ASON. 1989. Relationships
or and growth rates: A field
territories. Behav. Ecol. So-

NAKA. 1981. The relation-
. social behavior in juvenile
). Copeia 1981:422–434.
ICE. 1982. Ecological and
ants of relative clutch mass
ica 38:237–255.
. The effect of supplemental
ge size and activity patterns
sburiana. Oecologia (Berlin)

. WILEY. 1979. Mechanisms
ing in animals. Pp. 159–223.
. Vandenbergh (Eds.), Hand-
Neurobiology, Vol. 3: Social
unication. Plenum Press, New

NS, AND A. A. DHONDT. 1995.
ry fidelity and territory shifts
Sciurus vulgaris, females. Anim.

Territoriality and male mating
frog (Rana clamitans). Ecology

epted: 15 November 1995
ociate Editor: Richard Howard

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MOVEMENT, ACTIVITY, AND MICROHABITAT SELECTION IN THE WESTERN BOX TURTLE, *TERRAPENE ORNATA LUTEOLA*, IN NEW MEXICO

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ABSTRACT: Movement patterns in the western box turtle, *Terrapene ornata luteola*, were estimated from both repeated sightings on a road and radiotelemetry. Home ranges were smaller than those expected from random movements. Turtles in the study area may have larger home ranges (mean area of 1.6 ha, minimum polygon method, mean maximum diameter of 276 m) than box turtles in more mesic habitats. No significant differences in home range size or distances moved were observed between sexes, and overlap was considerable. Turtles moved farther on the road than off the road and the road may have increased the size of the home range of some turtles.

Turtles were most active when ambient temperatures were 13–24 C, solar radiation was <200 jules/cm²/h, and humidity was high (<20 mbar vapour pressure deficit). Turtles selected microhabitats with lower soil temperatures, higher ambient temperatures, and lower humidity levels than those observed at the meteorological station on the study site.

Key words: Box turtles; *Terrapene ornata luteola*; Movement; Home range; Microhabitat selection; Activities; Deserts

MOVEMENTS of organisms within and between populations are fundamental to the ecology of species and are important in both intra- and inter-specific interactions. An understanding of patterns of movement, both spatial and temporal, requires knowledge of environmental and social conditions under which movement occurs. It is often difficult, however, to acertain why an animal is moving and motivation usually has to be inferred.

I examined the intrapopulational movement of the western box turtle, *Terrapene ornata luteola*, in central New Mexico. This subspecies primarily inhabits arid grasslands of the southwestern United States and northern Mexico (Pritchard, 1979). It is thought to be a relict form of a mesically adapted box turtle (Milstead and Tinkle, 1967). A comparison between the western box turtle and conspecific forms in more mesic environments may give insights into the effect of habitat and resource density on movements.

Auffenberg and Weaver (1969) hypothesized that home range sizes of tortoises in Texas would be larger where there is a lower density of food and shelter; Auffenberg and Iverson (1979) showed that home range size in gopher tortoises was correlated with available food resources. Some xerically adapted tortoises have larger home ranges than mesically adapted tortoises (Diemer, 1992). Because western box turtles occur in drier areas than ornate box turtles, *T. o. ornata*, the only other subspecies (Legler, 1960), their home ranges may be larger than those for *T. o. ornata*. To date, there are no estimates of home range sizes for *T. o. luteola*, other than this study. Maximum diameters of home ranges for *T. o. ornata* range from 94–267 m (Table 1). Any study of home range in turtles must also consider the effects of roads; roads may increase the size of a home range (Diemer, 1992) and therefore can complicate comparisons.

Few studies (but see Rose and Judd, 1979) on home ranges of turtles have statistically examined whether turtles move randomly or non-randomly around an area. In both situations, a "home range" might be found, but even a water molecule moving at random will remain in a relatively restricted area (Munger, 1984). Because eastern box turtles display site fidelity over

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TABLE 1.—Home range sizes for ornate box turtles, *Terrapene ornata ornata*. Maximum diameter estimates in meters.

Geographic area	Habitat	n	Home range size	Authority
Northeastern Kansas	Farmland/ woodland	44	169.5	Legler, 1960
Southeastern Kansas	Prairie/ farmland	—	male: 152 female: 267	Metcalf and Metcalf, 1970
Kansas	?	13	167	Fitch, 1958
Texas	?	5 6	male: 105 female: 94	Blair, 1976

many years (Stickel, 1989), it is probable that western box turtles move non-randomly.

Previous studies on box turtles have shown that activity is closely related to environmental conditions (Legler, 1960; McRae et al., 1981; Reagan, 1974; Russo, 1972; Stickel, 1950) resulting in bimodal activity patterns when temperatures are high. Reptiles regulate their body temperatures by both behavioral and physiological means, and behavioral thermoregulation is carried out by selecting optimal thermal microhabitats (Adams and de-Carvalho, 1984). High mid-day temperatures in the area of my study should result in selection of thermally favorable microhabitats by box turtles, where it may be more critical than in more moderate climates.

This study was conducted to examine the size of home ranges and the extent of movements in general in the western box turtle. I tested the hypotheses that box turtles in drier habitats would have larger home ranges and that roads increase home range size. I predicted a strictly bimodal daily activity pattern. The question of what turtles do when they are above ground was also addressed. Finally, I expected box turtles to select microhabitats enabling them to increase the amount of time that they can be active during unfavorable temperatures.

METHODS

Description of the Study Area

Terrapene o. luteola occurs in a small part of the Sevilleta National Wildlife Refuge, about 85 km south of Albuquerque, New Mexico. This area consists of semi-arid grassland on the northern fringe of the Chihuahuan desert, at an elevation of 1600 m. The vegetation is characterized by various grasses, various cacti, yucca (*Yucca glauca*), snakeweed (*Gutierrezia glutinosa*), creosote (*Larrea tridentata*), and other small shrubs and annuals. Mean annual rainfall in Bernardo, 16.8 km from the study site, is 207 mm, most of it falling during July and August; annual temperatures range from −8 C (mean January minimum) to 35 C (mean July maximum) (Owenby and Ezell, 1992). The study site consisted of a 9.3-km dirt road, running approximately north–south, and an area about 500 m wide along each side of the road.

Home Range and Movements

Box turtles were encountered from May–October from 1990–1992 by driving on the dirt road several times weekly. Each turtle was weighed, measured, and permanently marked by filing notches into the marginal scutes of the carapace. The front right four marginals after the cervical scute represented 400–100, going left to right; the back right five marginals represented 5–1, going from left to right, and the back left five marginals represented 50–10, going from right to left. I painted an identification number on each side of the carapace, enabling turtles to be subsequently identified with minimal disturbance. I determined sex by looking at the shape of the tail, the orientation of the first toe of the hindfoot, and the colors of the eyes and front legs. Locations were estimated using odometer readings.

To supplement the information on movements along the road, I equipped

eight box turtles (three males
in 1990 and seven differer
(four males, three females)
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eight box turtles (three males, five females) in 1990 and seven different individuals (four males, three females) in 1992 with 11.8-g radio transmitters (AVM Co., SB2 type, with K7 batteries). Transmitters were attached to the front of the carapace to reduce interference with mating. All radio-tracked turtles were initially located along a 2.4-km stretch of road, where the density of turtles was highest. Radio-tracking took place from early or mid-June to mid-September in 1991 and from mid-August to early October in 1992. Turtles were located biweekly and not disturbed. I excluded fortuitous sightings from analyses, except in examination of home ranges with respect to the road. I measured the X and Y coordinates of each location from the first sighting of the turtle. Two individuals, denoted as 650 and 75, were intensively monitored by locating them four times a day for three days. This was done to determine when locations would be independent of each other, because independent sightings are an assumption of most methods for estimating home range area. To estimate the minimum length of time needed between sightings, Schoener's ratio was calculated and was graphed against time between observations (after Swihart and Slade, 1985). Independence of observations occurred in turtle 650 at two sightings/day, with eccentricity, e, of 4.79, and in turtle 75 at one sighting/day, with e of 1.74. However, sightings twice a week were at the borderline of being non-independent; in all subsequent analyses, I used only those observations that were three or more days apart, to compromise between independence versus reasonable sample sizes.

Home range area was calculated using an algorithm written by John Carey, in Turbo Pascal. To ease comparisons with other studies, I computed four estimates: the minimum polygon method (Mohr, 1947), the 95% ellipse method, the Dixon and Chapman (1980) method, and maximum diameters. To determine if box turtles move randomly around a site, home ranges were randomized sensu Munger (1984). For each individual, I used the X and Y coordinates to calculate vectors connecting the sightings. Each vector was divided into a north–south and east–west component. Direction (i.e., north or south, east or west) and the order of vectors was then randomized. New coordinates were calculated and a new home range area estimated. Twenty iterations of the randomized home range were computed; I compared means to the actual home range sizes.

I examined plots at which box turtles were sighted in relationship to the road. In addition, I estimated movements of radio-tracked turtles using straight line (minimum) distances between successive locations, as in Zeng and Brown (1987). On-road and off-road movement was compared. To test that distance increases with amount of time between sightings, I correlated distance moved with time between locations. Rate of movement was calculated by dividing the dispersal distance by the time between sightings.

Activities

Individual turtles were observed for 30 min to obtain detailed information on above ground activities during the times when turtles were active. I categorized behaviors as resting, feeding, walking, and social behavior. Sometimes the observation period was reduced because the turtle entered a burrow. No individual turtle was observed for more than a total of 1.5 h/yr, and never twice or more during the same day. Activities of radio-tracked turtles were noted on location, done during varying times of day, also to provide data on how many turtles were active (above ground) or inactive (below ground or stationary and sheltered by vegetation). Weather data were collected from the Deep Well Meteorological Station at the study site. Variables used included ambient temperature, soil temperature at 1 cm, precipitation, vapour pressure deficit, and solar radiation. I used principal component analysis, using centered, standardized data and a correlation matrix, to identify the most important weather variables for turtles. These were then analyzed using multiple regression to devise a model predicting the activity of box turtles when above ground.

To investigate the effect of environmental variables on activity more directly,

TABLE 2.—Mean home range estimates (±1 SD) for 15 radio-tracked box turtles, 1991 and 1992. Home ranges in m² or meters.

	D&C95[1]	D&C100[1]	Min pol[2]	Ellipse[3]	Max. diam.[4]
Total	9523	13,023	16,365	50,306	276
	±635	±111	±13,095	±47,015	±178
Males	12,804	17,243	21,067	71,440	237
	±14,198	±18,420	±14,888	±56,547	±141
Females	10,892	14,115	13,391	36,228	322
	±14,009	±18,190	±12,082	±34,038	±210
Range	66–43,857	67–56,183	300–41,357	783–164,139	32–526

Percentage change of actual home ranges compared to randomized home ranges (means ± 1 SD).

	D&C95[1]	D&C100[1]	Min pol[2]	Ellipse[3]
Total	353	403	382	571
	±390	±429	±323	±591
Males	362	398	366	573
	±362	±352	±284	±574
Females	345	408	396	570
	±412	±487	±553	±606

[1] D&C95/D&C100: Dixon and Chapman (1980) method, 95% or 100%.
[2] Min pol: minimum polygon method (Mohr, 1947).
[3] Ellipse: 95% ellipse method.
[4] Max. diam.: maximum diameter.

ambient temperature, soil temperature at 1 cm, vapour pressure deficit, and solar radiation were measured at the site where a turtle was located and were compared to variables obtained at Deep Well. Readings were made only when a turtle had been stationary for at least 20 min (and thereby considered to have selected this spot, rather than being in transition). Often turtles were inside burrows (detected by radio signals), and I obtained estimates by placing the sensor as far into the burrow as possible. Ambient temperature and vapour pressure deficit were measured using a digital thermometer/RH meter, at 2.5 cm above ground. Soil temperature was measured using a mercury thermometer placed 1 cm into the soil. Paired *t*-tests were used to test for differences between variables near the turtle versus at Deep Well. Because microhabitat selection was expected to change depending on the ambient temperature, I divided the data into three temperature regimes: cold (11–19.99 C), warm (20–25.99 C) and hot (26–33 C), and tested them separately. I also noted whether turtles were in burrows, under vegetation, or out in the open. Analyses were repeated using turtles in burrows only.

All statistics were carried out using the Statistical Analysis Systems package (SAS Institute, 1988) with $\alpha = 0.05$. Non-parametric tests were used when the assumptions for parametric tests were violated.

RESULTS

A total of 261 box turtles was encountered during the study, consisting of 27.4% males, 52.9% females, and 18.2% juveniles. Turtles hibernated in burrows of kangaroo rats (*Dipodomys spectabilis*), and they came out of hibernation (brumation) during May. Activity was sporadic until the monsoons started, usually in late June. By the middle to the end of October, most turtles were in hibernation.

Home Range and Movements

Male and female home ranges did not differ significantly in area (Table 2). Estimates of home range were extremely variable, especially for males. Most turtles had a smaller home range than expected if movement was random (Table 2). Turtles did not change the locations of their home ranges between years, nor did home ranges change appreciably between months among radio-tracked turtles. Considerable overlap of home ranges occurred, both between and within the sexes. Home ranges were roughly elliptical.

Four males and three females had home ranges with the major axis along the road

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FIG. 1.—Home range plots of indi
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urtles, 1991 and 1992. Home

Ellipse[3]	Max. diam.[4]
50,306 ±47,015	276 ±178
71,440 ±56,547	237 ±141
36,228 ±34,038	322 ±210
33–164,139	32–526

[1,2]	Ellipse[3]
3	571 ±591
4	573 ±574
5	570 ±606
53	

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Results

61 box turtles was encoun-
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Although a higher proportion of male non-radiotracked turtles travelled long distances over three years, the mean (±SD) of 375.1 m (±447) was not significantly different from females [326.5 m (±55)]. Juveniles moved significantly less far than adults [163.2 (±171], Kruskal-Wallis test, $F = 3.31$, $P = 0.013$) (Fig. 2). No relationship existed between time between sightings and distance moved. Total mean rate of dispersal (distance travelled between sightings/time between sightings) (±SD) was 13.4 m/day (±32) with males moving at a rate of 15.08 (±32, $n = 208$) m/day, females at 13.00 (±35, $n = 384$) m/day, and juveniles 7.50 (±8, $n = 56$) m/day. The speed for males was significantly higher than for females (Mann-Whitney U test, $U = 2.045$, $P = 0.041$).

Straight line dispersal distances of radiotracked turtles located twice weekly showed a similar pattern as in Fig. 2. Differences between the sexes were not significant. Movement occurring at least in part on the road was significantly greater than off-road movement (Mann-Whitney U test, $U = -4.639$, $P < 0.001$).

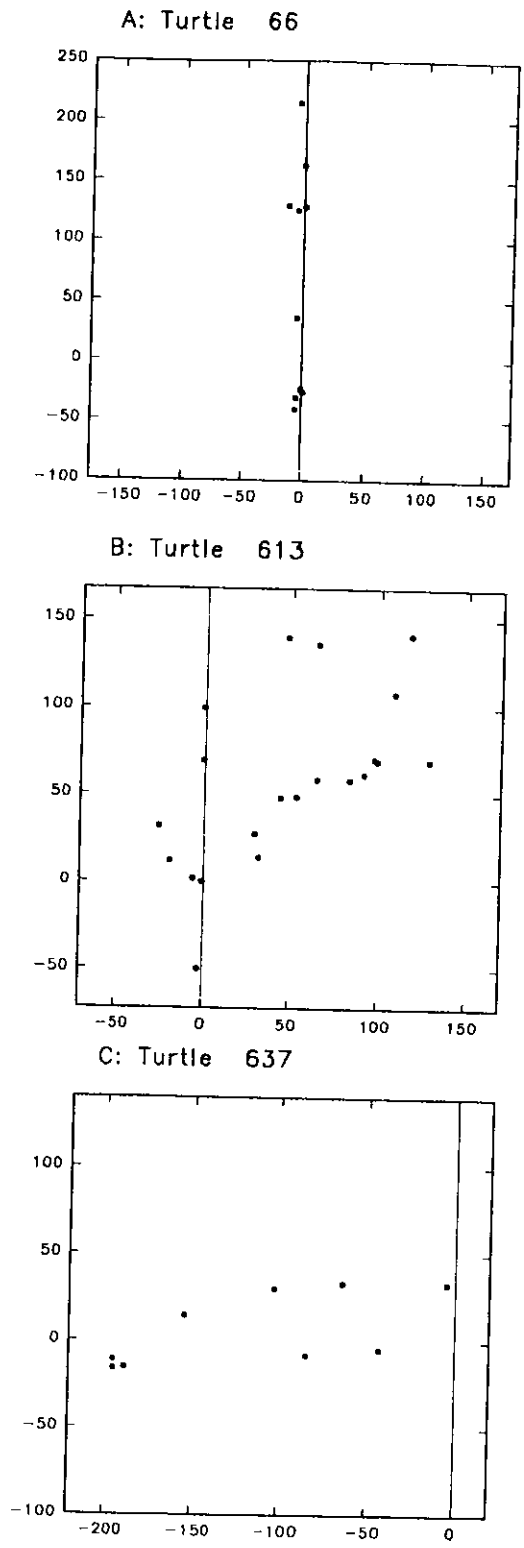

FIG. 1.—Home range plots of individual turtles. The road is represented by the line going from top to bottom through the plots. (A) a home range with the major axis along the road; (B) the major axis is slightly at an angle to the road; (C) the effect of the road on the turtle is less clear. Distances in meters.

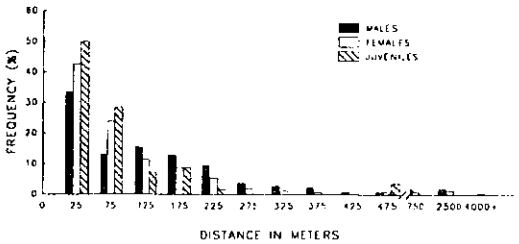

FIG. 2.—Dispersal of males (n = 209), females (n = 385), and juveniles (n = 57) along the road.

Activities

A total of 125.44 h of observations was made during the study, consisting of 258 observation periods of 30 min or less, on 143 turtles (39 males, 77 females, 25 juveniles, and two unknowns). Females rested significantly less and spent significantly more time walking than males and juveniles (χ^2 = 53.35, P < 0.0001 for resting, χ^2 = 71.50, P < 0.0001 for walking), and no significant differences were found between males and juveniles (Fig. 3). Because values for feeding and social behavior were low, differences between groups were not tested. No copulations were observed. One agonistic interaction was seen between two males on the road, taking just over 8 min. Turtle 33 approached turtle 111, lifted his front legs periodically over 111, and bumped his shell against him. Turtle 33 finally turned and walked away; 111 followed and bumped his shell against 33 from behind seven times. After the sixth bump, the turtles had their heads at right angles to each other and attempted to bite each other. Finally, 111 walked away and the interaction ended. Half an hour later, a female was found 114 m away; it is not known whether this interaction was related to her (or another female).

Ambient temperature was highly correlated with vapour pressure deficit and soil temperature (Table 3). Vapour pressure and soil temperature were also highly correlated. Solar radiation was not significantly correlated with any other variable. Ambient temperature, vapour pressure deficit, and soil temperature were relatively highly and equally correlated with the first principal component (Table 3), and thus are important in defining the immediate environment of a turtle. Only solar radi-

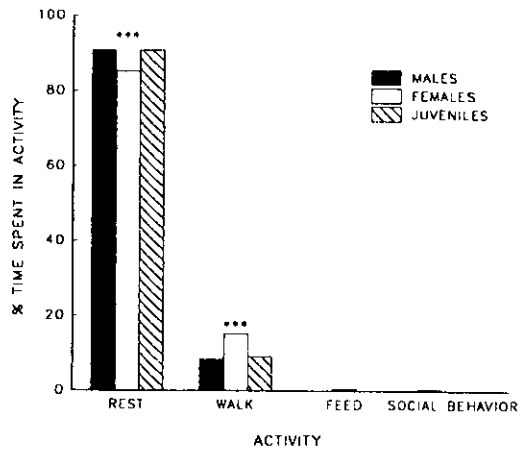

FIG. 3.—Activities of above ground turtles from observation periods (39 males, 77 females, and 25 juveniles). *** shows activities significantly different between the sexes at P < 0.001.

ation was highly correlated on the second component; it may be less important to turtles.

Environmental variables that correlated highly on the first component, used in a multiple regression analysis and alone, could not predict the activities of the turtles while above ground. However, for above ground turtles only, soil temperature was significantly higher for those found walking compared to those found resting or feeding (Kruskal-Wallis test, F = 3.42, P = 0.0356).

Environmental variables were important in predicting when turtles were active. Significant differences between all weather variables (ambient temperature, vapour pressure deficit, soil temperature, and solar radiation) were found between active versus inactive turtles (Mann-Whitney U test, U = 4.56, 5.67, 5.165, and 6.600 respectively, all P-values <0.0001). Data from radio-tracked turtles showed that activity was bimodal (Fig. 4). Turtles were active during ambient temperatures of 13–24 C, when the vapour pressure deficit was <20 mbars, and during solar radiation of 200 jules/cm²/h or less (Fig. 4). Turtles were less active at soil temperatures between 26–30 and >36 C. During periods of inactivity (36.31% of the time, not including nights), turtles stayed in kangaroo rat burrows or in clumps of vegetation.

TABLE 3.—Results of a

Correlation matrix	Ambient tem
Ambient temp.	1.000
VPD	0.918***
Soil temp.	0.605***
Sol. rad.	0.036

Eigenvalues of the correlation matrix:

	PC1	PC2
Eigenvectors: Variables		
Ambient temp.		
VPD		
Soil temp.		
Sol. rad.		

[1] VPD: vapour pressure deficit (mbar)
[2] Sol. rad.: solar radiation in jules/cm²/h.
*** P < 0.001

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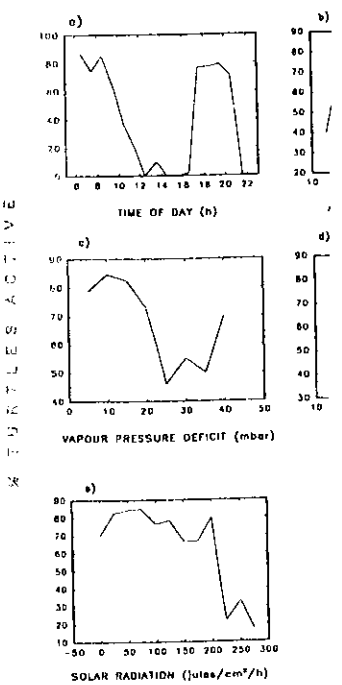
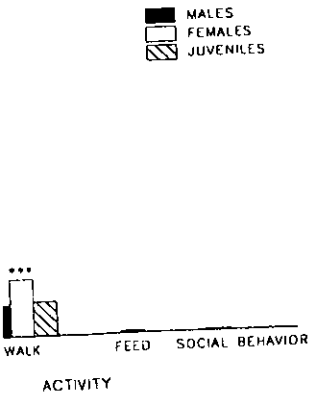


FIG. 4.—Activity of radio-tra tion to (a) time of day, (b) ambi vapour pressure deficit, (d) soil t solar radiation.



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or in clumps of vegetation.

TABLE 3.—Results of a principal component analysis of environmental variables.

Correlation matrix

	Ambient temp.	VPD[1]	Soil temp.	Sol. rad.[2]
Ambient temp.	1.000	0.918***	0.906***	−0.036
VPD	0.918***	1.000	0.861***	−0.004
Soil temp.	0.605***	−0.465***	1.000	−0.119
Sol. rad.	0.036	−0.097	−0.099	1.000

Eigenvalues of the correlation matrix:

	Eigenvalue	Difference	Proportion
PC1	2.800	1.807	0.700
PC2	0.993	0.853	0.248

Eigenvectors:

Variables	PC1	PC2
Ambient temp.	0.582	0.089
VPD	0.574	0.021
Soil temp.	0.571	0.018
Sol. rad.	−0.074	0.996

[1] VPD: vapour pressure deficit (mbar).
[2] Sol. rad.: solar radiation in jules/cm²/h.
*** $P < 0.001$

Precipitation was not used in the above analyses because of its rare occurrence and because field-work was not conducted during rain-storms. Turtles were observed to walk and feed during light rain, even when ambient temperatures were unusually high for normal activity.

When it was hot, soil temperature was significantly lower at the locations of the turtles than at Deep Well (Table 4). Ambient temperature and vapour pressure deficit at the turtle microsite was significantly higher than at Deep Well for all three categories, but the difference decreased with increase in temperature category. There were no significant differences between the sexes. Results for turtles in burrows were essentially the same as those for turtles above ground.

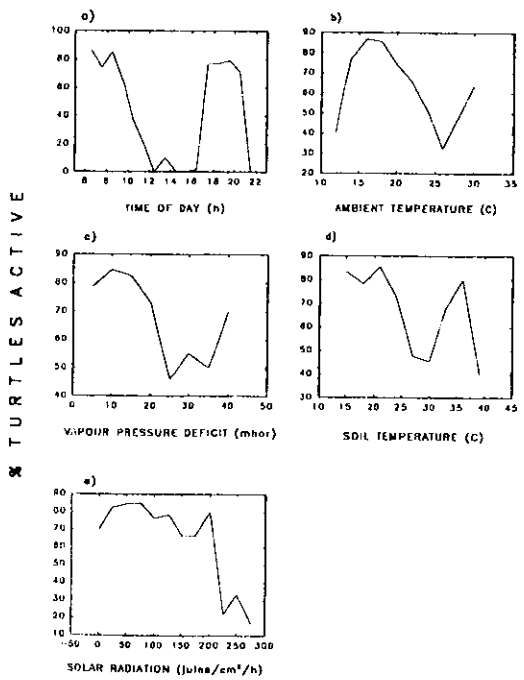

FIG. 4.—Activity of radio-tracked turtles in relation to (a) time of day, (b) ambient temperature, (c) vapour pressure deficit, (d) soil temperature, and (e) solar radiation.

DISCUSSION

Data from other turtle populations are equivocal with regard to differences in

TABLE 4.—Analysis of microhabitat selection data, showing t values from parametric and nonparametric tests, comparing values at turtles versus those from the Deep Well Meteorological Station. Cold: 11–19.99 C; warm: 20–25.99 C; hot: 26 C and above.

Variable	Cold (n = 15)	Warm (n = 30)	Hot (n = 37)
Soil temp.	1.592	−0.3571	−11.083***
Ambient temp.	8.448***	7.634***	5.542***
VPD[1]	4.129***	3.988***	2.238*

[1] VPD: vapour pressure deficit (mbar).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

home range size between sexes. For other box turtles, Blair (1976), Doroff and Keith (1990), Stickel (1950, 1989), and Williams and Parker (1987) found no differences between the sexes whereas Madden (1975) and Metcalf and Metcalf (1970) found females to have larger home ranges than males, and Kiester et al. (1982) found males moved larger distances than females. In aquatic turtles, there is a tendency for males to move more frequently and for longer distances than females (Gibbons, 1986). In tortoises, males seem to have larger home ranges (see references in Diemer, 1992; Ernst et al., 1994; O'Conner et al., 1994). The only significant difference obtained between sexes in this study was that males moved faster than females.

Desert box turtles have larger home range areas, measured by maximum diameter, than those in more mesic areas, as predicted. Only female ornate box turtles in southeastern Kansas had comparable home range sizes (Table 1). However, the present study was done on and alongside a road, and this may have led to estimates being larger than if no road were present. Some box turtles clearly used the road to do most of their movement; however, estimates of home ranges completely away from the road are needed, as in McRae et al. (1981), but are not presented in this study. Also notable was the large variation in home range estimates between methods; comparing methods other than maximum diameter, when more studies have been conducted, may lead to very different results.

Great variability in individual home range sizes have been obtained in other studies on turtles (e.g., Diemer, 1992; Doroff and Keith, 1990; O'Connor, 1994), and these could be responsible for non-significant differences between the sexes. Large sample sizes therefore are needed before conclusions can be drawn. However, the variability may provide clues as to what factors are important in determining home range size. All box turtles in this study lived within 2.4 km of each other; suitable habitats may therefore be patchy and may possibly be related to the presence of kangaroo rat burrows. Two radio-tracked turtles died (cause unknown) during the study, and ill health may have contributed to their small home ranges. One turtle brumated unusually early (beginning of September), and that may explain her small home range; another was apparently healthy, did not brumate early, but nevertheless had a very small home range.

Most of the time that a turtle is active (above ground) is spent resting. Although females spent more time walking than males or juveniles, they did not move larger distances. Little time is spent in social behavior; it is not thought to be important in influencing movements of box turtles, as found by Stickel (1950) for *T. carolina* and Legler (1960) for *T. o. ornata*.

Environmental variables alone were unable to explain the variation in behavior of active box turtles, but individuals were more active during conditions of low and medium temperatures and solar radiation, and high humidity. Extremes were avoided, as was predicted.

Box turtles consistently chose microhabitats with lower moisture and soil temperatures but higher ambient temperatures than those at the Meteorological Station. The results for ambient temperature and humidity were unexpected; *T. carolina triunguis* prefers moderate temperatures and high humidity (Reagan, 1974). *Terrapene o. luteola* may be unable to find as cool or moist conditions as those at the Meteorological Station and measurements were not made deep inside burrows. These differences decreased for the hotter categories, however. Soil temperature was obviously an important variable in microhabitat selection, due to conductive factors.

Movement in box turtles living in the desert is closely linked to the environment. However, there are still other factors, presumably motivational, that are difficult to quantify, and a model that would predict when and where turtles move is far from being worked out. Obviously many factors are in operation, and no simple series of variables will explain fully the movements of turtles.

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LITERATURE C

ADAMS, S., AND M. C. DECARVAL
of heat exchange in the orna
pene ornata. Comp. Biochem.
AUFFENBERG, W., AND J. B. I
mography of terrestrial turtles
Harless and H. Morlock (Eds
tives and Research. John Wiley
New York.
AUFFENBERG, W., AND W. G. V
pherus berlandieri in south
Florida State Mus. Biol. Sci. 1
BLAIR, W. F. 1976. Some asp
the ornate box turtle, *Terraper*
Nat. 21:89–104.
DIEMER, J. E. 1992. Home ra
of the tortoise *Gopherus poly*
Florida. J. Herpetol. 26:158–1
DIXON, K. R., AND J. A. CHAPMA
mean measure of animal activ
1040–1044.
DOROFF, A. M., AND L. B. KE
raphy and ecology of an orn
rapene ornata) population i
consin. Copeia 1990:387–399.
ERNST, C. H., R. W. BARBOUR
1994. Turtles of the United
Smithsonian Institution Press,
FITCH, H. S. 1958. Home ra
seasonal movements of vertel
sity of Kansas Natural Histor
Kansas Publ. Mus. Nat. Hist.
GIBBONS, J. W. 1986. Moven
turtle populations: Applicabili
the desert tortoise. Herpetolo
KIESTER, A. R., C. W. SCH
SCHWARTZ. 1982. Promoti
transient individuals in an oth
ulation of box turtles (*Terra*
guis). Evolution 36:617–619.
LEGLER, J. M. 1960. Natural
box turtle, *Terrapene ornata*
Kansas Publ. Mus. Nat. Hist.
MADDEN, R. 1975. Home ra
Orientation in the Eastern B
carolina carolina. Ph.D. Di
University of New York, Ne

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Literature Cited

Adams, S., and M. C. DeCarvalho, Jr. 1984. Rates of heat exchange in the ornate box turtle, *Terrapene ornata*. Comp. Biochem. Phys. 79A:359–361.

Auffenberg, W., and J. B. Iverson. 1979. Demography of terrestrial turtles. Pp. 541–570. *In* M. Harless and H. Morlock (Eds.), Turtles: Perspectives and Research. John Wiley and Sons, New York, New York.

Auffenberg, W., and W. G. Weaver. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Florida State Mus. Biol. Sci. 13:141–203.

Blair, W. F. 1976. Some aspects of the biology of the ornate box turtle, *Terrapene ornata*. Southwest. Nat. 21:89–104.

Diemer, J. E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. J. Herpetol. 26:158–165.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61: 1040–1044.

Doroff, A. M., and L. B. Keith. 1990. Demography and ecology of an ornate box turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1990:387–399.

Ernst, C. H., R. W. Barbour, and J. E. Lovich. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the University of Kansas Natural History Reservation. Univ. Kansas Publ. Mus. Nat. Hist. 11:63–326.

Gibbons, J. W. 1986. Movement patterns among turtle populations: Applicability to management of the desert tortoise. Herpetologica 42:104–113.

Kiester, A. R., C. W. Schwartz, and E. R. Schwartz. 1982. Promotion of gene flow by transient individuals in an otherwise sedentary population of box turtles (*Terrapene carolina triunguis*). Evolution 36:617–619.

Legler, J. M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. Univ. Kansas Publ. Mus. Nat. Hist. 11:527–669.

Madden, R. 1975. Home range, Movements, and Orientation in the Eastern Box Turtle, *Terrapene carolina carolina*. Ph.D. Dissertation, The City University of New York, New York, New York.

McRae, W., J. L. Landers, and J. A. Garner. 1981. Movement patterns and home range of the gopher tortoise. Am. Midl. Nat. 106:165–179.

Metcalf, E., and A. Metcalf. 1970. Observations on ornate box turtles. Trans. Kansas Acad. Sci. 73:96–117.

Milstead, W. M., and D. W. Tinkle. 1967. *Terrapene* of western Mexico, with comments on the species groups in the genus. Copeia 1967:180–187.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223–249.

Munger, J. C. 1984. Home ranges of horned lizards (*Phrynosoma*): Circumscribed and exclusive? Oecologia (Berlin) 62:351–360.

O'Connor, M. P., L. C. Zimmerman, D. E. Ruby, S. J. Bulova, and J. R. Spotila. 1994. Home range size and movements by desert tortoises, *Gopherus agassizii*, in the eastern Mojave Desert. Herpetol. Monogr. 8:60–71.

Owenby, J. R., and D. S. Ezell. 1992. Monthly station normals of temperature, precipitation, and heating and cooling degree days 1961–1990. New Mexico. Climatography of the U.S. No. 81, U.S. Dept. of Commerce, National Oceanographic and Atmospheric Administration and National Climatic Data Center, Asheville, North Carolina.

Pritchard, P. C. H. 1979. Encyclopedia of Turtles. T.F.H. Publications, Neptune, New Jersey.

Reagan, D. P. 1974. Habitat selection in the three-toed box turtle, *Terrapene carolina triunguis*. Copeia 1974:512–527.

Rose, L., and F. W. Judd. 1979. Home range estimates of *Gopherus berlandieri*. Proc. Sym. Desert Tortoise Council 1979:187.

Russo, P. M. 1972. Behavioral Thermoregulation and Energy Budget of the Eastern Box Turtle, *Terrapene carolina carolina* (Linne). Ph.D. Dissertation, Rutgers University, New Brunswick, New Jersey.

SAS Institute, Inc. 1988. SAS-STAT User's Guide. Version 6. SAS Institute, Inc., Cary, North Carolina.

Stickel, L. 1950. Populations and home range relationships of the box turtle. Ecol. Monogr. 20:351–378.

———. 1989. Home range behavior among box turtles (*Terrapene c. carolina*) of a bottomland forest in Maryland. J. Herpetol. 23:40–44.

Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66:1176–1184.

Williams, E., and W. S. Parker. 1987. A long-term study of a box turtle (*Terrapene carolina*) population at Allee Memorial Woods, Indiana, with emphasis on survivorship. Herpetologica 43:328–335.

Zeng, Z., and J. H. Brown. 1987. Population ecology of a desert rodent: *Dipodomys merriami* in the Chihuahuan desert. Ecology 68:1328–1340.

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