradient thermal preferences of northern (Nb)(N=8), central (Ks.)(N=8), and southern (Tx./Ok.)(N=8) ornate box turtle populations in 1992 and 1993 prior to being subjected to identical microclimates in a field enclosure in Wisconsin. Comparisons of the remaining northern (N=6) and southern (N=6) box turtles at the close of field studies in 1994 showed that significant differences (< 0.01) persisted after over a year in the field. The 0.1 difference in average body temperature variation between northern and southern box turtles (1.7° C ± 0.4 in 1993 versus the 1.8° C ± 0.5 in 1994), indicates that the lack of significant differences in the 1993 field season is likely the result of smaller sample sizes of southern animals during the 1993 field season (N in 1993 = 105 vs. N in 1994 = 160). This occurred because the Oklahoma animals were not introduced into the pen until mid-summer and thus were not counted in 1993 samples.

Figure 3 - Hatchling ornate box turtles from two clutches, from the same population in Wisconsin, in warm treatments with microclimates similar to prairie and savanna habitats

(N=4) and cool treatments similar to old field and wooded habitats (N=5) show significant differences in body weight after measurements were begun one month after the treatments started in September 1993.

Figure 4 - Measurement of field body temperatures of northern (Nb.)(N=8), central (Ks.)(N=8), and southern (Tx.)(N=4) box turtle populations did not show significant differences (<0.07) in 1993. In 1994 temperature measurements of northern (Nb.)(N=6) and southern (Ok./Tx.)(N=6) show significant differences (<0.01) in field body temperatures.

Figure 5 - Air temperatures (T_a)(shade 5cm - box turtle height) in model landscape located within 0.52 ha enclosure located near Muscoda, Wisconsin. Measurements taken at random within each plant association (designated according to Curtis 1959) on 22 different days at a variety of times ranging from 8:00 to 16:00 Hrs., indicate significant differences ($\leq$0.05) in the thermal structure of most plant assemblage types. The woods were significantly cooler than all grassland habitats and the arid sand blow was significantly warmer than transitional and mesic prairie.

Figure 6 - a) Map created from a survey by Wisconsin Power & Light personnel illustrates composition of the field enclosure. Warm and cool season box turtle locations (derived from 10 days of spring and 10 days of summer field data), illustrate typical warm and cool season habitat use. b) Contrasts of percentage of habitat area and the proportion of the observations of turtles where located within a given habitat indicate disproportional use of warmer dry prairie and sand blow habitats in the cool season and cooler wooded areas in the warm season. Mesic prairie saw a disproportionate amount of use during both warm and cool seasons.

Figure 7 - The proportion of each population either basking or moving varied between Tx., Ok. and Ks., and Nb. populations. Particularly striking was the rapid drop in activity during mid-summer by the southern populations (when temperatures closely approximate those of

Texas). The drop in activity by southern populations during mid-summer, when temperatures most closely approximate those of Texas, indicates that the reduced body temperatures and activities seen by southern and central animals in the enclosure in Wisconsin are not a result of the southern animals being in an alien environment, but a reflection of the animals actual field preference.

Figure 8 - Calculated from 12 random surveys of activity in 1993 (4 taken at each period of the day), this interaction plots illustrates that northern turtles are significantly more activity that central or southern animals in the morning. A cooler thermal preference may allow northern animals to expand their daily activity periods by allowing them to be out and active earlier in the day than more southerly animals. At the same time northern turtles are no more limited by mid-day temperatures then their southern counterparts. Similar significant differences in activity also existed in 1994 between northern and southern individuals.

Figure 9 - Air temperatures, taken at 5 cm (turtle height) in old field and woods assemblages were significantly cooler (<0.01) than native savanna and prairie communities. This suggests that shifts in plant community structure resulting from changing land-use can significantly alter microclimate.

Figure 10 - Hollow clay replica's of box turtle attached to data loggers where used to determine the range of environmental temperatures (T_e) in native and exotic plant communities (Curtin In Press). The physical models demonstrate how shifts in plant community composition can affect box turtle life history. Exotic woods and agricultural plant communities (e.g. old field and corn) limit activity during the cool season while conferring little advantage during the warm season. This decline in activity is predicted to reduce time for feeding, growth, and reproduction and lead to population declines.

Figure 11 - Map of the Mazomanie study area illustrates differential seasonal use of habitat types (derived from 10 days of spring and 10 days of summer field data). Burning and clearing in the winter of 1992/1993 cleared pine plantations and opened up old field habitat (Table 5). Comparisons of habitat use between 1992 and 1993 suggests that turtles are able to shift their habitat use in response to shifts in landscape structure and microclimate. In 1993 95% percent of cool season activity was located in a hot-dry section of south-east facing sand prairie covering >5% of the site. During the summer 70% of activity was concentrated in prairie and savanna habitats covering 50% percent of the site. Old field and woods locations were usually avoided. In 1994 Wooded areas saw greater use in the warm season. The more open, warmer structure of the old field areas in 1993 allow turtles to shift their habitat use to these areas.

Figure 12 - Seasonal distributions of activity from my studies of Nebraska turtles (1993 N=8, 1994 N=6) in field enclosures in Wisconsin, studies in Kansas (N= $100^{+}$by Legler (1960), and Texas (N=50^{+} by Blair are contrasted between observed numbers of animals in the field and computer simulation calculations to examine the similarity between computer output and field data. The proportion of a population located in field censuses is assumed to be roughly equivalent to the number of hours of box turtle activity. Because Legler and Blair censused populations in the field without telemetry their recapture rate is lower than mine from the Wisconsin enclosure yet the pattern of distribution should still hold. The results indicate that computer simulations are indicative of box turtle activity in the field.

Figure 13 - a) the contour plot shows the computer simulations calculations of activity times contrasted with plots of actual activity patterns of Nebraska animals in the field enclosure (1993 N=8, 1994 N = 6). The simulations succeeded in estimate the morning, evening, and the bimodal distribution of warm season activity periods. b) Activity potential calculations and observed hours of activity are contrasted. Because the computer program is written to estimate

maximum potential activity it overestimates hours of activity yet succeeds in closely approximating daily activity periods.

Figure 14 - Periods of activity simulated under current climates, microclimate cooling resulting from shifts in plant community structure, and climatic warming resulting climate change indicate that northern and central populations will have a similar loss of activity potential under either scenario. Southern populations exhibit a net gain under microclimate cooling and a net loss under climatic warming.

Figure 15 - Laboratory (Legler 1960, Packard et al. 1985, Hay pers. comm.), and field data (Legler 1960, Doroff and Keith 1990, Curtin In press), on egg incubation times were used with computer simulation microclimate data on soil temperature profiles and adult box turtle activity periods to illustrate how a cooling in microclimate can affect reproductive potential. Solid lines indicate incubation periods likely to result in successful hatching of the clutch while dashed lines indicate clutches which are unlikely to successfully hatch. The figures indicate, as has been shown by Wisconsin field data (Doroff and Keith 1990, Curtin in press), that the 4 ° C cooling in microclimate can reduce the box turtles ability to hatch before winter resulting in lower recruitment. In Kansas populations are unlikely to successfully hatch their second clutch and in many instances the first clutch may be compromised. Texas populations show little change in reproductive potential in response to microclimate cooling.

Figure 16 - The combination of laboratory (Legler 1960, Packard et al. 1985, Hay pers. comm.) and field data (Legler 1960, Doroff and Keith 1990, Curtin In press) with computer simulation output indicate northern populations will increase their reproductive output while central or southern reproductive success will remain constant or decline. Solid lines indicate incubation periods likely to result in successful hatching of the clutch while dashed lines indicate clutches which are unlikely to successfully hatch.

Figure 1

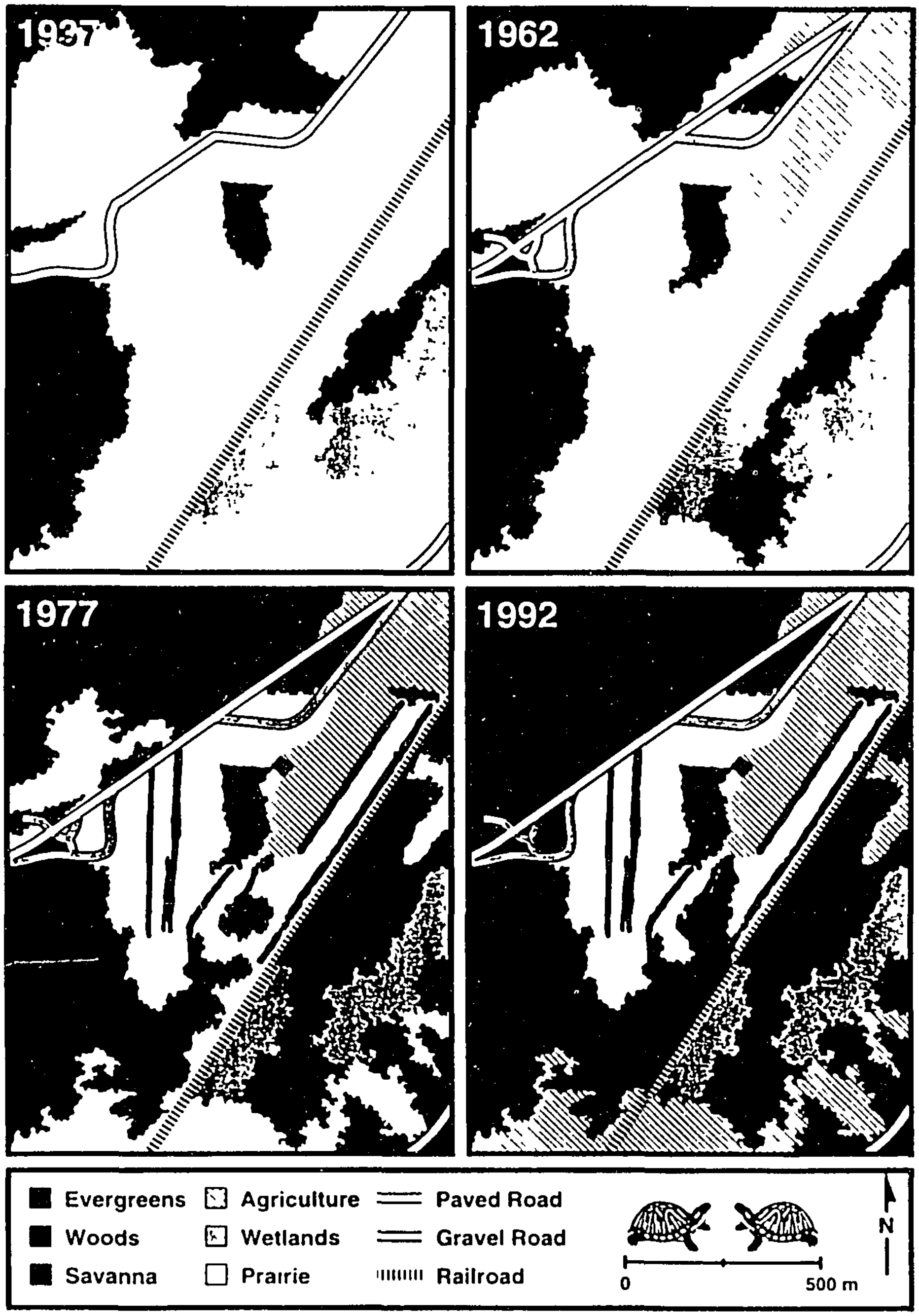
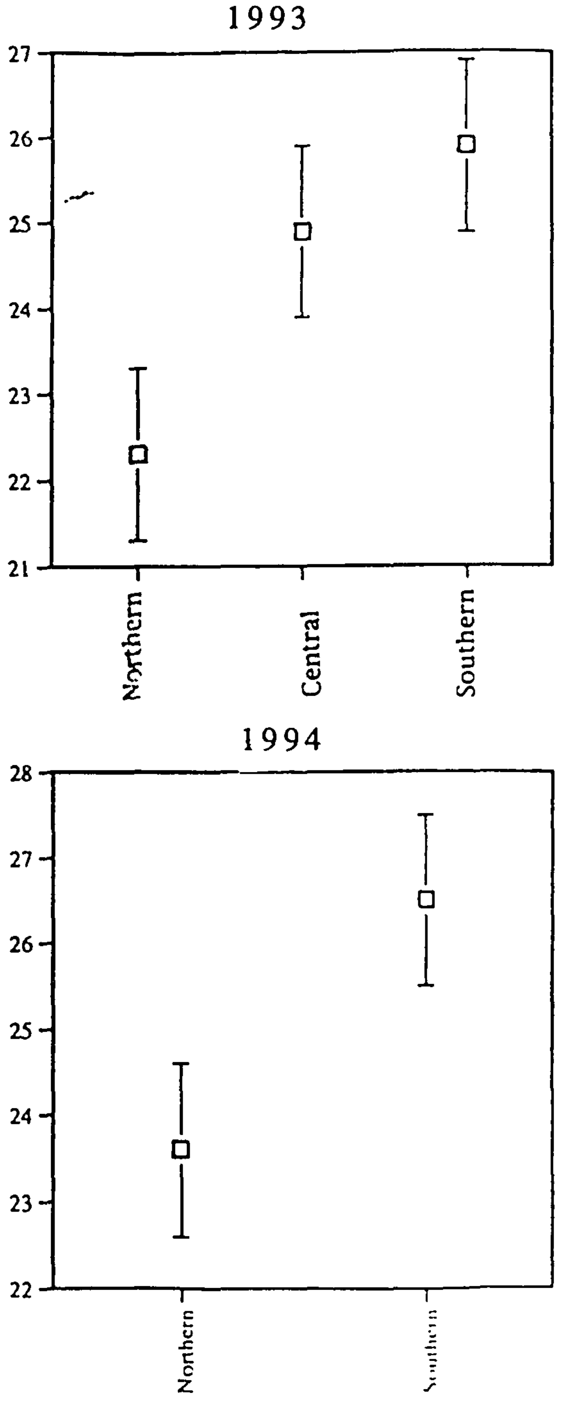

1937
1962
1977
1992
Evergreens
Woods
Savanna
Agriculture
Wetlands
Prairie
Paved Road
Gravel Road
Railroad
0
500 m
N

Figure 2

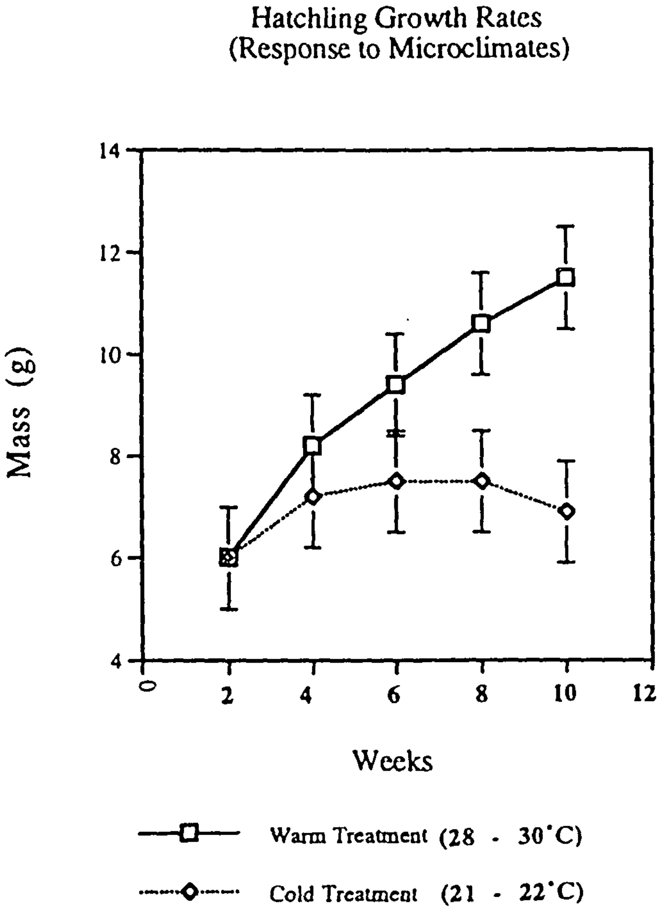
Laboratory Gradient



1993

1994

Figure 3


Hatchling Growth Rates
(Response to Microclimates)
Mass (g)
14
12
10
8
6
4
0
2
4
6
8
10
12
Weeks
Warm Treatment (28 - 30°C)
Cold Treatment (21 - 22°C)

Field Preference

Figure 4

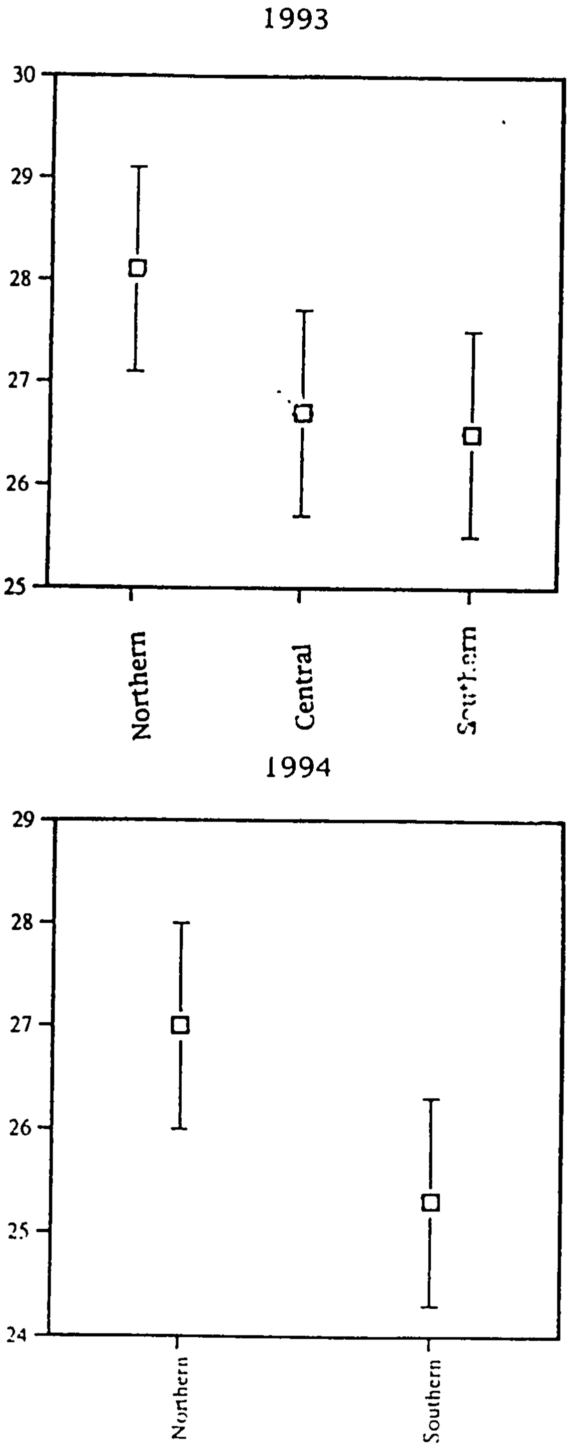
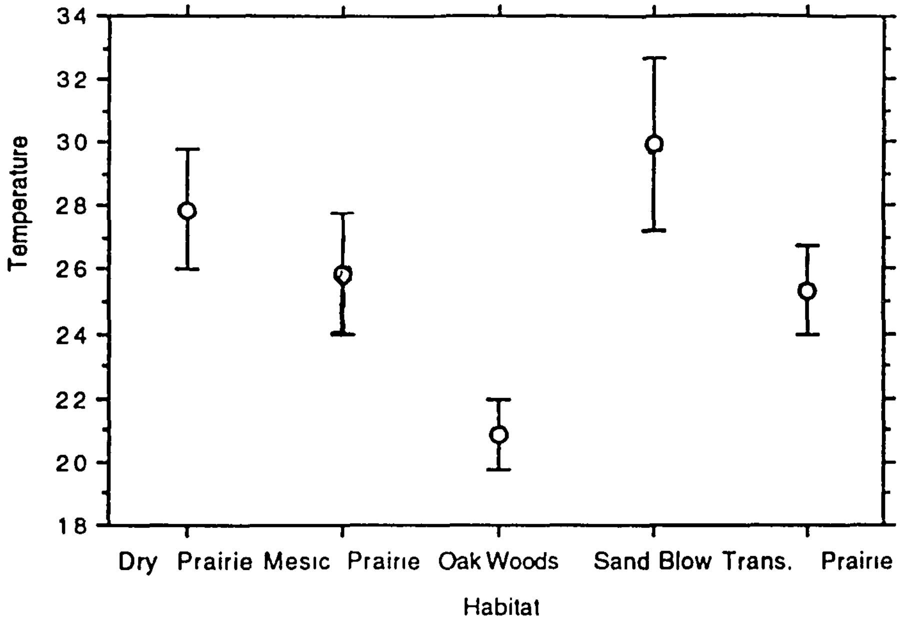


Figure 5



Interaction Plot
Effect: Habitat
Dependent: Temperature
With 95% Confidence error bars.

Figure 6

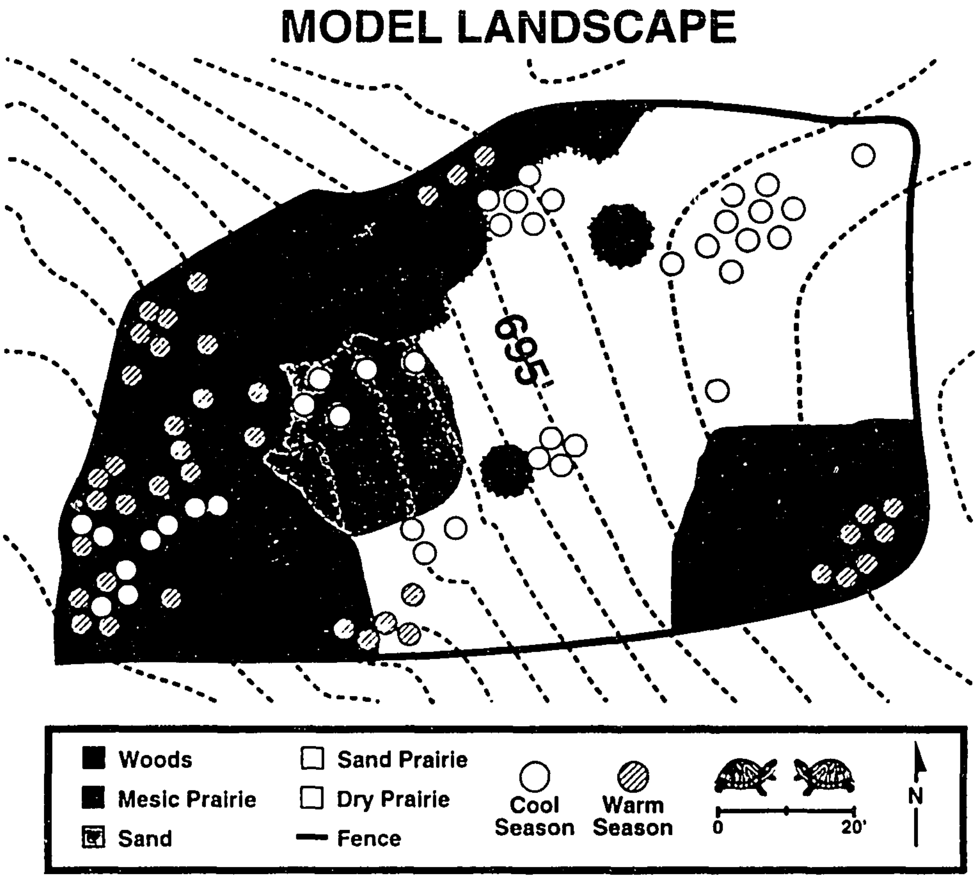

MODEL LANDSCAPE
695'
Woods
Mesic Prairie
Sand
Sand Prairie
Dry Prairie
Fence
Cool Season
Warm Season
0
20'
N

Figure 7

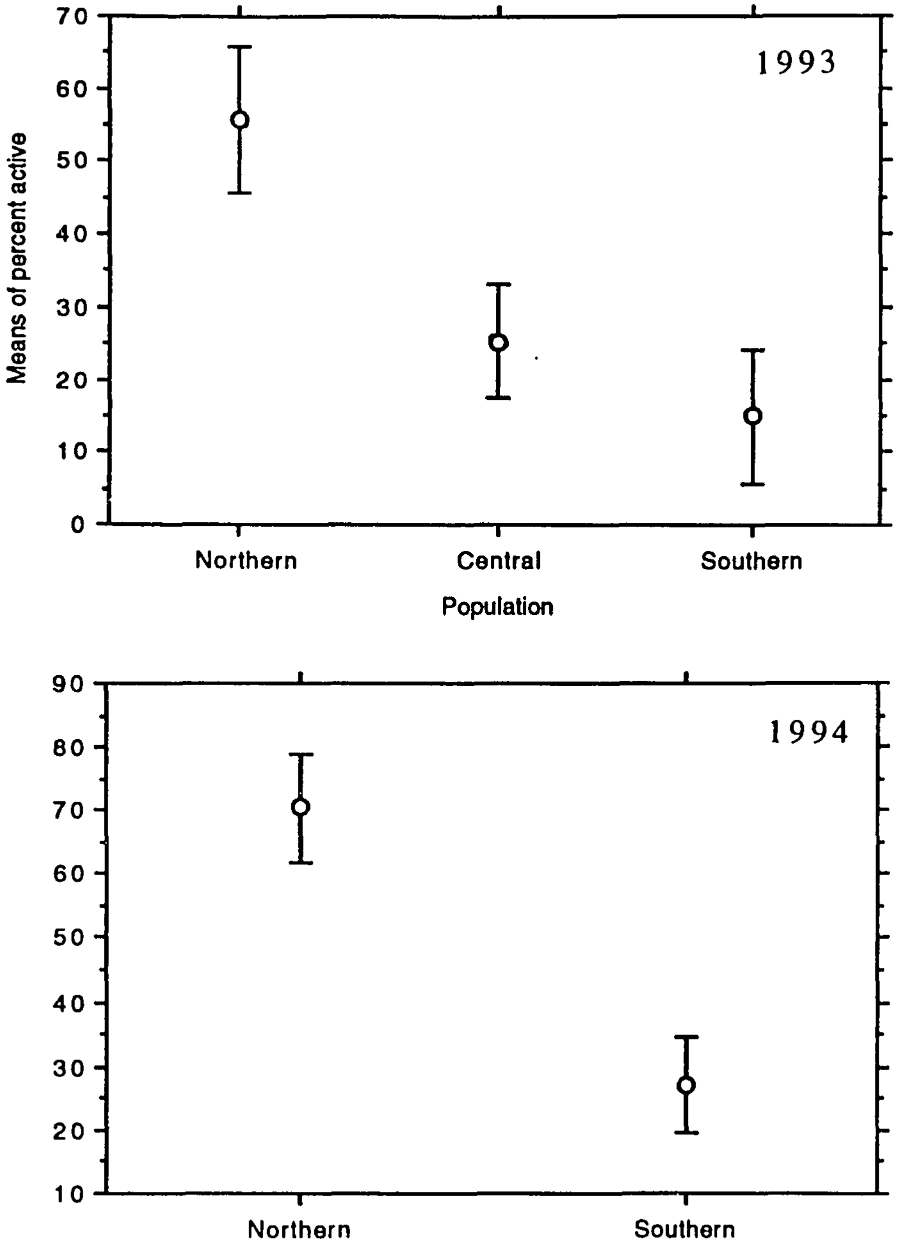
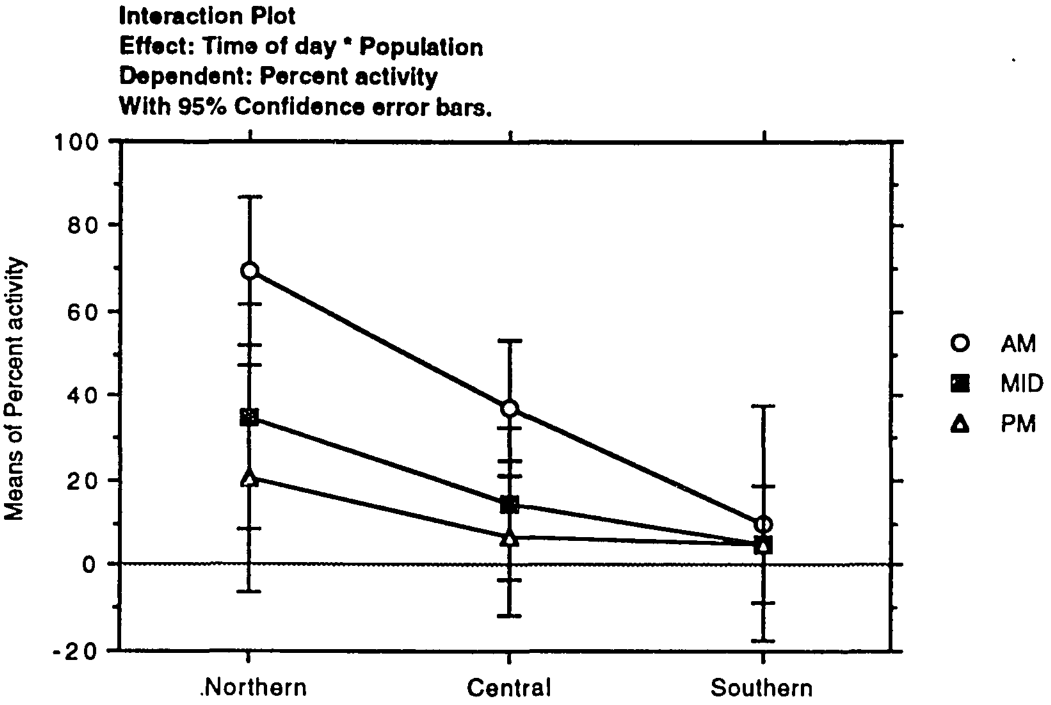

1993
Means of percent active
0
10
20
30
40
50
60
70
Northern
Central
Southern
Population
1994
10
20
30
40
50
60
70
80
90
Northern
Southern

Figure 8

Distribution of daily activity



Tukey-Kramer
Effect: Time of day
Dependent: Percent activity
Significance level: .05

	Vs.	Diff.	Crit. diff.	
PM	MID	7.533	12.266	
	AM	28.200	12.907	S
MID	AM	20.667	12.266	S

S = Significantly different at this level.

Figure 9

Interaction Plot
Effect: Habitat
Dependent: Temperature
With 95% Confidence error bars.

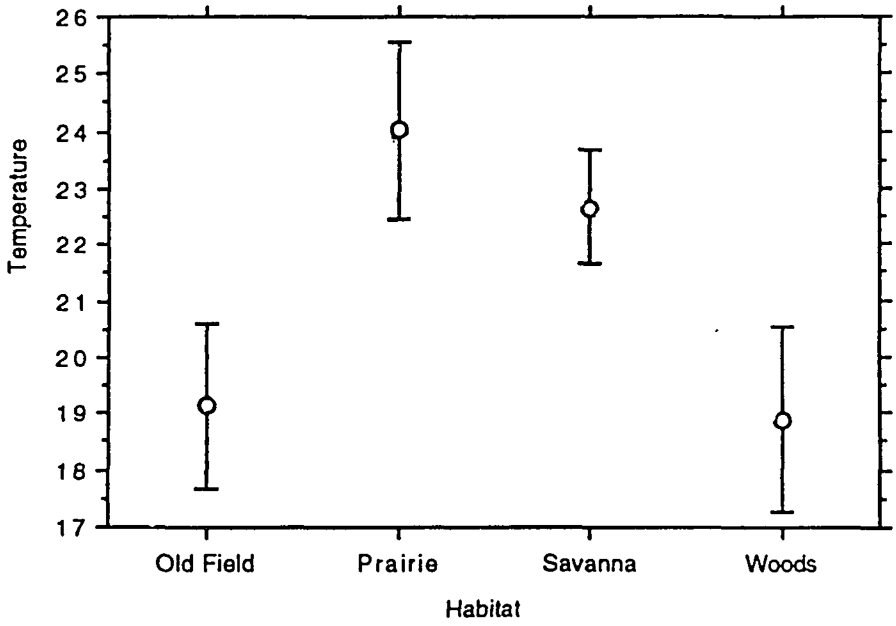
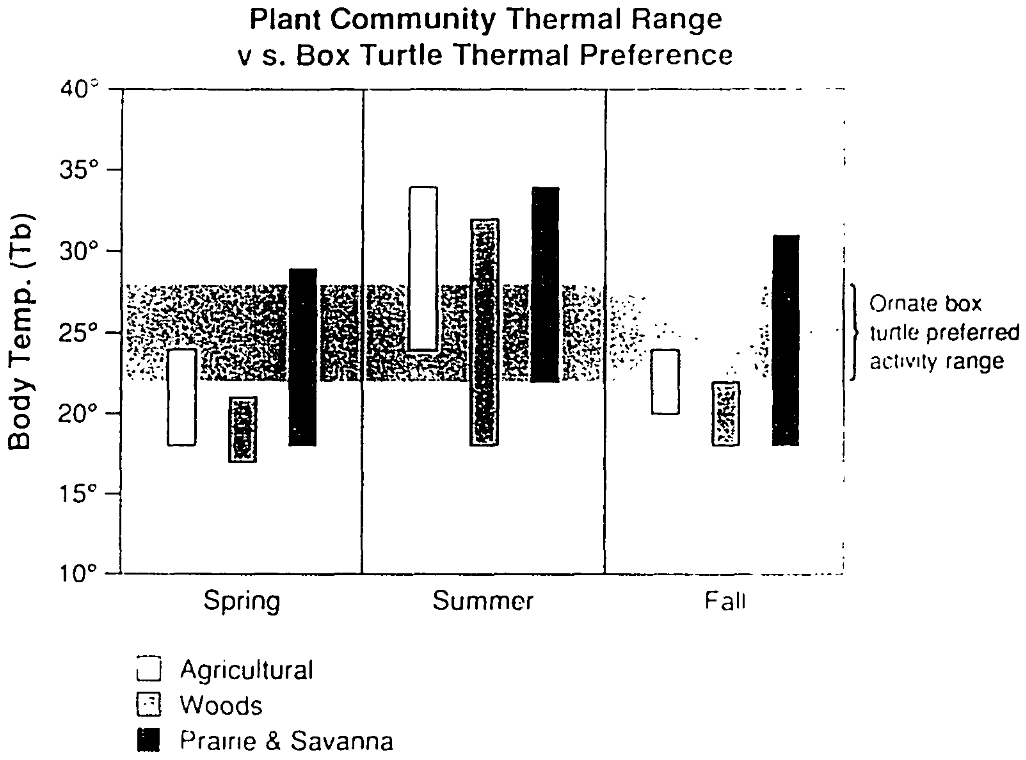
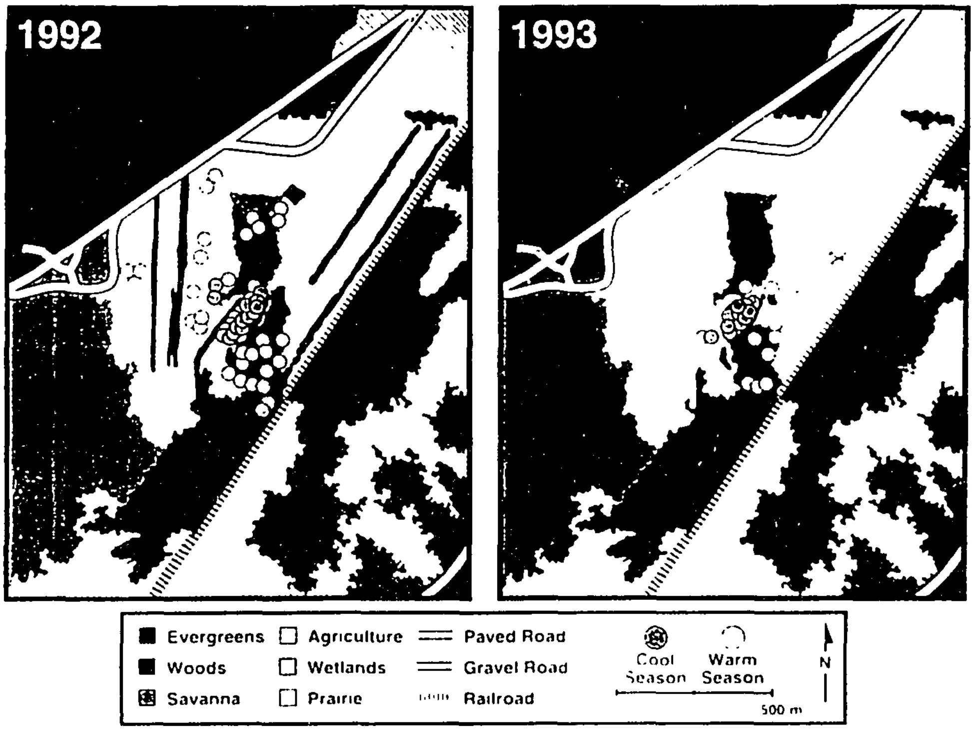


Figure 10



Plant Community Thermal Range
v s. Box Turtle Thermal Preference

Figure 11



Habitat Usage (1992)

Habitat	Prairie & Savanna	Old Field	Woods
Percent of Area	50%	30%	20%
Percent of Cool Season Use	95%	0	05%
Percent of Warm Season Use	70%	10%	20%

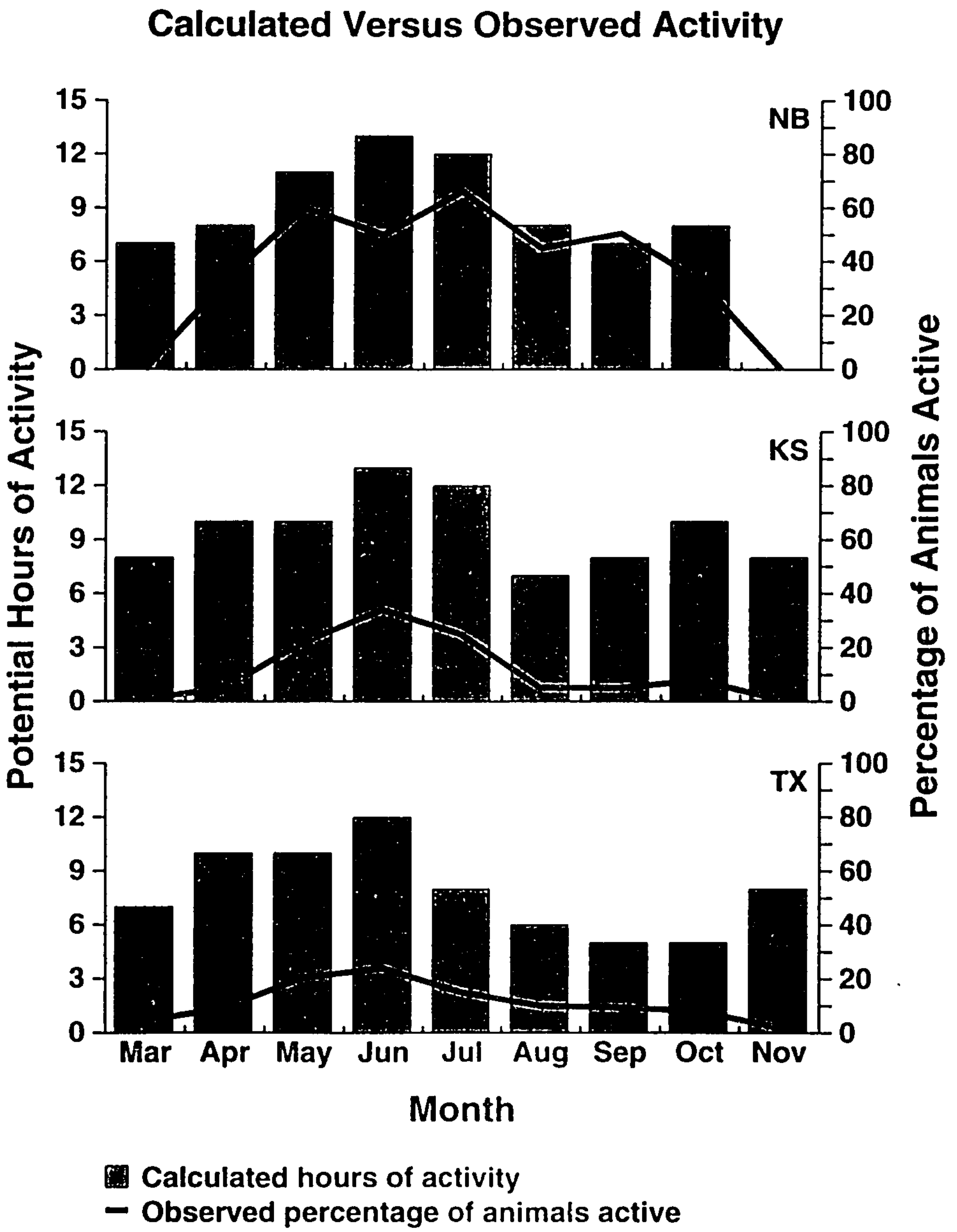
(N = 8)

Habitat Usage (1993)

Percent of Area	70%	20%	10%
Percent of Cool Season Use	95%	05%	0
Percent of Warm Season Use	35%	35%	30%

(N = 5)

Figure 12


Calculated Versus Observed Activity
Potential Hours of Activity
Percentage of Animals Active
NB
KS
TX
0
3
6
9
12
15
0
20
40
60
80
100
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month
▨ Calculated hours of activity
— Observed percentage of animals active

Calculated Versus Observed Activity

Figure 13

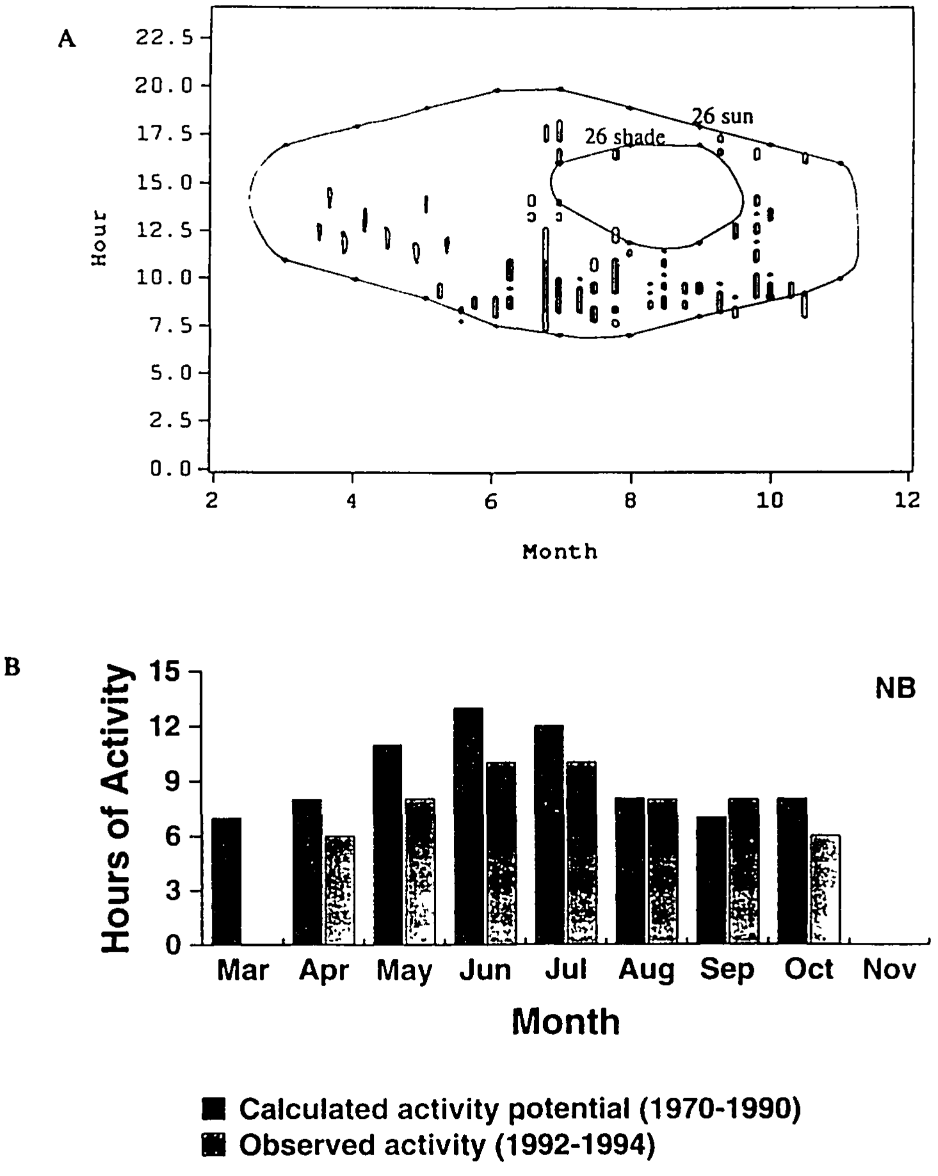


Figure 14

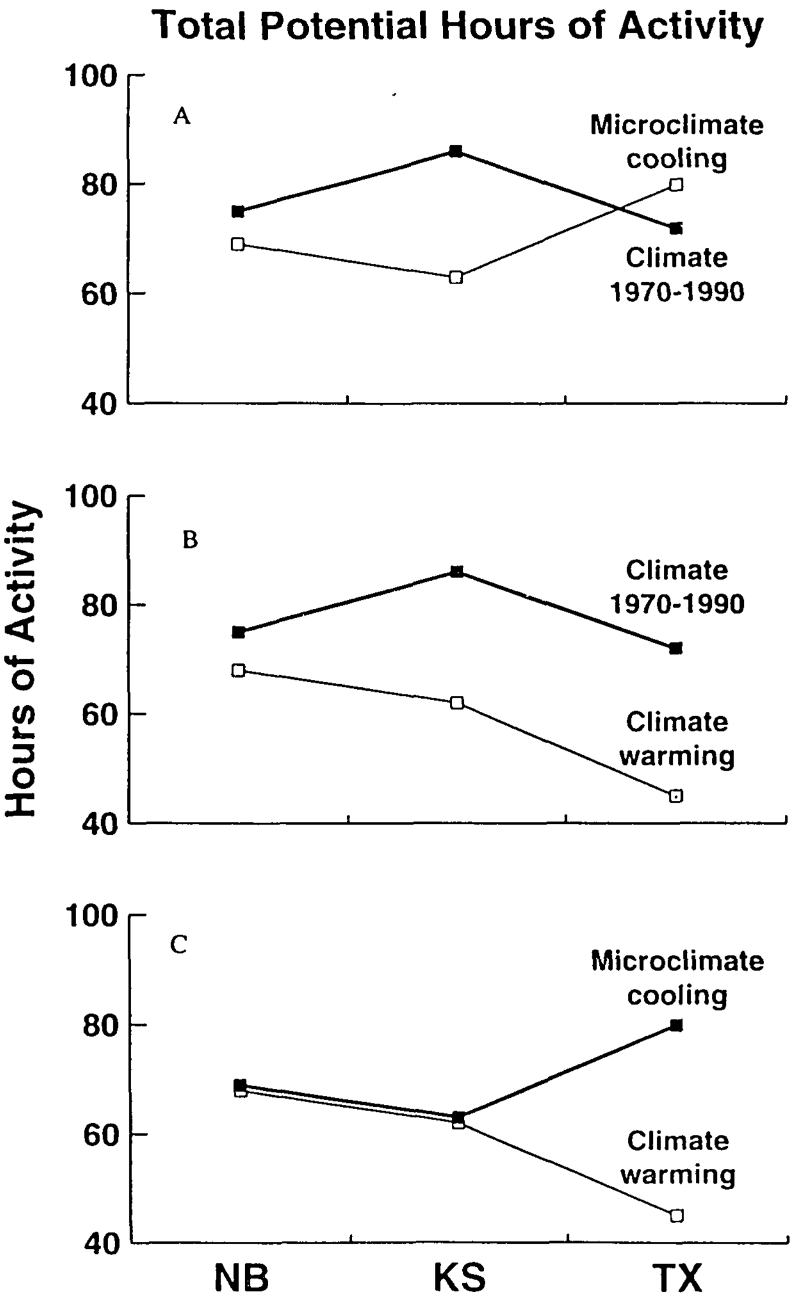

Total Potential Hours of Activity
Hours of Activity
100
80
60
40
A
Microclimate cooling
Climate 1970-1990
B
Climate 1970-1990
Climate warming
C
Microclimate cooling
Climate warming
NB
KS
TX

Figure 15

Impact of Microclimate Change on Reproductive Potential

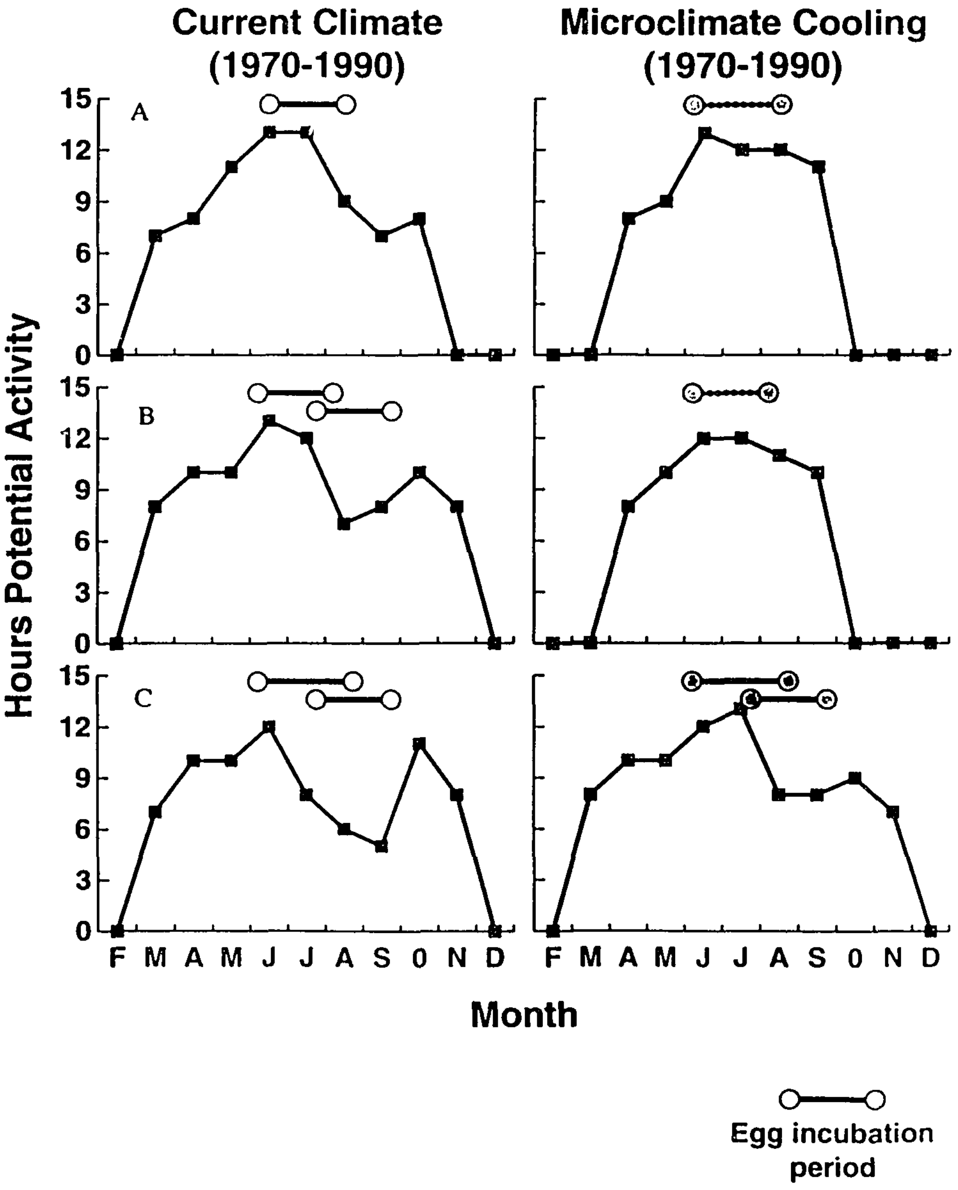
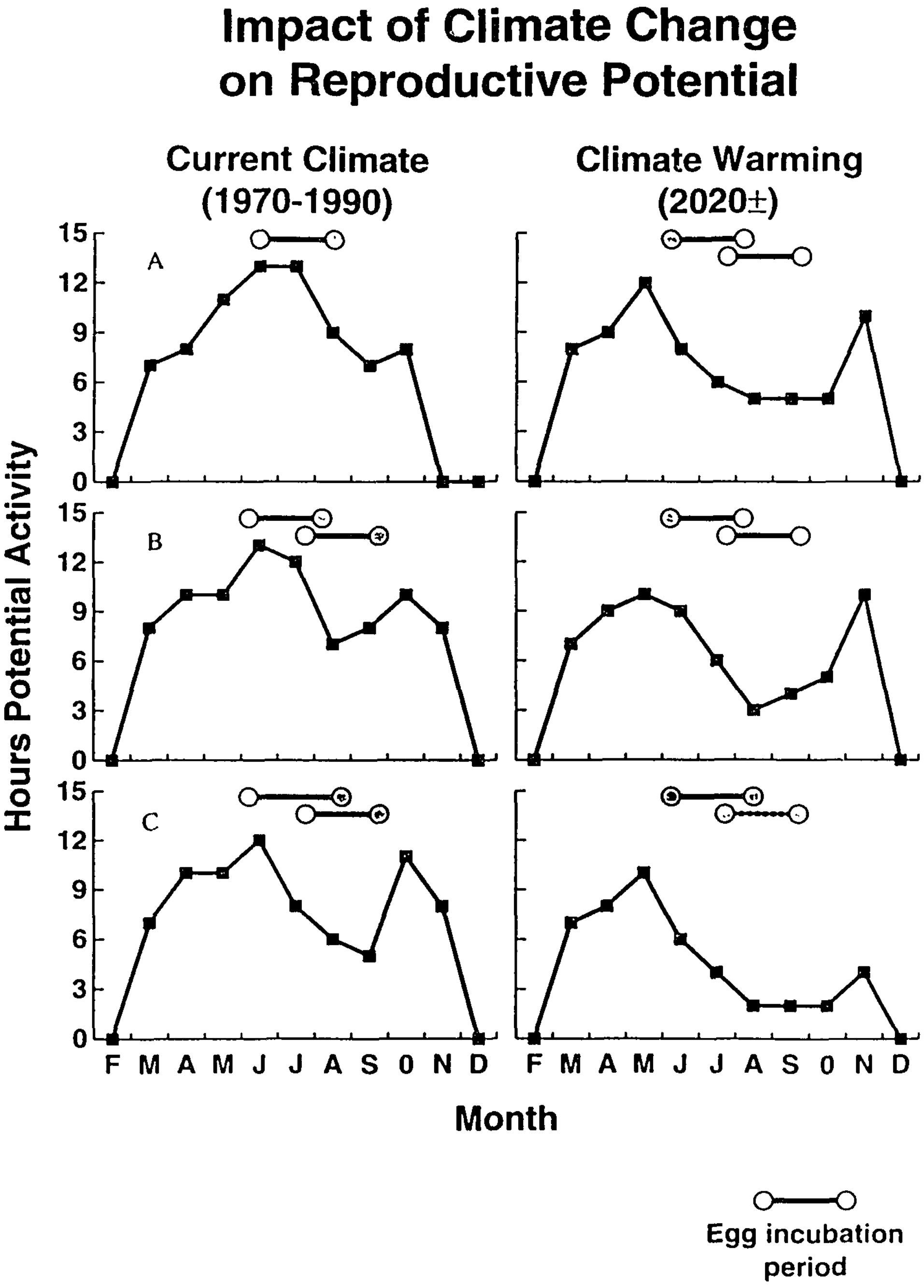


Figure 16


Impact of Climate Change on Reproductive Potential
Current Climate (1970-1990)
Climate Warming (2020±)
Hours Potential Activity
15
12
9
6
3
0
A
B
C
F M A M J J A S O N D
F M A M J J A S O N D
Month
Egg incubation period