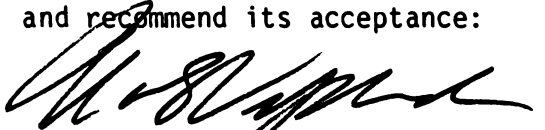


To the Graduate Council:

I am submitting herewith a dissertation written by Marilla Davis entitled "Aspects of the Social and Spatial Experience of Eastern Box Turtles, Terrapene carolina carolina." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

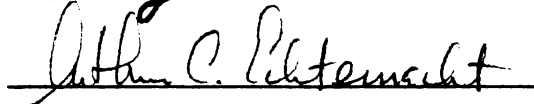

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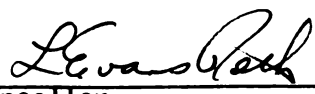








Accepted for the Council:


Vice Chancellor
Graduate Studies and Research

ASPECTS OF THE SOCIAL AND SPATIAL EXPERIENCE OF EASTERN
BOX TURTLES, TERRAPENE CAROLINA CAROLINA

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Marilla Davis

March 1981

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DEDICATION

To my mother, Irma Davis; the memory of my father, Harry Davis; my uncle, Milton Krakower; my grandmother, Anna Krakower; my grandfather, Robert Krakower; and the memory of my "godmother," Dobi Topkins Cohen; whose love, ideas, and ideals have shaped my life.

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Rewgalduin and Galladrial

ABSTRACT

An investigation of the ways in which eastern box turtles experience their social and spatial environment was conducted using an ethological approach in combination with a phenomenological orientation. The primary question of what the turtles experienced was addressed by determining what they could discriminate. Discrimination between other individuals and between areas of space was investigated. The inquiry was extended to investigate the quality of this experience by assessing the functional significance of the cues and behavior patterns involved in such discriminations. The approach was to observe behavior in relation to its context in a combination of naturalistic, semi-naturalistic, and laboratory settings.

Discrimination of spatial areas was studied in the field by repeatedly locating turtles through the use of telemetry. Most turtles were found to use only prescribed areas within the larger area of suitable habitat. Difficulties in unobtrusively observing the turtles in the field made it impossible to assess directly the basis of this discrimination.

Direct observations of turtles' movements and more detailed information about their locations were obtained from turtles introduced into an outdoor enclosure. The turtles showed significant individual preferences for different areas of the enclosure, indicating their ability to discriminate among such areas. The resident turtles were subsequently removed from the enclosure while new shelter sites were installed. A new group of turtles was then introduced into the enclosure

simultaneously with the reintroduction of the residents. A significant difference in use of resting sites by new and resident turtles was obtained, with more of the new turtles using the new shelter sites and more of the previous residents using previously established sites. The turtles also showed overall patterns of area use: they tended to move along the perimeter and to rest in corner locations, suggesting certain cues which they plausibly might have used to guide their movements.

The functional significance of two such potential cues, darkness and slope, was investigated by presenting them to hatchling box turtles under controlled laboratory conditions. The turtles moved significantly more often to a dark rather than a light wall of a chamber, regardless of color, and showed a tendency to move uphill rather than downhill. This suggests that darkness may be experienced as attractive by the turtles even in the absence of other factors which would frequently accompany it in the natural habitat.

The turtles' experience of other turtles was investigated by addressing the basic question of recognition of other individuals, or classes of individuals, within a spatial context. Proxemic studies of turtles in an outdoor enclosure and of hatchlings housed indoors demonstrated that in both settings turtles who touched each other were significantly more likely to be found together again than those who were found close together but not touching.

Discrimination between neighbors and strangers was investigated in two parallel studies. One tested wild-caught "neighbors," (trapped near each other) vs. "strangers," (found farther apart); the other tested hatchlings housed together vs. separately. Turtles discriminated between neighbors and strangers by displaying higher levels of agonistic

and investigatory behavior toward strangers, with some of these differences attaining statistical significance. This study progressed beyond the basic issue of neighbor recognition to an investigation of the meaning of certain potentially communicative gestures.

The existence of individual styles of interacting was investigated by comparing the behavior of turtles across contexts. A hierarchical pattern of feeding success was obtained within groups of hatchlings. Hatchlings who were more successful in feeding competition were found to react less to human contact. Wild turtles who reacted with less head retraction and movement to human approach and contact traversed greater distances per day in the field, thus suggesting the presence of individual styles of experiencing both the social and spatial environment.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION.	1
The Study of Experience	1
Past Investigations	6
General Natural History	6
Individual Use of Space	9
Home range size	10
Population density.	13
Home range tenacity	14
Movements	15
Differential use of areas within the home range	17
Spatial cues.	18
Summary	20
Individual Interactions with Other Turtles.	21
Individual Styles of Interacting.	25
The Present Investigation	27
II. INDIVIDUAL USE OF SPACE	29
Study 1. Movements and Home Ranges in the Natural Habitat. .	29
Introduction.	29
Methods	29
Setting	29
Apparatus	36
Procedure	40
Subjects.	44
Results	46
Observations.	46
Locations	47
Discussion.	55
Study 2. Area Preferences in a Semi-Naturalistic Setting .	60
Introduction.	60
Methods	60
Results	63
Discussion.	74

CHAPTER	PAGE
Study 3. Responses to Spatial Cues	76
Introduction.	76
Methods	77
Results	80
Discussion.	82
III. PREFERENCE FOR INDIVIDUALS AND RECOGNITION OF NEIGHBORS . . .	86
Study 4. Preference for Individuals.	86
Introduction.	86
Methods	86
Results	88
Zoo turtles	88
Hatchlings.	89
Discussion.	91
Study 5. Recognition of Neighbors.	93
Introduction.	93
Methods	98
Subjects.	98
Apparatus	100
Procedure	100
Results	101
Discussion.	106
IV. INDIVIDUAL STYLES OF INTERACTING.	109
Study 6. Individual Consistencies in Social and Spatial Relations	109
Introduction.	109
Methods	109
Results	110
Discussion.	111
V. GENERAL DISCUSSION AND SUMMARY.	117
LITERATURE CITED	124
VITA	133

LIST OF TABLES

TABLE		PAGE
1.	Estimates of box turtle home range size.	11
2.	Important flora in the study site, arranged by topographic area in approximate order of prevalence.	32
3.	Common and scientific names of important flora in the study area	34
4.	Behavior states recorded during field observations	42
5.	Behavior events recorded during field observations	43
6.	Basic information on turtles observed in the study area, 1978.	45
7.	Estimated home range areas and lengths	54
8.	Daily displacement (straight-line distance between sightings divided by number of intervening days)	56
9.	Gender and number of observed locations of 21 box turtles in the enclosure at the Zoological Park	64
10.	Median temperature and humidity for introductions to the zoo enclosure during which turtles crossed the center of the enclosure vs. moved along the perimeter vs. remained in the initial quadrat.	67
11.	Mean proportions of each turtle's locations within Areas 1, 2, 3, and 4 compared with the proportion of total square meters contained within each area	70
12.	Daily area preference compared with initial choice of resting area	73
13.	Differential use of new vs. established shelter sites by new vs. reintroduced turtles	75
14.	Turtles' choices of dark (D) vs. light (L) portions of the test chamber in each experimental condition.	81
15.	Turtles' choices of uphill (U) vs. downhill (D) portion of the test chamber in each experimental condition.	83
16.	Number of turtles choosing dark vs. light by uphill vs. down- hill portions of the test chamber in three experimental conditions	84

TABLE

PAGE

17. Number of touching vs. close pairs which were observed together once vs. more than once	90
18. Number of touching vs. close pairs which were of mixed vs. same sex	90
19. Behavior categories recorded during neighbor recognition testing.	94
20. Mean and median frequencies of nosing, biting or snapping, and head-ducking by neighbor vs. stranger pairs.	102
21. Mean and median frequencies of gaping, neck-arching, and mouthing by neighbor vs. stranger pairs.	104
22. Mean and median duration of contact, number of squares entered, and duration of feeding for neighbor vs. stranger pairs.	105
23. Number of neighbor vs. stranger pairs in which the food was won by one turtle vs. divided.	107
24. Correlation between hatchlings' reactions to human contact and their success in food competition against other hatchlings	113
25. Correlation between wild turtles' mean head extension subsequent to human contact or approach and mean displacement per day.	114
26. Correlation between wild turtles' mean activity score subsequent to human contact or approach and mean displacement per day.	115

LIST OF FIGURES

FIGURE	PAGE
1. Topographic map of the study site and surrounding area. . . .	30
2. A view of the study area.	37
3. A transmitter-equipped turtle in the study area	37
4. Locations of Turtle A in and near the study site from 6/22/78 to 8/19/78.	48
5. Locations of Turtle C in and near the study site from 6/29/78 to 7/17/78.	49
6. Locations of Turtle E in and near the study site from 7/14/78 to 8/20/78.	50
7. Locations of Turtle F in and near the study site from 7/17/78 to 8/6/78	51
8. Estimated home ranges of Turtles A, C, E, and F. -----: Longest axis.	53
9. Box turtle enclosure at the Knoxville Zoological Park	61
10. Composite map of the location of all 21 box turtles during their first 45 minutes in the enclosure. Quadrat locations 1 minute apart are connected by straight lines. Turtles' initials indicate their locations at the end of 45 minutes.	65
11. Four areas of the box turtle enclosure. Areas 1, 2, and 3 were preferred by turtles	69
12. Number of times each turtle was found in each area of the enclosure	71
13. Orientations of test chamber with slope and starting position as shown. Light lines indicate light walls; heavy lines indicate dark walls. Direction of arrows indi- cate direction of upward slope.	78
14. Food competition setting.	95
15. Head-ducking and biting	95
16. Nosing.	95
17. Neck-arching and gaping	95
18. Competing for food.	95

FIGURE

PAGE

19. Food competition hierarchies based on single paired encounters with members of own group and other group	112
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CHAPTER I

INTRODUCTION

The Study of Experience

. . . . We must first blow, in fancy, a soap bubble around each creature to represent its own world, filled with the perceptions which it alone knows. When we ourselves then step into one of these bubbles, the familiar meadow is transformed. . . . This we may call the phenomenal world or the self-world of the animal (Von Uexküll, 1934, p. 5).

Von Uexküll approached the study of the animal's experience though this concept of the Umwelt, or the "surrounding self-world," of the animal.

In order to understand the structure of the Umwelt, one must identify the animal's perceptual cues among all possible stimuli in its environment. To color the Umwelt appropriately, one must specify the "functional tones" of these elements by determining the significance of the behavior directed toward them (Von Uexküll, 1934). The ongoing experience of an animal may thus be investigated as a way in which that individual perceives and relates to the world in which it lives.

This subject has been largely ignored as a topic for recent psychological investigation. The experience of non-human animals was, however, the subject of several early, well-considered investigations. In addition to Von Uexküll (1934), careful observations and thoughtful discussions pertinent to this issue were provided by Darwin (1872), Jennings (1906, 1910, 1933), and Washburn (1908, 1916).

Other workers sometimes replaced careful observations with casual anecdotes, however, and combined these with interpretations based upon a human context rather than the animal's own (e.g. Romanes,

1882, 1884). Such problems led to a reaction in the form of Morgan's Canon (1894), which stated that behavior should not be ascribed to a "higher" psychical faculty when it can be explained by one which stands "lower" in the "psychological scale." In psychology in general, introspectionism and the study of consciousness as practiced by Wundt and Titchner gave way to the behaviorism of Watson, Pavlov, and eventually Skinner.

The field of ethology has emphasized the study of behavior which is meaningful to the animal in the context of its natural existence and has been critical of the behavioristic tradition for its failure to do so (reviewed by Burghardt, 1973; Dewsbury, 1978). Classical ethologists, in particular, conducted many studies which revealed much about the meaning of certain cues for the animal (Lorenz, 1935; Tinbergen, 1951). Ethologists, however, have generally not overtly discussed the study of experience or, at most, have discussed it equivocally: "Do animals undergo subjective experience? If I were able to give the answer, I would have solved the problem of body-and-mind" (Lorenz, 1963, p. 323). Verplanck, however, has dealt with the issue directly, asserting, "Experiencing is doing Phenomena cannot be conceptualized independently of acting" (1971, p. 484).

This is the view of the phenomena of experience taken by phenomenologists such as Merleau-Ponty (1942, 1945). Pollio (in press) states, "Whatever we do always carries its meaning within itself; there is no way in which to separate the meaning from the movement."

Recent work on experience has dealt almost exclusively with humans, often relying upon language to convey the experience of the subject. Of those studies which have involved other animals, most have

dealt with language, both as a means of communicating experience and as an indication of a "level" of experience similar to our own (Fouts, 1973; Gardner and Gardner, 1969; Lilly 1961, 1967; Premack, 1972). They therefore have been limited to apes and other animals which may possess the ability to use language.

Recently there have been calls for increased study of experience in humans (Lieberman, 1979) and other animals (Griffin, 1976). Lieberman, however, suggests a cautious return to introspectionism and Griffin, after raising a number of interesting issues about the problems of studying awareness in non-humans, falls back on the limited solution of using a shared language (such as sign language with the appropriately trained apes) to ask the animal about its experience. He cautions, however: "It is very easy for scientists to step into the passive assumption that phenomena with which their customary methods cannot deal effectively are unimportant or even nonexistent" (Griffin, 1976, p. 56).

A more direct, generally applicable, behavioral approach to the study of experience is suggested by Thinès (1970, 1977; Thinès and Zayan, 1975). Thines interprets experienced phenomena as "a mode of expression functionally included in the behavioral acts themselves" (1977, p. 149). This avoids the implication "that subjective experience is an epiphenomenon, i.e. an accompanying realm of events devoid of biological significance" (1977, p. 149) and includes it in scientific studies of behavior.

Thinès presents closely reasoned discussions of the nature of scientific investigation and argues that experience is an essential subject-matter of psychology (1977). To exclude it as unsuitable for

scientific investigation is only to attain "the purity of that which is devoid of life" (1970, p. 72).

With reference to the study of experience, Thinès states, "The method is that of experimental ethology but the hypothetical framework is in line with the phenomenological standpoint" (1977, p. 147). By posing different questions, one is led to investigations which may reveal previously unexplored phenomena. The method, however, is not incompatible with a behavioral approach; phenomenal experience may be regarded as an activity, a behavior, and an accurate description of such experience is essential in psychology (Malone, 1975).

Specifically, one may gain an initial understanding of the experience of another animal through behavior which reveals which aspects of its social and physical environment are discriminated by the animal (Von Uexküll, 1934). Choice is a form of discrimination by the animal (Burghardt, 1977a; Buytendijk, 1932).

The same behavior will often indicate preference as well as discrimination (Buytendijk, 1932; Dawkins, 1977). This represents a step toward the goal of identifying the immediate significance to the animal of the cues in its environment and of its own behavior patterns. This goal may be approached by studying the relationships of specific behavior patterns to such cues and to other behavior patterns, or, in other words, by studying behavior in context (Buytendijk, 1962; Thinès and Zayan, 1975).

Certain types of behavior are particularly amenable to the investigation of experience. Three interrelated and especially suitable topics are mentioned below:

1. The complex processes inherent in orientation and use of space, with the attendant simple measure of location, are conducive to this type of investigation. Tolman's (1948) work on maze learning in rats led him to formulate the idea of a "cognitive map" as Griffin's (1946, 1950) discovery of echolocation in bats and work on orientation led him to formulate The Question of Animal Awareness (1976). Furthermore, use of space provides a context within which other types of behavior occur. Spacing is an integral component of social behavior.

2. Social behavior provides especially rich opportunities for the study of experience because it affords the investigator an opportunity to "eavesdrop" upon communication occurring between members of the same species and to observe reactions of individuals to each other's behavior, thus multiplying the opportunities for relating behavior to its context.

3. Finally, individually consistent ways of relating to both the social and spatial environment may be investigated as modes of experiencing or, in other words, styles of interacting.

The behavioral study of experience is based upon the ethological approach, with a thorough descriptive foundation, but focuses attention more directly upon the experience of the subject. Such a phenomenological ethology extends possible research on experience to a wide range of animals.

The present study explores the experience of eastern box turtles, Terrapene carolina carolina (Emydidae), by investigating individual box turtles' recognition of and preference for spatial areas and for other box turtles and by investigating individual turtles' styles of interacting with their spatial and social environments.

Past Investigations

General Natural History

Box turtles comprise the genus Terrapene. Two species of box turtles inhabit the United States of America, Terrapene carolina in the eastern portion and Terrapene ornata in the west. Terrapene carolina carolina, the eastern box turtle, is the subject of the present investigation. Its range extends from the southeastern tip of New Hampshire west to the Mississippi River in the southern half of Illinois and south to northern Mississippi, central Alabama, and southern Georgia (Conant, 1975; Pritchard, 1979). Other subspecies include T. c. triunguis, the three-toed box turtle; T. c. major, the Gulf Coast box turtle; and T. c. bauri, the Florida box turtle. Terrapene ornata includes the subspecies T. o. ornata, the ornate box turtle, and T. o. luteola, the desert box turtle.

The box turtles are one of the most terrestrial genera in the family Emydidae, which includes many of the common pond turtles. In their terrestrial habits box turtles resemble tortoises, which are completely terrestrial and which comprise the closely related family Testudinidae (Carr, 1952; Pritchard, 1979). Eastern box turtles inhabit woodland habitat; ornate and desert box turtles inhabit more open, arid land.

Box turtles are inactive at night, usually resting in body-shaped depressions which they dig in the undergrowth or earth. Such "forms" may also be used during the heat of the day (Dolbeer, 1969; Legler, 1960; Schwartz and Schwartz, 1974). Box turtles may remain inactive for several days at a time even during favorable weather conditions

when others are active (Dolbeer, 1969; Schwartz and Schwartz, 1974; Stickel, 1950). During periods of very hot or cold weather box turtles dig deeper into the substrate and survive in a quiescent state (Legler, 1960; Stickel, 1950).

Spring emergences are followed by a peak in mating activity with one another, perhaps larger peak of mating behavior in the fall (Dolbeer, 1969; Legler, 1960; Schwartz and Schwartz, 1974). Females typically lay one clutch of two to seven (usually four or five) eggs in a season (Carr, 1952). It is thought that the eggs usually hatch in two to three months, but this period can be much longer, depending upon temperature and possibly other environmental conditions (Allard, 1948; Legler, 1960).

Hatchlings average about 3 cm in length (Conant, 1975). Box turtles may not reach sexual maturity for 8 to 14 years (Legler, 1960; Nichols, 1939a) and there are numerous records of box turtles living more than 40 years, according to Conant (1975) and Pritchard (1979). Stickel (1978) found that 11-15% of marked turtles estimated to be 20 years old in 1945 were still alive and in the same general area 30 years later in 1975. Some individuals were estimated to be over 80 years old (Nichols, 1939a; Stickel, 1978). A length of 11-16 cm is typically attained by adulthood according to Conant (1975). This is compatible with estimates of 11-12 cm and 13-14 cm by Stickel (1950) and Nichols (1939a), respectively. After this, growth may slow and become almost imperceptible (Legler, 1960; Nichols, 1939a; Stickel, 1978).

Each plate of the carapace and plastron contains a series of concentric rings, known as growth-rings or annuli, which are formed by the alternation of seasons of growth and quiescence. These have been

found to be a fairly reliable indication of age in appreciably growing turtles. In a population of marked turtles studied for 30 years, the number of new rings indicated the number of elapsed years to within one year in 77% of the growing turtles (Stickel, 1978). Nichols (1939a) presents case by case data on 18 turtles which may be analyzed to show that in 14 of these turtles (78%) the number of new rings indicated the number of elapsed years to within 1 year. In the remaining four turtles the number of rings underestimated the number of elapsed years. As these four turtles all had at least 13 rings, it seems possible that they were no longer growing enough to form distinguishable rings.

Adults possess a high-domed, calcified shell with a single hinge in the lower shell (the plastron) which enables it to close upward until the edges contact the edges of the upper shell (the carapace), thus completely enclosing the turtle. Adult box turtles are thought to have few potential predators and to be relatively secure from predation (Legler, 1960). Hatchling box turtles do not possess a functional hinge, nor can they fully retract into their still-soft shells. Perhaps in part because their greater vulnerability may occasion different habits, hatchlings are rarely observed even in areas where older turtles are common.

Adults possess several external characteristics which may be used to distinguish females from males. Females have smaller tails with the opening of the cloaca closer to the body, more convex plastrons, and brownish eyes, in contrast to the red eyes of the adult males (Carr, 1952; Legler, 1960; Nichols, 1940).

Box turtles are omnivorous, opportunistic feeders. Common food items include mushrooms, fruits (especially berries) and other high

quality vegetation, as well as various invertebrates (Legler, 1960; Stickel, 1950).

Individual Use of Space

Individual recognition of, and preference for, spatial areas may be demonstrated if individuals consistently occupy circumscribed areas (referred to as home ranges) despite a surrounding region of suitable habitat and activity levels which would enable them to traverse greater distances.

Individual preferences may be demonstrated further by the differential use of areas within the home range, as, for instance, when certain areas are repeatedly selected as resting sites. That such choices represent individual recognition and are not solely the result of micro-habitat limitations may be established if individuals whose overlapping home ranges permit them access to the same area differentially use features of that area. At times, such differential use of space may also have social implications.

One may progress from an initial level of establishing whether individuals know and prefer certain areas to the next level of understanding the nature of this experience by investigating the relationship between the animal's movements and specific cues in its environment. Experimentation may be particularly useful at this level.

All phases of such an investigation must be based upon a thorough descriptive foundation in order to elucidate the animal's relation to its spatial environment and to understand other activities, such as social behavior, which have important spatial components.

The majority of the limited behavioral research on box turtles has focused upon their use of space. Occupation of home ranges is consistently reported (Breder, 1927; Dolbeer, 1969; Fitch, 1958; Legler, 1960; Medsger, 1919; Metcalf and Metcalf, 1978; Nichols, 1939b; Schneck, 1886; Schwartz and Schwartz, 1974; Stickel, 1950; Williams, 1961; Yahner, 1974).

Home range size. Home range sizes reported in the literature are shown in Table 1. (Measures reported here have been converted to metric units to facilitate comparisons. For the same reason, diameters were calculated on the basis of reported areas and are indicated in parentheses.) Home range size estimates were generally based upon adult turtles because of the scarcity with which juveniles are found. "Trips" by females outside their established home ranges were excluded from their calculations by Fitch (1958) and Stickel (1950). Such trips are discussed on pp. 15-17.

The discrepant measures reported in the literature do not facilitate comparisons. Further, the most commonly reported measure was a "diameter" which, in actuality, was usually the longest axis of an irregular figure enclosing the known locations of a turtle. The use of such a linear measure to describe the size of an area seems questionable. The area of the convex polygon enclosing all sightings seems a more realistic measure. Perhaps the reliance upon "diameters" is partly attributable to the lack of sufficient sightings to calculate a meaningful area. Home range sizes were reported for turtles sighted only two or three times by Dolbeer (1969), Fitch (1958), Legler (1960) and Williams (1961).

Table 1. Estimates of box turtle home range size.

Size	Method	No. of Turtles	Mean Obs./ Turtle	State	Source
<u>Terrapene c. carolina</u>					
74 m	Diameter of smallest circle enclosing all locations	76	4	TN	Dolbeer, 1969
113 m (♀) 100 m (♂)	Greatest diameter of figure enclosing all locations	55	8	MD	Stickel, 1950
114 m	Diameter of smallest circle enclosing all locations	130	3	IN	Williams, 1961
229 m	"normal diameter"	?	?	NY	Nichols, 1939b
<u>Terrapene c. triunguis</u>					
1.5 ha (Diameter of 1.5 ha circle = 138 m)	Smallest rectangle enclosing all locations (?)	239	8	MO	Schwartz and Schwartz, 1974
<u>Terrapene o. ornata</u>					
2.0 ha (Diameter of 2.0 ha circle = 160 m)	Area of figure connecting peripheral locations	8	(minimum of 6 obs.)	KS	Legler, 1960

Table 1. (Continued)

Size	Method	No. of Turtles	Mean Obs./ Turtle	State	Source
<u>Terrapene o. ornata</u>					
2.3 ha 169 m	Area and diameter of circle determined by equating radius with mean distance between successive locations	44	3	KS	Legler, 1960
2.2 ha 167 m	Same as above	14	3	KS	Fitch, 1958

Despite these problems, estimated home range sizes were of the same order of magnitude. Generally, larger home ranges were reported for ornate box turtles, Terrapene o. ornata, who live in drier, more open habitat and are reported to have lower population densities (see below).

Population density. There have been no reports of territorial defense in the field. Boice (1970) however, reports exclusive occupation of an area in an enclosure by a dominant male box turtle and a female with whom he mated. Field work indicates that box turtles' home ranges overlap greatly without apparent regard for age or sex classes (Dolbeer, 1969; Stickel, 1950). Thus, despite relatively large home range sizes, relatively high population densities may be achieved.

Terrapene carolina carolina were estimated to have densities of 19-23 adult turtles per hectare in hilly, wooded habitat in Knox County, Tennessee (Dolbeer, 1969). Densities were estimated at 10-12 turtles per hectare in lowland wooded habitat in Maryland (Stickel, 1950), although there has since been evidence of decreasing population density (Stickel, 1978). Ten adults per hectare were reported in Indiana (Williams, 1961).

Population densities decreasing from 26-34 turtles per hectare in 1967 to 18-19 turtles per hectare in 1973 were reported for Terrapene carolina triunguis in central Missouri (Schwartz and Schwartz, 1974). They used trained dogs to locate turtles and included adult and large juvenile turtles in their population estimates.

Terrapene ornata ornata were estimated to occur with densities of 6-16 turtles, including juveniles, per hectare, in favorable habitat in Kansas (Legler, 1960).

Home range tenacity. Box turtles have been found to occupy the same home ranges for many years (Nichols, 1939b; Stickel, 1950). Yahner (1974) located turtles sighted by Dolbeer (1969) 3 or 4 years earlier and found 89% of the turtles within one average home range diameter (74 m) of their previous locations. Turtles were found to have yearly ranges which overlapped extensively over a 6 year period (Schwartz and Schwartz, 1974). Eastern box turtles were found within their previously established home ranges even after flooding had submerged the area to a depth of almost one meter (Stickel, 1950).

Box turtles which were experimentally displaced by as much as 1.2 km were reported to home in early studies by Breder (1927) and Nichols (1939b). Later experimental work has confirmed the ability of box turtles to home from somewhat greater distances. Eleven of fourteen eastern box turtles confined in closed containers, displaced 0.6-2.0 km, and then released and trailed for an average of 45 days were found to head within 90° of their homeward directions (Lemkau, 1970). Twenty-two of forty-three eastern box turtles confined in closed containers, displaced 0.4-9.3 km, and released in an open field were found to move an "appreciable" distance in an "approximately homeward direction" during observation sessions of 10 minutes to 2 hours (Gould, 1957, p. 337). In a later study using similar methods, eight eastern box turtles selected for their ability to home were displaced more than 0.15 but less than 4.5 km a total of 44 times. They assumed headings within 30° of their homeward directions 26 times, compared with the 7.3 times expected by chance (Gould, 1959). One hundred ornate box turtles were displaced, in equal numbers, 1.6, 2.0, 2.4 or 2.8 km. Eighteen were later found near their original point of capture. Only

four of these had been displaced more than 2.0 km, although a turtle displaced 3.2 km was later found near its initial point of capture (Metcalf and Metcalf, 1978). A dichotomy in homing when turtles were displaced more or less than 2 km was also found for wood turtles, Clemmys insculpta (Emydidae) (Carroll and Ehrenfeld, 1978).

Box turtles showed individual differences in homing. Some turtles homed, while others, transported equal or lesser distances, failed to do so and were sometimes later found near the release point (Fitch, 1958; Metcalf and Metcalf, 1978; Legler, 1960; Lemkau, 1970). Some appear to establish new home ranges near the point of release (Schwartz and Schwartz, 1974). Nichols (1939b) reported that adults are more likely to home than juveniles.

Movements. Displaced turtles often move in relatively straight lines while moving homewards (Breder, 1972; Lemkau, 1970), whereas one turtle displaced within its home range showed only irregular movements (Breder, 1927). Two turtles who had been displaced from their home ranges moved considerably farther per day than turtles moving within their home ranges (Legler, 1960). Possible cues used in homing are discussed below (pp. 18-20).

Box turtles are known to leave their established home ranges spontaneously, on occasion. Females often lay their eggs some distance from their normal ranges (Fitch, 1958; Legler, 1960; Stickel, 1950); turtles of either sex may leave their home ranges for brief periods unrelated to egg-laying (Stickel, 1950). There is some evidence that turtles may visit the same locations on different occasions, in which case, travel outside the home range may differ only in degree from

possessing two home ranges (Stickel, 1950). Some turtles do have two home ranges, which they travel between infrequently (Stickel, 1950). A few turtles appear to be transients. One male was tracked for 15 months, during which time he moved in a virtually straight line, becoming inactive in the winter and resuming the same course in the spring. This turtle crossed obstacles, including a river, and had travelled more than 9.7 km when tracking was discontinued. Two other turtles radio-tracked for shorter intervals travelled 3-5 km (Kiester, Schwartz and Schwartz, unpubl.).

Within their home ranges, box turtles (which were trailed by attaching to the carapace a spool of thread which unrolled as the turtle moved) were found to intersperse periods of circuitous movements with more direct travel, crossing and recrossing their home range every few days or weeks (Stickel, 1950). Turtles were also found to alternate a few days of activity with a few days of quiescence without apparent synchrony among turtles in the same general area (Dolbeer, 1969; Legler, 1960; Stickel, 1950).

Eastern box turtles wandered a mean of 20 m per day with a maximum recorded distance of 116 m (Dolbeer, 1969). Displaced eastern box turtles moved a mean of 23 m per day for females and 28 m per day for males (Lemkau, 1970). Schwartz and Schwartz (1974) reported that 92% of daily movements by three-toed box turtles were less than 61 m, but recorded a maximum straight-line distance of 229 m.

Ornate box turtles, which occupy more open, grass-land habitat and are thought to have larger home ranges (see pp. 10-13), were trailed by Legler (1960) in June. Males moved a mean of 88 m per day, non-gravid females moved 69 m (compared with 79 m in July), and gravid

females moved 111 m per day. Two males which had been displaced from their home ranges moved an average of 130 m per day. A maximum distance of 579 m in one day was recorded for one gravid female before her thread was expended. She moved in a generally straight line.

Turtles frequently do not move in straight lines. After moving 15-45 m during the day, turtles sometimes returned to within 2 m of the previous day's resting place (Dolbeer, 1969).

Differential use of areas within the home range. Box turtles typically rest in "forms," body-sized depressions which are dug in the leaf-litter and soil. Forms may be used repeatedly, sometimes by different turtles on successive nights (Stickel, 1950). A. Ross Kiester (pers. comm.) indicated that a resting site used by one three-toed box turtle may be more likely to be used again by that turtle than by other turtles occupying the same area. Legler (1960) however did not observe reuse of forms by ornate box turtles. In captivity, Boice (1970) found some evidence of individual preferences for quadrants of 1 x 3 x 3 m terraria in which six to seven turtles were housed. This finding was based mostly on resting sites.

Eastern box turtles were sometimes found hibernating close to their previous hibernation sites (Stickel, 1950). Box turtles usually hibernate separately, but a group hibernation of ornate box turtles has been reported (Legler, 1960).

Within their home ranges, box turtles travel over some routes more than others. A turtle may make frequent returns to a particular feature, such as a bush or log, and partially circle it in the course of changing direction (Stickel, 1950). Repeatedly displaced eastern

box turtles showed a tendency to follow the same routes when they traversed the same areas. They frequently followed natural boundaries when moving in straight lines (Lemkau, 1970).

Spatial cues. In order to understand box turtles' movements more fully, it is necessary to discover which features have significance for the turtles. Little is known about this problem.

Although box turtles have been known to home from distances of several kilometers, the mechanisms involved are unknown. Local landmarks were suggested as important cues by Lemkau (1970). Gould (1957) reported that turtles homed better on sunny than on overcast days and that reflected sunlight from a mirror when turtles were in the shade caused them to change their heading. On the basis of these data, he suggested that the turtles might use some form of celestial navigation. The navigational feats of sea turtles, such as green turtles, Chelonia mydas (Cheloniidae), some of which migrate well over 1600 km to nest on a tiny island in the middle of the Atlantic Ocean (Carr, 1964, 1967, 1975), must be borne in mind when considering such possibilities. Carroll and Ehrenfeld (1978), however, stated that the short distances involved make accurate celestial navigation implausible and suggested the use of olfactory or, possibly, magnetic cues as alternatives. In support of this, they reported a blind female wood turtle, Clemmys insculpta (Emydidae) which was displaced 1.35 km across streams, rock walls, and an intervening area of suitable habitat, and was found, three years later, mating with a male at her original home site.

Different modes of orientation need not be regarded as mutually incompatible. Lemkau (1970) suggested that turtles may have an ability

to maintain a heading which would help them to travel when more precise cues are only sporadically available. Gould (1957, 1959) reported some tendency for displaced turtles to assume headings which they took after previous displacement despite being displaced in different directions. Painted turtles, Chrysemys picta (Emydidae), developed strong position habits in operant conditioning studies of visual discrimination (Casteel, 1911, Spigel, 1963).

Even the routine use of space by box turtles in their home ranges is not understood. Observations by Stickel (1950) suggest that box turtles may recognize local features and Reagan (1974) identified temperature, cover, and moisture as important variables in habitat selection; however, the proximal factors involved in use of space have been largely unstudied, as is true for reptiles in general (Heatwole, 1977).

A few studies have addressed this issue. In a pioneering work, Yerkes (1904) used the reluctance of eastern box turtles to walk over an apparent edge (using what has come to be referred to as a "visual cliff") as evidence of depth perception. Burghardt (1977a) points out that differential responding, either spontaneously or after training, defines discrimination. He reviewed studies which demonstrate that visual discrimination in turtles, as well as other reptiles, may be revealed through operant conditioning as well as other techniques.

Several studies have been conducted which reveal spatial cues that are used by different turtle genera. Aspects of space use by snapping turtles, Chelydra serpentina (Chelydridae), including cues involved in choice of substrate, were studied by Froese (1974) using a combination of field and laboratory techniques. Sexton (1958) explored the roles of cover and support, as provided by experimental

vegetation models, in attracting snapping turtles. The geometric configuration of vegetation was found to be important in attracting painted turtles, on the basis of a combination of observation and experimentation (Meseth and Sexton, 1963; Sexton, 1959).

Numerous studies have investigated the cues used by hatchling sea turtles to find the sea. They generally concluded that brightness or openness of the horizon (Daniel and Smith, 1947; Hooker, 1908; Mrosovsky and Shettleworth, 1968; Parker, 1922) and also downward slope (Hooker, 1908; Parker, 1922) are important. Interestingly, newly hatched diamondback terrapins, Malaclemys terrapin (Emydidae), which inhabit brackish swamps, were found to move downhill but toward, rather than away, from clumps of vegetation (Burger, 1976). The phototactic behavior of freshwater turtles was reviewed by Mrosovsky and Boycott (1965).

Summary. A review of the literature on use of space by box turtles reveals the consistent finding that box turtles occupy overlapping home ranges for long periods of time. Data on home range sizes and population densities also appear to be roughly consistent, although the use of discrepant methods must be taken into account.

These results were obtained through mark-recapture techniques in which turtles' locations were sporadically recorded. At most, trailing devices allowed turtles' paths to be followed; in neither case were the turtles' movements directly observed. This would seem to reflect the ecological, population-level emphasis of such research.

Evidence for differential use of resting sites or other differential use of space within the home range is extremely limited and

contradictory, although some local features may play a role in turtles' movements.

Box turtles have been reported to home when experimentally displaced and spontaneously to leave and return to their established home ranges on occasion, but the mechanisms whereby this is accomplished are unknown. Even the cues which box turtles employ in daily movements within their home ranges are not understood. Limited information is available about cues to which other genera of turtles respond. Individual differences in use of space have been repeatedly reported but rarely discussed or related to other behavior.

In order to understand the ways in which box turtles experience their spatial surroundings, it is necessary to focus observations upon the individual and to relate box turtles' movements to potential social factors and environmental cues, as well as other aspects of the turtles' own behavior, thereby learning about the significance of each.

Individual Interactions with Other Turtles

Little is known about the social behavior of box turtles, despite substantial field studies. Indeed, the general consensus of the researchers who conducted these studies seems to be that box turtles are essentially non-social with the exception of mating (Brown, 1974; Legler, 1960; Stickel, 1950). "Meetings with other individuals in the course of foraging, basking, or seeking shelter, are fortuitous and have no social significance" (Legler, 1960, p. 367). Such conclusions may, however, reflect the limited expectations of the researchers more than the limited repertoires of their subjects, as pointed out by Boice, Quanty and Williams (1974), and Burghardt (1977b).

Relatively complex courtship and mating, involving reciprocal interactions between the female and male and lasting several hours were described by Evans (1953) in a manner consistent with earlier reports (Allard, 1939; Brumwell, 1940; Cahn and Condor, 1932) and personal observations.

Agonistic encounters have been reported occasionally in the field. Latham (1917) observed a larger male Terrapene c. carolina rush at a smaller male which was approaching, knock it over, and pin its head to the ground for approximately 2 minutes before crawling over the smaller turtle and walking away. Brumwell (1940) observed Terrapene ornata males snapping at each other while pursuing the same female, and Stickel (1950) observed one male Terrapene c. carolina biting at the front of the shell of another who had withdrawn into his shell. Brown (1974), Dolbeer (1969), Legler (1960), and Schwartz and Schwartz (1974) did not report any agonistic encounters.

Box turtles were regarded as essentially solitary by Legler (1960), and Schwartz and Schwartz (1974). The latter do report finding pairs of turtles together but conclude that this is probably related to sexual behavior. They did, however, observe several male-male pairs. Stickel (1950) reported frequently finding box turtles near each other, sometimes so close that their shells nearly touched. The turtles were not infrequently in clusters of three or four which sometimes were comprised of turtles of only one sex or included juveniles. At times 35-63% of turtles were found within 6 m of at least one other turtle. Stickel concluded that although these might have been aggregations, they were at least indicative of social tolerance. Brown (1974), Dolbeer (1969), and Legler (1960) occasionally observed turtles together;

however, these associations were regarded as devoid of social significance.

Such conclusions may have been drawn too hastily. These were all essentially capture-recapture studies which focused upon ecological and population parameters. No unobtrusive observation, or any formal observation, was mentioned, except by Legler (1960) who used binoculars and a blind to observe turtles for an unspecified length of time. Yet box turtles have been found to be extremely wary, freezing and remaining motionless for half an hour or more in reaction to an observer as far as 60 m away (Legler, 1960).

Personal observations suggest that box turtles are aware of human observers and react by remaining motionless as long as the observer is present; 15 eastern box turtles were observed for a total of more than 11.5 hours. Even during 5.5 hours of observation in which special care was taken not to disturb turtles by noises, sudden movements, close approaches, or handling, no movements were observed in 13 turtles, after their initial freezing upon the approach of the observer, except for occasional, almost imperceptible, head motions. There were two exceptions. One turtle, who was missing an eye, turned her head toward the observer when a paper was rustled on her blind side; another turtle ducked its head when a wasp landed on its face. Two turtles did not change position during 105 minutes and 60 minutes of continuous observation, respectively; each moved away during a 15 minute absence of the observer. Each was again motionless during a subsequent 10 minute observation, suggesting that they reacted to the presence of an observer.

Due to the difficulty of observing any behavior in the field, conclusions about a lack of social behavior may be premature. This is especially true in view of numerous interactions observed among captive box turtles, who may be presumed to have become habituated to the presence of humans. Boice (1970) frequently observed biting, pushing, blocking with the side of the shell, and sometimes holding down another turtle's head with a foreleg during and immediately after food competition. He was able to obtain stable dominance hierarchies (Boice, 1970; Boice, Quanty, and Williams, 1974). Dominance hierarchies were also obtained in captive snapping turtles (Froese and Burghardt, 1974) and wood turtles (Harless, 1970).

Lack of reports of social behavior in the field often may reflect the restricted range of behavior considered. In most cases social behavior seems to have been equated with courtship or combat. Less obvious forms of behavior may well have been overlooked. Dominance hierarchies obtained with snapping turtles by Forese and Burghardt (1974) were not maintained through frequent agonistic encounters; rather, deference may have been based upon individual recognition (Burghardt, 1977b).

Individual recognition or preference is perhaps even more indicative of sociality than courtship or competition as, in the latter case, social behavior might sometimes be regarded as incidental to obtaining a necessary resource. Such recognition or preference in box turtles is indicated only by anecdotal evidence. Boice (1970, p. 709) incidentally noted that one dominant male Terrapene c. carolina and a female who was his "usual consort" exclusively occupied one quadrant of an enclosure. Evidence of short-term discrimination between individuals

was provided by Brumwell (1940) who observed four males simultaneously courting a female Terrapene ornata in the field. The female snapped at three of the males but mated with the fourth.

Among other groups of turtles a wood turtle, Clemmys insculpta, stopped and then resumed fighting twice when the turtle with whom he was fighting was replaced by other turtles and then returned (Dinkins, 1954). Stable individual preferences for other individuals were observed in a captive herd of Galapagos tortoises, Geochelone elephantopus (Evans and Quaranta, 1951). These observations were based upon patterns of association and sleeping positions.

Individual recognition of other turtles is an ideal topic for the study of experience. What, or rather who, a turtle knows is directly manifest in its behavioral discrimination between other individuals. The rich context of social behavior may enable one to assess the basis of such recognition or preference.

Individual Styles of Interacting

Box turtles were reported to show a "striking individualism in their behavior" by Allard (1949, p. 149). Individual differences in patterns of activity within the home range were reported by Stickle (1950). ". . . . Some individuals regardless of sex, live a more sedentary life while others are more active . . .", according to Schwartz and Schwartz (1974, p. 23). Individual differences in homing after experimental displacement were reported by Metcalf and Metcalf (1978), and others, as discussed on p. 15. Individual preferences for resting sites are discussed on pp. 60-76.

Stable dispositions in box turtles were reported by Nichols (1939b) on the basis of their reactions to human handling. Twenty-two of twenty-four turtles who struggled or withdrew into their shells when disturbed did so consistently every time they were found over as many as four captures and 15 years. Gould (1957) also reported individual differences in the reactions of eastern box turtles following human handling. Some withdrew and did not emerge from their shells for more than an hour, some were active, and others "were completely at ease even when approached or picked up" (p. 337). Harless and Lambriotte (1971) found individual differences in activity following human handling, which they related to prior experience, in ornate box turtles. Consistent individual patterns of behavior across various measures of activity and feeding precedence were reported in captive ornate box turtles (Harless and Lambiotte, 1971). Boice (1970) reported that a male eastern box turtle which lost in food competitions with another male did not mount females in the other's presence but did so when removed from the male.

Evidence of meaningful, individually consistent, patterns of behaving across various situations is necessary to indicate individually consistent modes of experiencing or styles of relating to the world. An investigation of such consistencies across contexts in which box turtles have manifested individual differences is indicated. This might encompass use of space, interactions with other turtles, and interactions with humans.

The Present Investigation

The present investigation focused upon box turtles' experience of social and spatial aspects of their environment and upon their individually consistent modes of relating to both. Social and spatial factors are interwoven because social interactions occur in spatial contexts and movements through space may be influenced in social factors. Certain less obvious forms of sociality may consist largely of differential spatial relationships between individuals. Three general questions were addressed in the present study:

1. The primary question concerned which aspects of their social and spatial environments box turtles do experience; this question was addressed by investigating whether box turtles recognize particular individuals and areas. Such recognition is directly observable as discrimination between the different individuals or areas.

2. The subsequent question of how such aspects are experienced was addressed by identifying the significance to the turtles of specific facets of their social and spatial interactions. This was investigated by observing the relationships between particular cues and behavior patterns.

3. The final, integrating, question was whether box turtles manifest individual styles of interacting. This is significant because such styles indicate the active role which the individual takes in determining the way in which its world is perceived and acted upon, thereby providing evidence for the importance of individual experience. This aspect was addressed by searching for consistent individual patterns of behavior across social and spatial contexts.

In the present study, these three questions pertaining to individual social and spatial experience were investigated using ethological methods. A combination of descriptive and experimental studies were conducted in the turtles' natural habitat, in an outdoor enclosure, and in the laboratory.

The first part of this investigation consisted of a descriptive study of individual patterns of space use in the natural habitat, a study of preferential and possibly exclusive use of smaller areas of space in an outdoor enclosure, and an experimental investigation, conducted in the laboratory, of certain cues which box turtles may employ in their movements through space.

The second part consisted of an investigation of turtles' recognition of and preference for other individuals. In one phase, differential spacing between individuals was used as a measure of preference. In another phase, turtles' discrimination between individuals who lived at different distances from them was investigated. Specific behavior patterns involved in their interactions were studied.

The third part of the total investigation consisted of an investigation of individually consistent styles of interacting with both the spatial and social environment.

CHAPTER II

INDIVIDUAL USE OF SPACE

Study 1. Movements and Home Ranges in the Natural Habitat

Introduction

Use of space by individual eastern box turtles in their natural habitat was investigated in a descriptive study. Use of telemetry allowed individuals to be located repeatedly. Formal observation sessions were conducted and locations recorded when turtles were found. On the basis of these data, rates of movement and home range sites and shapes were estimated. Different methods of estimation may result in different conclusions; hence, problems of methodology are also discussed.

Individual differences in movements were investigated and are related to other aspects of these individuals' behavior on pp. 109-116.

Methods

Setting. The study area consisted of a square, four hectare, plot on privately owned land, adjacent to The University of Tennessee Cherokee Woodlot in Knox County, Tennessee.

The plot was laid out along north-south and east-west axes and divided into 100 quadrats of 20 x 20 m each. These were arranged in a 10 x 10 grid. Each quadrat was marked by flagging and stake-wire flags labelled with a unique letter-number combination. Numbers progressed from north to south and letters from east to west. The north-east corner of the study area was an identifiable point which facilitated plotting the quadrats on a topographic map of the area (see Figure 1).

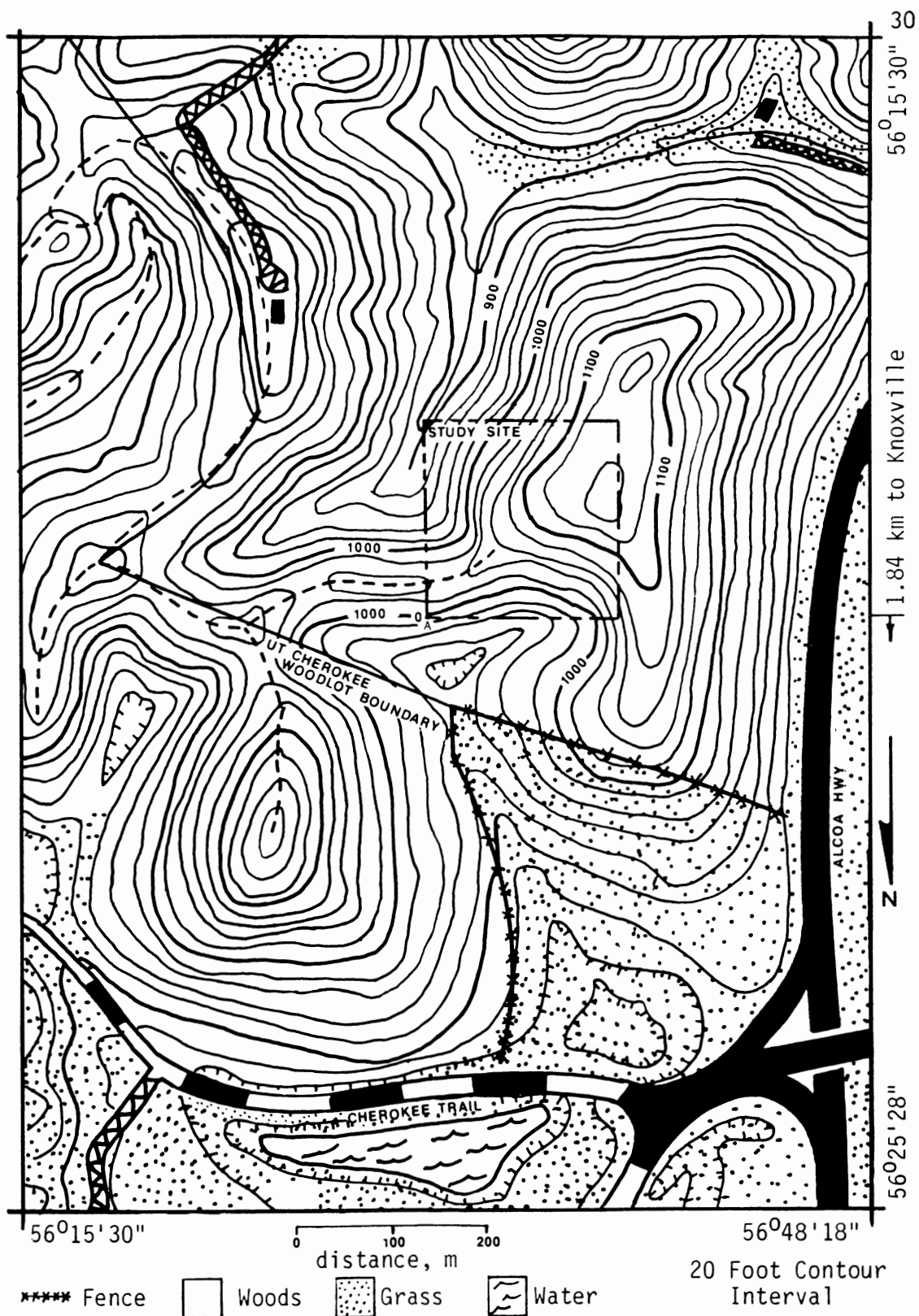


Figure 1. Topographic map of the study site and surrounding area.

Source: U.S. Geological Survey, Knoxville, Tennessee (N3552.5-W8352.5/7.5) 1978.

A staff compass with level and sights and a 30 m steel tape were used to establish the boundaries of each quadrat. Markers were placed in each corner of every quadrat. The locations of virtually all of these points were checked against at least two other points. Occasionally adjustments were required. An estimated accuracy of 90-95% was achieved.

The topography of the study area is shown in Figure 1. It featured a ridge which entered the eastern border toward the northern side of the study area at an elevation of 1040 feet (317 m). This rose and broadened into a hilltop with an elevation of 1140 feet (347 m) in the southwest sector of the study area. On either side of the ridge, portions of two valleys, with minimum elevations of 940-1000 feet (286-304 m), were included in the northern and southeastern parts of the study area.

The important forms of vegetation found in each of the major areas of the study site are listed in Table 2. Their scientific names are provided in Table 3. The north valley and slope were moist with low, herbaceous groundcover. The ridge and hill top were more open with less ground cover and larger trees. Higher portions of the south and especially the east slopes were covered with extremely dense tangles of vines and shrubs which were often at least 2-3 m in height and width and many meters in length. The investigator was able to penetrate these only with considerable difficulty by working through them in a prone position. The remaining portions of these slopes also contained dense vegetation. Some of the most prevalent plants in the study site, such as Japanese honeysuckle, Lonicera japonica, are not native to the region. The tip of the south valley was an enclosed area which contained primarily a tall stand of tree-of-heaven, Ailanthus altissima.

Table 2. Important flora in the study site, arranged by topographic area in approximate order of prevalence.

Vines	Ground-Cover	Shrubs	Understory	Canopy
<u>North Valley</u>				
	glade fern	spicebush	red mulberry	box elder
	Canada violet			maple
	clearweed			
	enchanter's nightshade			
<u>North Slope</u>				
poison ivy	Canada violet	spicebush	dogwood	tulip poplar
Japanese honeysuckle	Christmas fern	slippery elm	sassafras	maple
Virginia creeper	clearweed		maple	oak
grape	enchanter's nightshade			beech
	Solomon's seal			hickory
	false Solo- man's seal			
<u>Ridge and Hill Top</u>				
Japanese honeysuckle	leafcup	shrub honey- suckle	box elder	tulip poplar
grape	pokeweed	spicebush	dogwood	maple
Virginia creeper	clearweed	slippery elm	red mulberry	oak
poison ivy	enchanter's nightshade		redbud	hickory
	periwinkle			sassafras
				hackberry

Table 2. (Continued)

Vines	Ground-Cover	Shrubs	Understory	Canopy
<u>Ridge and Hill Top</u>				
				black walnut
				black locust
<u>South and East Slopes</u>				
Japanese honeysuckle	leafcup	blackberry	red mulberry	tulip poplar
grape	periwinkle	spicebush	dogwood	hackberry
poison ivy	Indian strawberry		box elder	hickory
	Solomon's seal		sassafras	oak
	false Solomon's seal		redbud	
	Christmas fern			
	ebony spleenwort			
<u>South Valley</u>				
	mondo grass	spicebush	tree-of-heaven	box elder
	clearweed	blackberry	red mulberry	tulip poplar
	enchanter's nightshade	black raspberry		cherry
	jewelweed	redbud		

Table 3. Common and scientific names of important flora in the study area.

Common Names	Scientific Names	Common Names	Scientific Names
beech	<u>Fagus grandfolia</u>	hickory	<u>Carya</u> sp.
black locust	<u>Robinia pseudoacacia</u>	Indian straw-berry	<u>Duchesnea indica</u>
black raspberry	<u>Rubrus occidentalis</u>	Japanese honeysuckle	<u>Lonicera japonica</u>
black walnut	<u>Juglans nigra</u>	jewelweed	<u>Impatiens capensis</u>
blackberry	<u>Rubrus</u> sp.	leafcup	<u>Polymnia canadensis</u>
box elder	<u>Acer negundo</u>	maple	<u>Acer</u> sp.
Canada violet	<u>Viola canadensis</u>	mondo grass	<u>Microstegium uimineum</u>
cherry	<u>Prunus</u> sp.	oak	<u>Quercus</u> sp.
Christmas fern	<u>Polystichum acrostichoides</u>	periwinkle	<u>Vinca minor</u>
clearweed	<u>Pilea pumila</u>	poison ivy	<u>Rhus radicans</u>
dogwood	<u>Cornus florida</u>	pokeweed	<u>Phytolacca americana</u>
ebony spleen-wort	<u>Asplenium platyneuron</u>	red mulberry	<u>Morus rubra</u>
enchanter's nightshade	<u>Circaea</u> sp.	redbud	<u>Cercis canadensis</u>
false Solomon's seal	<u>Smilacina racemosa</u>	sassafras	<u>Sassafras albidum</u>
glade fern	<u>Athyrium pycnocarpon</u>	shrub honeysuckle	<u>Lonicera</u> sp.
grape	<u>Vitus</u> sp.	slippery elm	<u>Ulmus rubra</u>
hackberry	<u>Celtis occidentalis</u>	Solomon's seal	<u>Polygonatum biflorum</u>

Table 3. (Continued)

Common Names	Scientific Names	Common Names	Scientific Names
spicebush	<u>Lindera</u> sp.	tulip poplar	<u>Liriodendron</u> <u>tulipifera</u>
tree-of- heaven	<u>Ailanthus</u> <u>altissima</u>	Virginia creeper	<u>Parthenocissus</u> <u>quinquefolia</u>

Farther south, the valley opened into an exposed area with grass and brambles.

A small, dry stream bed touched the southeast corner of the study area. The stream emerged above ground outside of the study area.

Views of the study area and a turtle in the study area are presented in Figures 2 and 3, respectively.

Apparatus. Turtles found in the study area were equipped with transmitters (Mini-Mitter Company, model L) each of which operated on a different frequency between 26.870 and 27.545 MHz. A citizens' band "walkie-talkie" (Lafayette, model HA-420) and a hand-held directional antenna were used to receive the signals from these transmitters and locate the turtles. Figure 3 shows the complete transmitter package mounted on a turtle.

To increase range and visibility the transmitters were modified by the addition of an external antenna (suggested by A. Ross Kiester, pers. comm.). These antennae consisted of guitar strings, not longer than 40 cm, inserted into polyethylene tubing which was painted bright orange with acrylic spray paint. The lengths of the antennae were adjusted in relation to the wave lengths of the transmitted signals in laboratory trials to maximize the range at which the signal could be received.

Each transmitter was housed in one end of a two-part plastic capsule. The antenna extended through the empty end of the capsule. The point at which it pierced the capsule was water-proofed with silicone stop-cock grease (Dow Corning High Vacuum Grease) and covered with black silicone glue and seal (General Electric). This end of the



Figure 2. A view of the study area.



Figure 3. A transmitter-equipped turtle in the study area.

capsule, including the point at which the antenna emerged, was embedded in a pad of epoxy putty which was shaped so as to provide a smooth contour with one slightly concave surface to provide maximum area for attachment to the turtle's shell. This was allowed to harden at least 24 hours before use.

To make the transmitter operational, two or three 1.5 V camera batteries (Eveready S76) were inserted into the embedded capsule. The free end of the capsule, which contained the transmitter, was then inserted after being coated with stop-cock grease as a sealant. Care was taken to drive air from the capsule so that firm contact was established between the batteries and transmitter. It was possible to change batteries or even the transmitter in the field in this manner. The complete transmitter package weighed approximately 25 g and measured approximately 3.5 cm in length and 1.5 cm in diameter.

Care was taken to minimize disturbance to the turtle when attaching the transmitter. The transmitter was attached to the turtle's carapace in the rear and to one side with no portion of the transmitter package extending beyond the highest or widest parts of the turtle's shell. It was felt that this placement would minimize interference with the turtle's movements and mating activities.

Transmitters were attached to turtles without picking up or moving the turtles. After inserting batteries in the transmitter as described above, the appropriate area of the turtle's shell was lightly roughened with fine emory cloth and cleaned with alcohol. The concave surface of the hardened epoxy pad was coated with black silicone glue and seal and this was affixed to the turtle's shell. Masking tape was sometimes used to hold the transmitters in place while the glue dried.

The turtle was watched for at least one-half hour following attachment of the transmitter. All turtles were generally inactive during this time.

Considerable experimentation in the laboratory, using turtle shells, was required to devise this method of attaching transmitters. The method was found to be generally successful. It was possible to remove the transmitter by peeling the silicone glue and seal from the turtle's shell without damage to the shell. It also seemed likely that transmitters which were not recovered would eventually loosen from the turtles' shells and that the elasticity of the glue would allow growth prior to this time.

No transmitters attached in this fashion came off prematurely in the course of 1 to 2 months of observation. They did not seem to interfere with the turtles' movements. The resiliency of the antennae wires allowed them to be trailed by turtles without kinking or snagging. The orange antennae greatly facilitated finding the turtles.

The paint, however, tended to flake off the polyethylene tubing and the tubing tended to slip off the antenna wire. Corrosion of the exposed wire did not seem to be a problem. Some of these wires were painted orange to increase their visibility. However, they remained less visible than the painted tubing.

The transmitted signals were received at a maximum range of less than 100 m. The range was often much less, depending upon the degree of interference from other citizens' band transmissions and upon topographic and weather conditions. In valleys, the signals echoed and, consequently, direction was difficult to determine. It usually required from 1 to several hours to locate each turtle.

Expected battery life was 1 to 2 months; however, contact was lost with three of four turtles, presumably because of battery failure, after their batteries had been in use 20, 29, and 37 days, respectively.

Procedure. Turtles were initially located by searching the study area. Subsequent locations were accomplished through the use of telemetry. The first time each turtle was located, it was inspected, sexed according to the external characteristics described on p. 8, then measured and designated as mature or immature on the basis of size and number of growth rings (see pp. 7-8). The turtle was then paint-marked and outfitted with a transmitter as described above (pp. 36-39). At no time were turtles picked up or moved. On subsequent occasions, turtles were not touched, except as necessary to maintain their transmitters. It was found necessary to pick up one turtle (Turtle A) 1 month after he was initially located in order to change the batteries in his transmitter.

Every time a turtle was located, the observer froze and then noted the turtle's general behavior and surroundings as well as its distance and orientation relative to the observer. The observer either remained stationary or moved away to an observation position, in which case distance and orientation were again noted.

Orientation was recorded as the observer's position on an imaginary circle surrounding the turtle and divided into eight 45° sectors, with sector eight the direction in which the turtle was facing. Thus, Orientation 8 indicated that the observer was in front of the turtle, Orientation 4 that the observer was behind the turtle, and 2 or 6 that the observer was to the turtle's right or left. Odd numbers

represented intermediate positions.

Temperature, humidity, and general weather conditions were recorded. A 30 minute formal observation period was then conducted. (These observation sessions were discontinued at the end of July for reasons discussed on pp. 46-47.)

Five types of behavior, regarded as states, were recorded during the observation period using an instantaneous time sampling technique in which the turtle's behavior at the beginning of each minute was recorded. The behavior categories employed, with the addition of orientation as described above, are presented in Table 4.

The frequencies of four behavior categories, regarded as events, were also recorded during the observation period. These are presented in Table 5. These behavior types are discussed more fully on pp. 93-98. Notes were made of other types of activities. The observer remained as still as possible during the observation period.

Finally, each turtle was slowly approached. Care was taken to avoid sudden movements which previous observations had indicated were often followed by startle responses and head retraction. The turtle's reaction to close approach was recorded, using the behavior categories discussed above. Close approach consisted of holding a ruler and a compass several centimeters directly above the turtle's carapace. This allowed a stakewire flag to be positioned 30 cm south of the center of the turtle's shell.

The position of each turtle was then measured by sighting the direction to the nearest quadrat marker, using a hand-held compass with sights, then measuring this distance with a steel tape. The stakewire flag positioned near the turtle facilitated this process by

Table 4. Behavior states recorded during field observations.

Behavior Category	Code	Definition
Head Extension	1	Head withdrawn with eyes inside shell
	2	Eyes to full head exposed
	3	Neck partially extended, skin folded
	4	Neck fully extended, skin smooth
Shell Openness	1	Closed
	2	Partly open, sufficient for head extension
	3	Open, sufficient for extension of legs
Exposure	1	Turtle more than half covered by earth, leaf litter, or tangled vegetation immediately over the turtle
	2	Turtle less than half covered
	3	Turtle uncovered, on surface
Activity Level	1	Motionless
	2	Shift in posture
	3	Change in position relative to the substrate

Table 5. Behavior events recorded during field observations.

Behavior Category	Definition
Neck-arching	Fully extending the neck with a stiff upward arch
Head-ducking	Retracting the head with a sudden jerk
Gaping	Opening the mouth, holding it at its fullest extension, then closing it more rapidly than it was opened
Mouthing	Opening and closing the mouth very slightly, sometimes while making a soft "chewing" noise, in the absence of food

increasing the visibility of the turtle's location and allowed the measurements to be checked even if the turtle moved.

Successive locations of each turtle were later mapped by measuring the distance and angle from points which represented the quadrat markers on maps of the study area. Three triangulated positions were found to be accurate to better than ± 0.5 m. These maps represent diagrams of observed home ranges. Estimated home range sizes were calculated by connecting the outermost locations to form a convex polygon and measuring the enclosed area. The length of the longest axis of this figure was also measured. A Spearman rank-order correlation was calculated between the estimated home range size and the number of sightings on which this was based to check for bias based on sample size.

Straight-line distances between sightings were measured using these graphs. Daily displacement was calculated by dividing the distance between sightings by the number of days between sightings.

Subjects. Subjects were six eastern box turtles who initially were observed within the study area. Transmitters were attached to four of these turtles, allowing relocation and subsequent observations. Background information concerning these turtles is presented in Table 6. The turtles' locations were obtained between June 22 and August 20, 1978. A total of 24 formal observation sessions were conducted on six turtles. The four relocated turtles were found a total of 46 times.

All subjects were adult males except for one juvenile of indeterminate sex who was not relocated and one adult female who was relocated. One of the turtles classified as a male was later observed mounted on another turtle in a male courtship position.

Table 6. Basic information on turtles observed in the study area, 1978.

Turtle	Sex	Curved Carapace Length	Number of Locations	Number of Formal Observations	Dates of First and Last Locations
A*	Male	148	21	12	6/22-8/19
B	(Juvenile)	87	1	1	6/26
C*	Female	149	5	4	6/29-7/17
E*	Male	153	11	3	7/14-8/20
F*	Male	164	9	3	7/17-8/6
G	Male	117	1	1	7/19

*Transmitter attached.

Results

Observations. Despite careful precautions to minimize disturbance to the turtles, attempts to observe their movements in the field directly were not successful. The behavior categories were clearly distinguishable; however, turtles almost never moved during the observation periods despite evidence of prior activity on several occasions. During 24, 30-minute observation sessions conducted on six different turtles, the turtles changed their positions relative to the substrate (Activity Level 3) on only five occasions. These movements occurred during a total of 7 minutes. They consisted of walking during minutes 1 through 3 of observation, after which turtles froze, having apparently noticed the observer. The only exception was Turtle A, who turned toward the observer, such that the observer's relative position changed from Orientation 4 (directly behind the turtle) to 5 (diagonally behind the turtle), during the 14th minute of the 12th observation session. The same turtle changed his posture (Activity Level 2) by gradually protruding his head (Head Extension 1 changing to 2) while opening his shell (from Openness 2 and 3) during the 3rd and 4th minutes of his seventh observation session. He appeared to be watching the observer. The only other change in posture was a head movement which occurred during one minute in which a fly was walking about this turtle's eye. A head-duck also occurred during this time. Turtle E once froze in a neck-arch position. These were the only occurrences of the behavior events listed in Table 4. Thus, in 12 hours of formal observation, turtles only moved during a total of 10 minutes. For this reason formal observation sessions were discontinued near the end of July, although locations continued to be recorded.

The seven observation sessions during which any change of posture or position was observed (Activity Level 2 or 3) occurred between June 30 and August 2, 1978. Initial times varied between 10:04 am and 4:40 pm. The remaining 17 observation sessions occurred between June 22 and August 21 and started between 10:17 am and 5:08 pm.

The mean temperature at the beginning of the observation sessions during which movement occurred was 24°C (range, 21-27°C); the mean temperature of those without movement was 25°C (range, 22-29°C). This difference did not approach statistical significance ($t_{22df} = 0.72$, NS). The mean relative humidity at the beginning of the trials with movement was 79% (range, 72-92%) as compared with a mean of 72% (range, 59-92%) for the other trials. This difference was not statistically significant ($t_{22df} = 1.34$, NS).

All 48 sessions in which a turtle was located, including those for which formal observation sessions were not conducted, occurred between June 22 and August 19, starting between 9:15 am and 4:55 pm. The mean temperature was 24°C (range, 21-29°C); the mean relative humidity was 80% (range 56-100%). Turtles were often observed for several minutes and found to remain motionless even during those sessions for which a formal half-hour observation session was not conducted.

Locations. All locations of each of the four relocated turtles are shown in Figures 4-7. The date of each location is indicated. Turtles were relocated a mean of once every 3.17 days (range, 1-11 days).

The turtles were most frequently found on the southeast slope which, as discussed on p. 31, was covered with dense vegetation, including huge tangles of vines and shrubs which were almost impenetrable

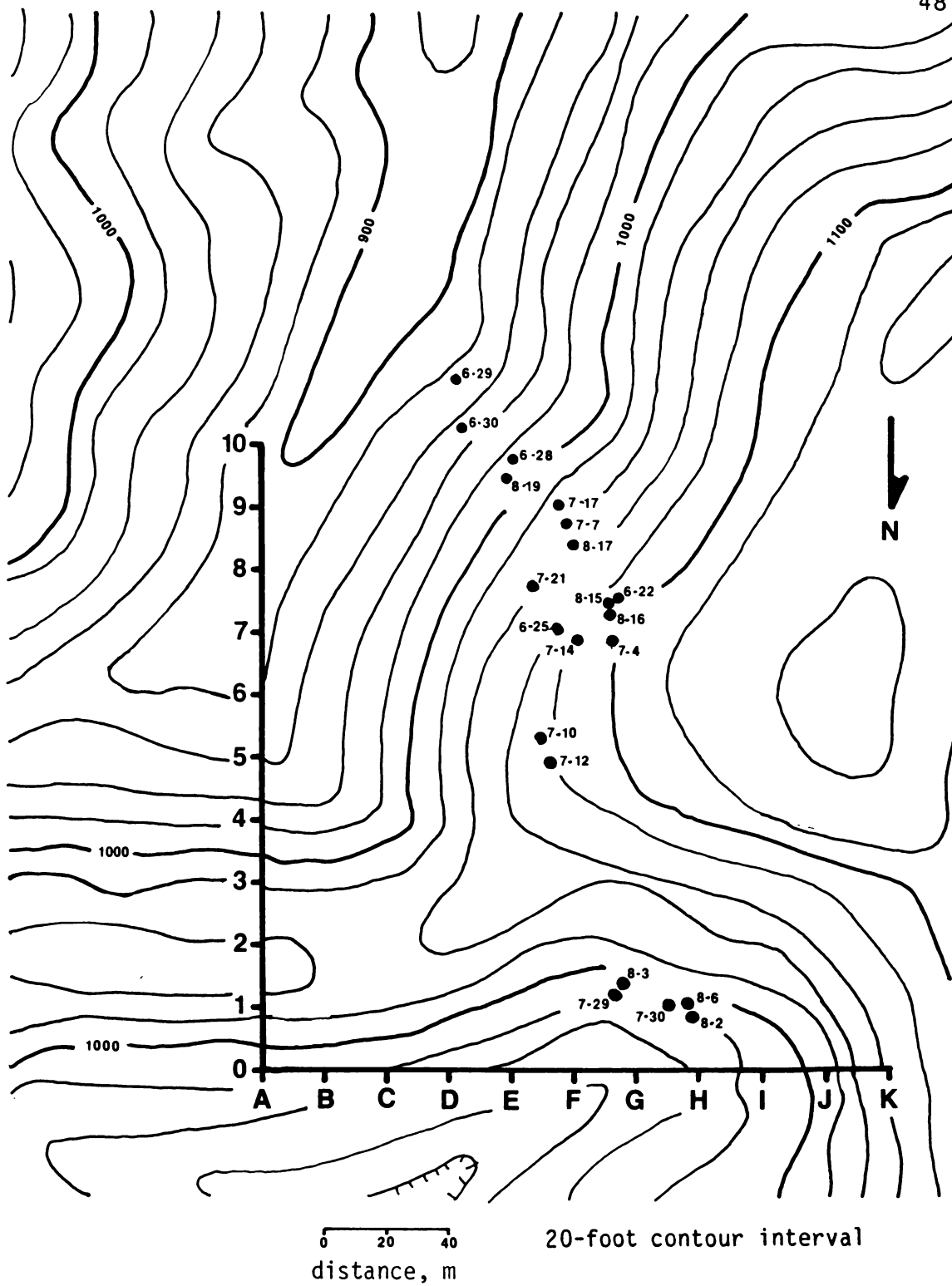


Figure 4. Locations of Turtle A in and near the study site from 6/22/78 to 8/19/78.

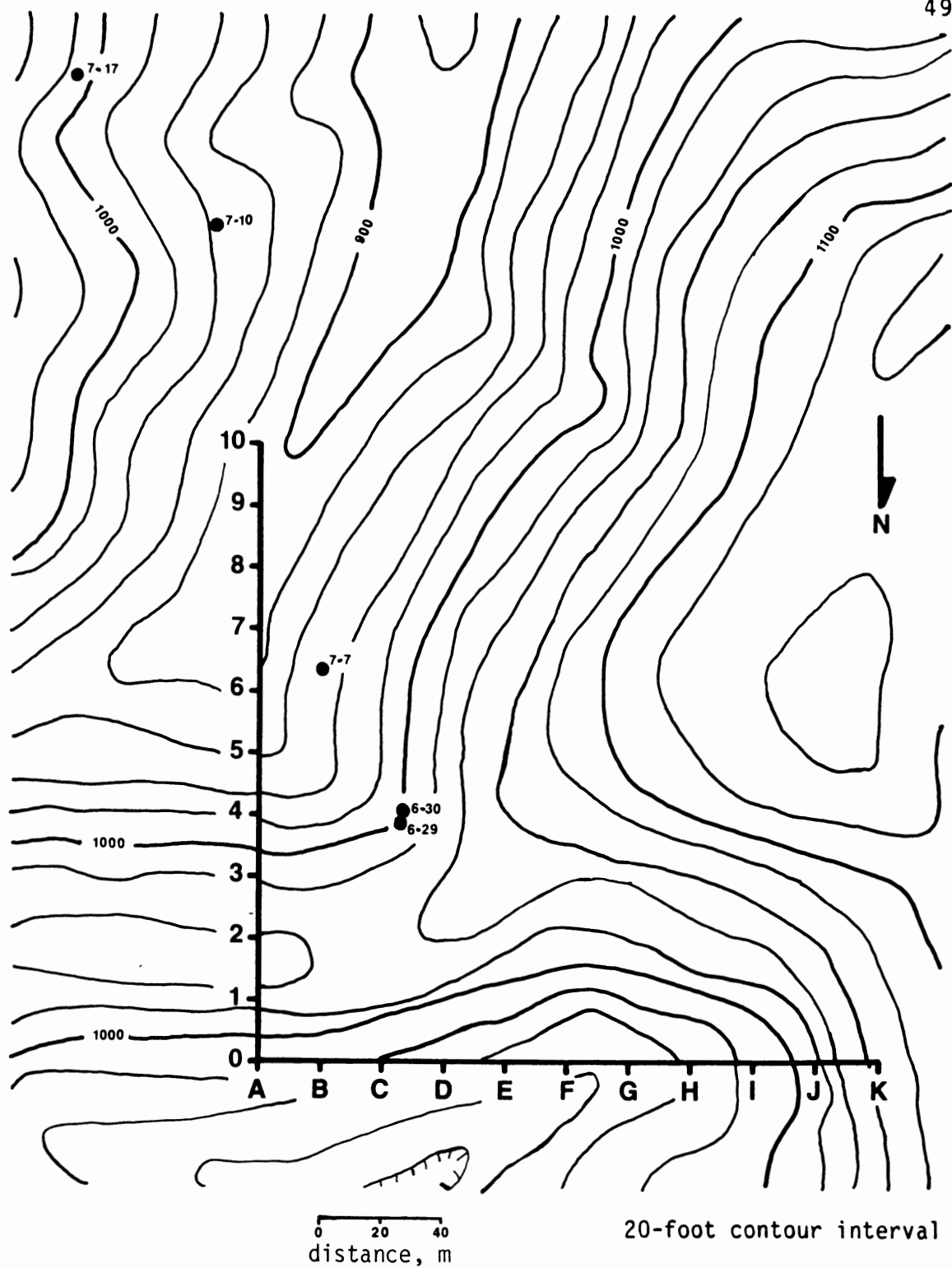


Figure 5. Locations of Turtle C in and near the study site from 6/29/78 to 7/17/78.

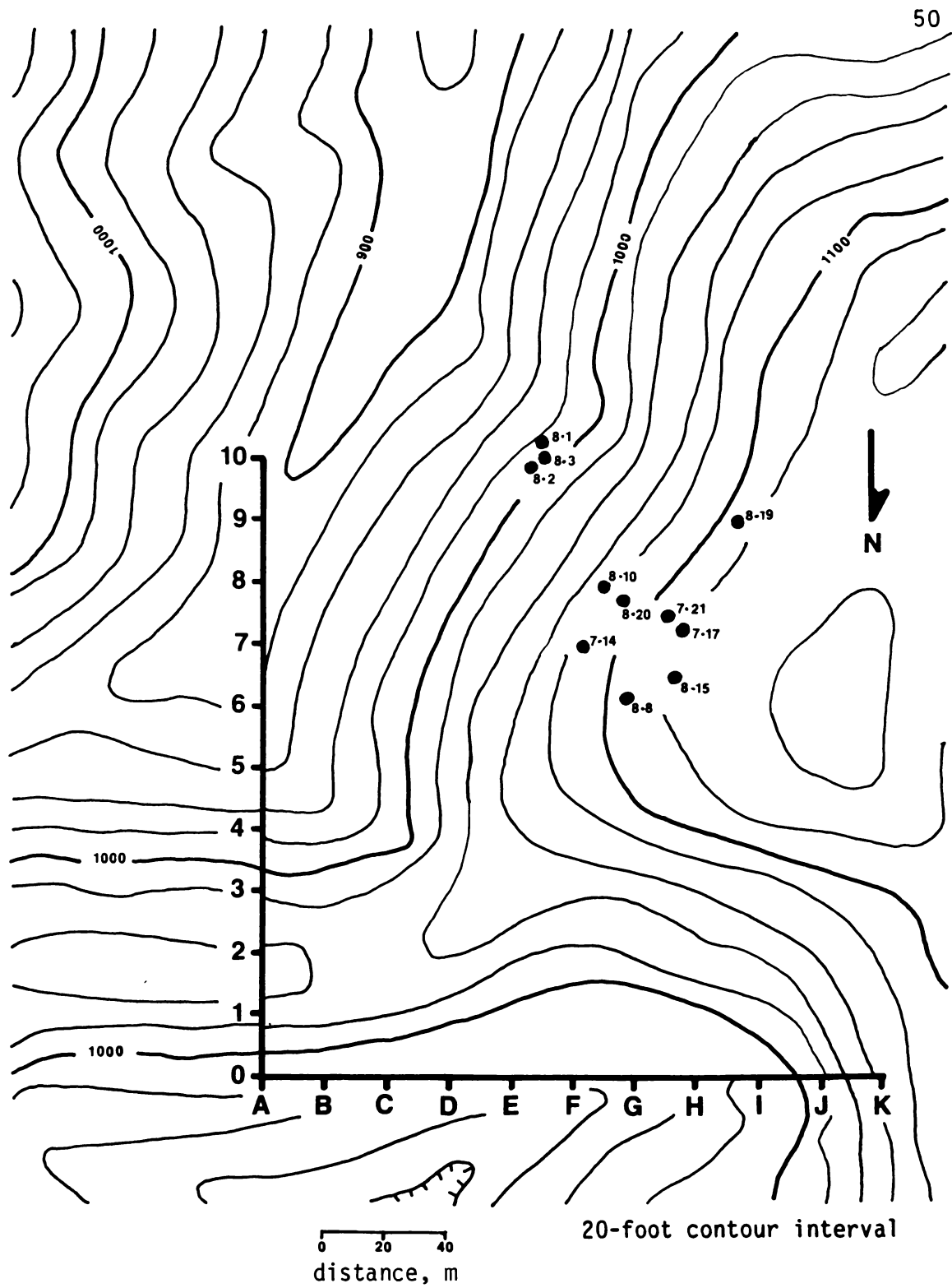


Figure 6. Locations of Turtle E in and near the study site from 7/14/78 to 8/20/78.

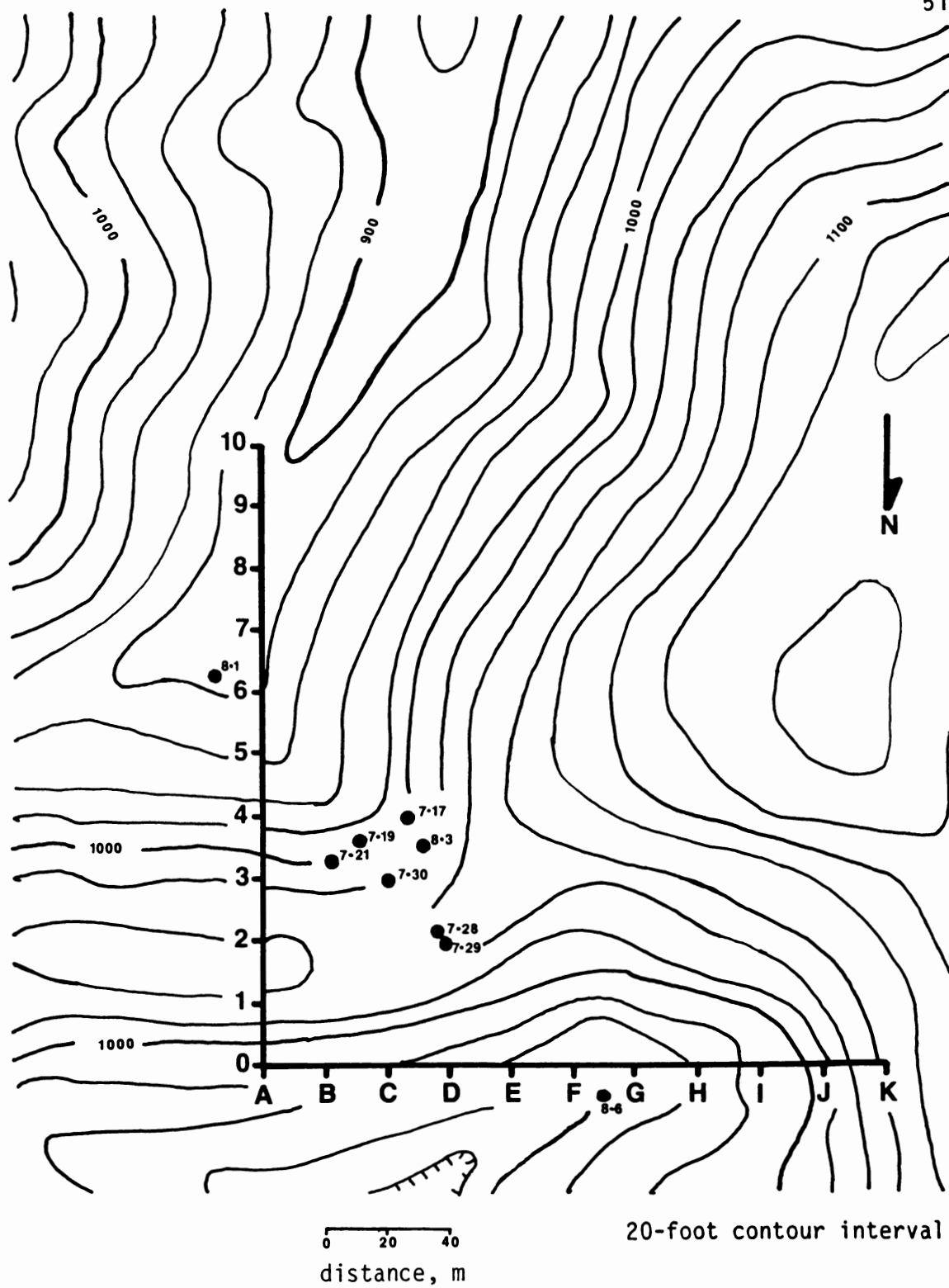


Figure 7. Locations of Turtle F in and near the study site from 7/17/78 to 8/6/78.

to the observer. The turtles utilized cover extensively by resting beneath it and even by moving beneath a layer of vines interlaced with other vegetation. Turtles were occasionally sighted on the north slope but were rarely found on the more open ridge and hilltop in either the north valley or the grassy south valley.

Examination of Figures 4-7 reveals that each turtle generally moved within one confined area with two possible exceptions.

Turtle A, a male, appears to have moved from one area to another located more than 130 m north and slightly west, then, after spending at least 9 days in that area, to have returned to the original area (see Figure 4). The unusually long times between sightings (8 and 9 days, respectively) which correspond with the periods of movement between the two areas make it possible that lack of intervening sightings accounts for the apparently dichotomous home range.

Turtle C, a female, moved in a generally straight line until she was lost outside the study area after five sightings (see Figure 5). The straight line distance between most distant sightings was 265 m. This is greater than that for any other turtle. The next largest maximum distance between sightings was 218 m. This was achieved by Turtle A, discussed above, who was located 21 times. It is interesting to note that Turtle C was the only female of the four relocated turtles.

The estimated home ranges of all repeatedly located turtles are shown in Figure 8. Overlap occurs between Turtles A and E, with slight overlap between C and F. Estimated home range sizes are presented in Table 7. The median area was 0.336 ha. The median length was 202 m. Turtle C was observed over the greatest length and second largest area despite having been sighted the least. If she is regarded as a

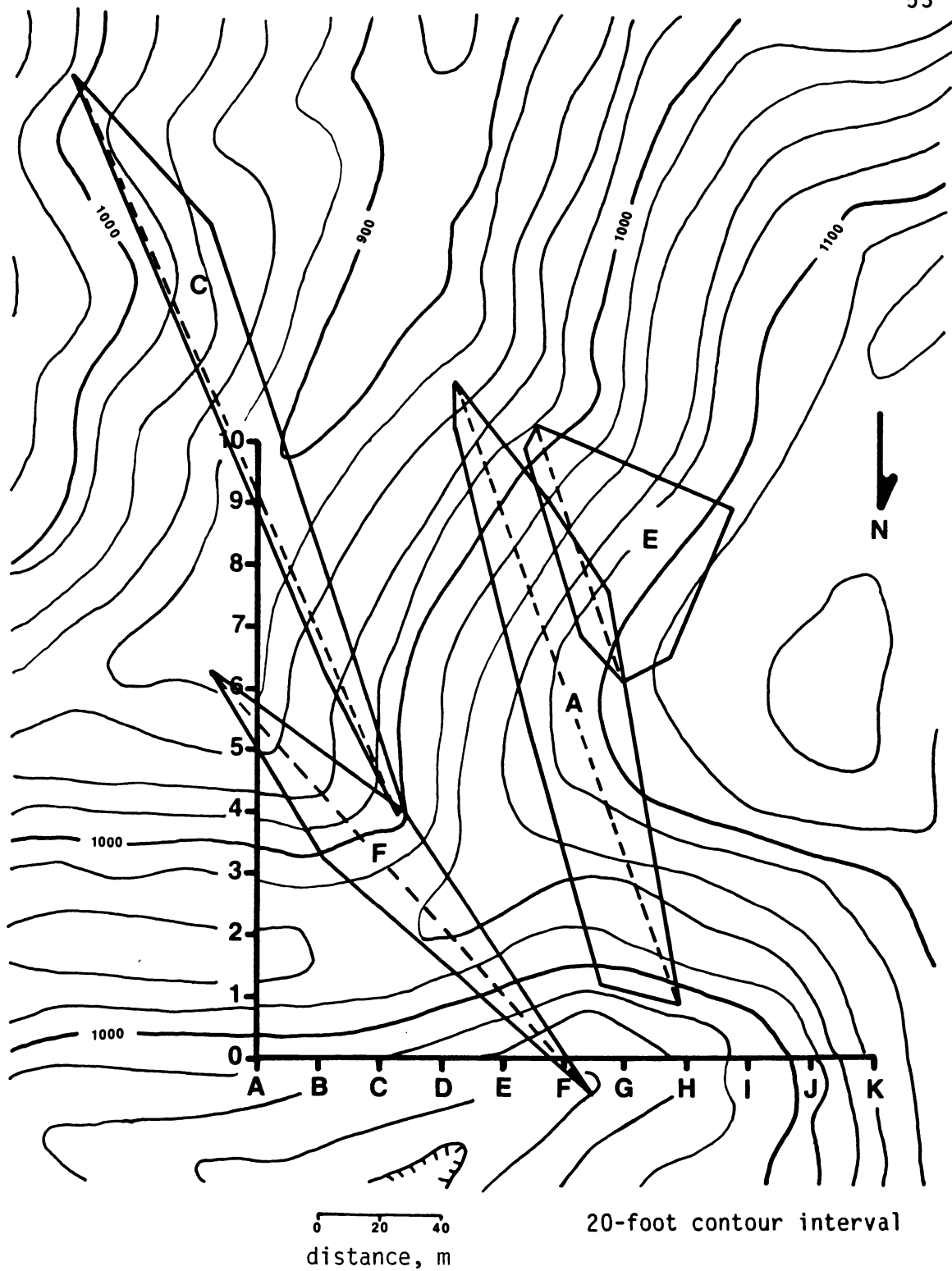


Figure 8. Estimated home ranges of Turtles A, C, E, and F.
 -----: Longest axis.

Table 7. Estimated home range areas and lengths.

Turtle	Sex	Area (ha)	Longest Axis (m)	Number of Observations
A	Male	0.571	218	21
C	Female	0.360	265	5
E	Male	0.312	89	9
F	Male	0.266	186	11
Mean		0.377	190	12
Median		0.336	202	10
Median Excluding Turtle C		0.312	186	11

transient and excluded, the median area and length are 0.312 ha and 186 m, respectively. The Spearman rank-order correlation between area and length is $r_s = 0.60$ (NS) for all turtles.

The Spearman rank-order correlation between the estimated area and the number of sightings upon which this estimate was based is $r_s = 0.20$ (NS); the correlation between observed length and number of observations is $r_x = -0.20$ (NS). Both values, however, were influenced by the atypical behavior of Turtle C.

Daily displacement (straight-line distance between sightings divided by the days between sightings) was calculated because the number of days between sightings varied and because the distance between the sightings was significantly correlated with the number of intervening days ($r_{40df} = 0.55$, $p < .001$). The median displacement per day was 14 m, as shown in Table 8. The turtles did not differ significantly from each other on this measure (Kruskal-Wallis one way analysis of variance, $H = 1.28$, NS).

Discussion

The box turtles were found mostly on hillsides, which accords with Dolbeer's (1969) report for an adjoining area. Personal observations of box turtles' tank-like strategy of persistently moving through obstacles rather than around them, which can be rather amusing in an otherwise open laboratory or living room, become understandable in the dense vegetation which they were found to inhabit where clear paths often do not exist.

Most box turtles were found to use individually prescribed areas within the suitable habitat studied. This is consistent with previous

Table 8. Daily displacement (straight-line distance between sightings divided by number of intervening days).

Turtle	Daily Displacement (m)			Number of Displacements
	Mean	Median	Range	
A	15	16	3-33	20
C	17	9	2-50	4
E	13	10	2-45	10
F	21	18	3-44	8
Overall	16	14	2-50	42

reports that box turtles occupy individual home ranges (e.g. Dolbeer, 1969; Legler, 1960; Schwartz and Schwartz, 1974; Stickel, 1950). The only relocated female presents a possible exception to this general rule. She moved through the study area in a generally straight line, covering a greater length than that estimated for any of the other home ranges. Much of the terrain through which this female travelled was grassy valley land. This, with the time of year (late June to early July) makes it plausible that this was an egg-laying trip. Turtles of both sexes, however, are known to make occasional "visits" outside their home ranges (Stickel, 1950) and long distance transients have been reported moving in relatively straight lines (Kiestler, Schwartz, and Schwartz, unpubl.). Experimentally displaced turtles may also move relatively great distances in relatively straight lines (Breder, 1927; Lemkau, 1970).

Home range areas, estimated by taking the area of the convex polygon drawn through the peripheral observed locations of each turtle, showed only moderate correlations with the length of the greatest axis through this area. The latter measure corresponds to the home range "diameters" most commonly reported as an indication of box turtle home range size. The low correlation between area and length obtained in the present study raises the question of the suitability of using a two-dimensional measure to represent the size of an area. To have taken the areas of the circles produced by these diameters, a method used by Fitch (1958) and Legler (1960), would have produced areas many times as great as those obtained by connecting the peripheral points. This may be seen by inspection of Figure 8. Taking the area of the smallest rectangle enclosing all points (Schwartz and Schwartz, 1974) would have

produced intermediate results.

Home range lengths obtained in the present study ($\bar{x}$ = 190 m) are considerably larger than those obtained by Dolbeer (1969) for an adjacent area ($\bar{x}$ = 74 m; range, 15-168m) or for Terrapene c. carolina in other parts of the country: $\bar{x}$ = 100-113 m (Stickel, 1950), $\bar{x}$ = 114 m (Williams, 1961), with the exception of an estimated diameter of 229 m reported by Nichols (1939b). The studies by Dolbeer and Williams used a minimum of three and two sightings per turtle, respectively. Mean home range diameters of 169 m and 167 m were calculated, by using average distance between successive captures as one radius, by Legler (1960) and Fitch (1958) for Terrapene o. ornata with a minimum of two locations per turtle. In the present study, turtles were located 5-21 times (median = 10). The smaller home range lengths reported in other studies may reflect the smaller number of sightings per turtle.

The differences obtained may reflect differences in the turtles' behavior, perhaps as a function of specific locality, terrain, or year. The present observations were made in 1978 following two severe winters. Possibly, lowered population densities corresponded with larger home range sizes. The elongated home ranges obtained in the present study may partially account for the greater home range lengths obtained. If so this reflects a weakness in the use of a linear measure.

The mean home range area of 0.377 ha obtained in this study is considerably less than the 1.5 ha reported for Terrapene carolina triunguis (Schwartz and Schwartz, 1974) and 2.0-2.3 ha reported for Terrapene ornata ornata (Fitch, 1958; Legler, 1960) using less conservative methods as discussed above (p. 57). Terrapene ornata would be expected to have larger home ranges than Terrapene carolina on the basis

of a comparison of published reports of home range lengths, habitat types, and population densities (see pp. 10-13). Unfortunately, estimates of home range areas of Terrapene carolina carolina are not available for comparison, as these studies relied upon length.

As would be expected, the average displacement per day found in the present study was somewhat less than actual distances moved per day as reported for traileed turtles by other investigators (Dolbeer, 1969; Legler, 1960; Lemkau, 1970). In view of the often circuitous nature of turtles' movements reported in the above studies, the median straight-line displacement per day of 14 m may actually reflect greater activity than Dolbeer's (1969) measure of 20 m total movement per day.

The difficulties encountered in attempting to observe turtle's movements directly, like those encountered in previous attempts (see pp. 23-24), suggest that the turtles were aware of the presence of the observer and reacted by "freezing." This underscores the danger of drawing conclusions about the limits of their repertoire on the basis of which types of behavior have not been observed. Although the turtles rarely even changed posture while observed, successive locations indicated that they traversed a median of 14 m per day as measured in a straight line. Even this lower limit of their actual wandering presents a very different picture of their activity from that which might be construed on the basis of direct observation.

Although the data collected confirm that box turtles do discriminate between certain areas (their home ranges) and surrounding suitable habitat, more detailed investigations of the basis of this discrimination and of discrimination of particular land marks did not prove feasible in the field. Such discrimination might well prove adaptive in allowing

turtles to locate resources such as seasonally shifting food sources, shelter sites, and possibly other individuals.

Study 2. Area Preferences in a Semi-Naturalistic Setting

Introduction

Field studies have revealed that box turtles occupy home ranges; however, such studies have not proven conducive to the direct observation of movements and investigation of differential use of features within the home range which would clarify the turtles' experience and facilitate an understanding of their behavior. Reports which do exist of differential reuse of particular resting sites by turtles occupying the same area, or even of any reuse of resting sites, are extremely limited and contradictory (A. Ross Kiester, pers. comm.; Legler, 1960; Stickel, 1950).

In the present study, movements and use of resting sites within a relatively large outdoor enclosure were observed in order to elucidate factors which affect box turtles' choices of locations and to determine whether turtles showed patterns of area use indicative of individual recognition of and preference for specific locations. Social implications of spacing are discussed on pp. 86-108.

Methods

This study was conducted in an outdoor enclosure at the Knoxville Zoological Park as shown in Figure 9. The enclosure measured about 8 m on a side and encompassed 58 m^2 (= 0.0058 ha). The enclosure was marked with wooden stakes in a grid of 0.5 x 0.5 m quadrats. Each quadrat was designated by a unique combination of letter and number.

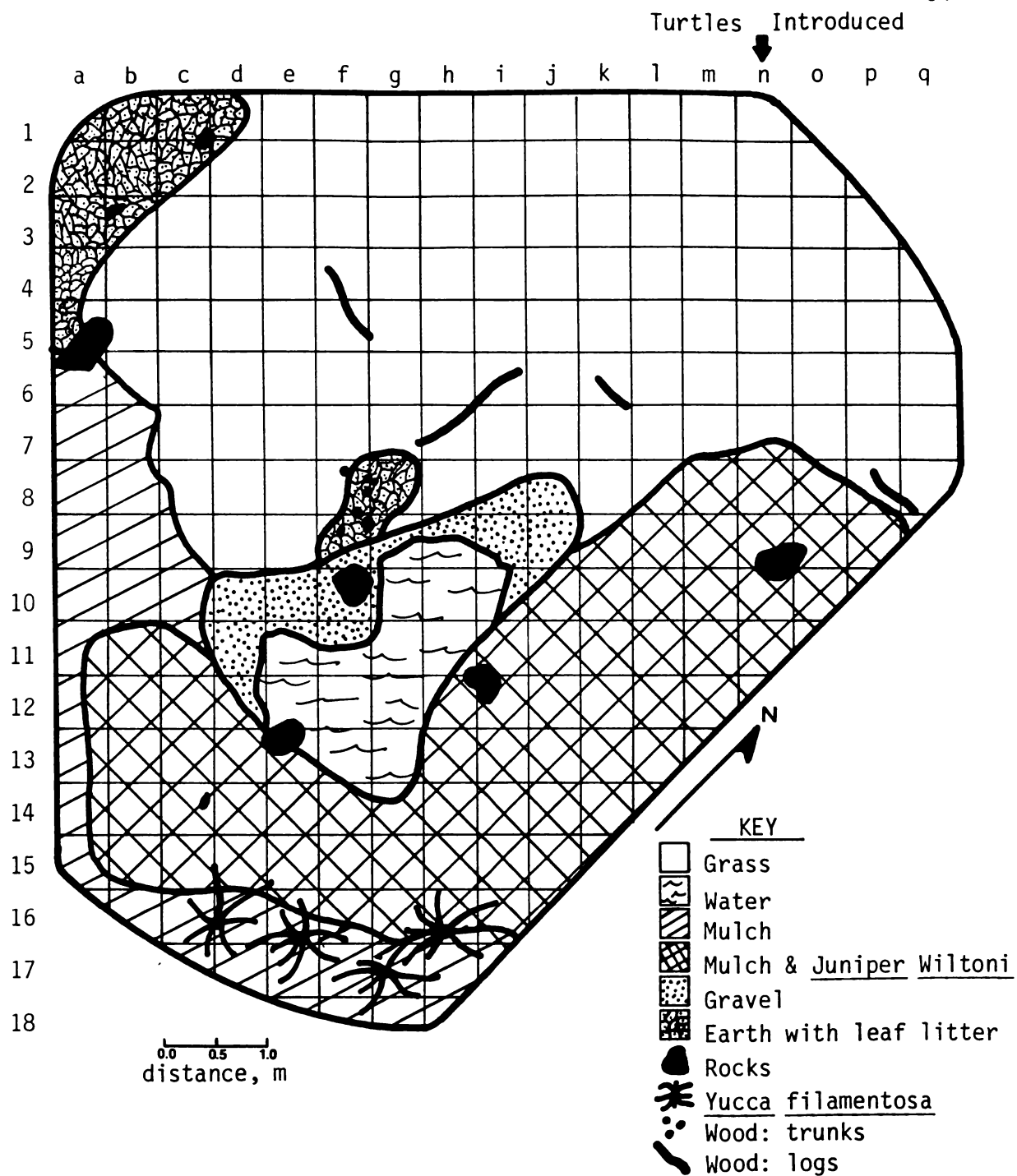


Figure 9. Box turtle enclosure at the Knoxville Zoological Park.

Subjects were 21 eastern box turtles, who were captured and donated to the Zoological Park in May, 1976 by individuals responding to a public request, with the exception of Turtle 1, who had been housed indoors at the Knoxville Zoological Park for several years. Turtles were classified according to age and sex on the basis of size and external characteristics as described on pp. 7-8. Sixteen adults, eight females, and eight males, as well as five juveniles, served as subjects. An additional 24 eastern box turtles were used in a later phase of this study. These were almost all adults and included individuals of both sexes.

Twenty-one turtles were picked up, weighed, measured, and paint-marked, then introduced to the enclosure at a rate of slightly less than one per day. Turtles were introduced in a uniform manner into the same, unshaded, corner of the enclosure (see Figure 9).

Weather conditions were noted prior to each introduction. Air and ground temperature, relative humidity, and whether it was sunny, hazy, shady, or raining were recorded.

Each of these turtles was observed for 45 minutes immediately subsequent to its introduction into the enclosure. Its location at the beginning of each minute was recorded by noting which 0.25 m^2 quadrat the turtle was in. This will be referred to as the turtle's initial locations. These locations were later plotted on a map of the enclosure and connected by straight lines to indicate the approximate paths taken by the turtles.

Subsequently, the locations of all turtles in the enclosure were recorded prior to the introduction of each new turtle. A turtle's location was not recorded until it had been in the enclosure overnight.

A total of 180 locations were recorded for 19 turtles during 19 days of observation between May 10 and June 10, 1976 (see Table 9). These turtles were located a median of 10 times (range, 1-19). On seven occasions, turtles known to be in the enclosure could not be located. The social implications of the turtles' locations relative to each other are discussed on pp. 86-92.

All turtles were placed in the center of the enclosure (Area 4) twice a week and fed a mixture of chopped vegetables, fruits, eggs, and meat by zoo personnel.

One day after the observation period, zoo personnel removed the turtles from the enclosure and maintained them indoors for 11 days. During this time five privet bushes, Ligustrum sp., were planted in an open area bounded by rows 1-6 and columns k-o. The original "resident" turtles and 24 new turtles were then simultaneously placed in the enclosure by zoo personnel. The locations of all turtles were recorded 9 days after the reintroduction of turtles to the enclosure.

Results

The locations of each 21 box turtles during its first 45 minutes in the enclosure are shown in Figure 10. Turtles tended to move along the perimeter of the enclosure, which was bounded by a wooden-pole fence approximately 1 m high. Only 4 turtles crossed the central part of the enclosure. These were Turtle 1, an adult male who had previously been maintained in captivity, Turtles E and R, adult females, and Turtle S, a juvenile. Turtle 1 repeatedly crossed the open central part of the enclosure; each of the others crossed it once. In contrast, Turtle I, an adult male, and Turtles K and N, juveniles, did not move

Table 9. Gender and number of observed locations of 21 box turtles in the enclosure at the Zoological Park.

Turtle	Gender if Adult	Number of Daily Locations	Number of "Missing" Locations
I	Male	19	
A	Male	18	
B	Female	17	
C	Male	15	1
D	Male	13	2
E	Female	14	
F	Male	12	1
H	Female	12	
I	Male	11	
J	Female	10	
K	Juvenile	6	*
L	Male	8	
M	Female	7	
N	Juvenile	3	3
O	Female	5	
P	Female	4	
Q	Male	3	
R	Female	2	
S	Juvenile	1	
T	Juvenile	0	
U	Juvenile	0	

*No missing observations prior to accidental death.

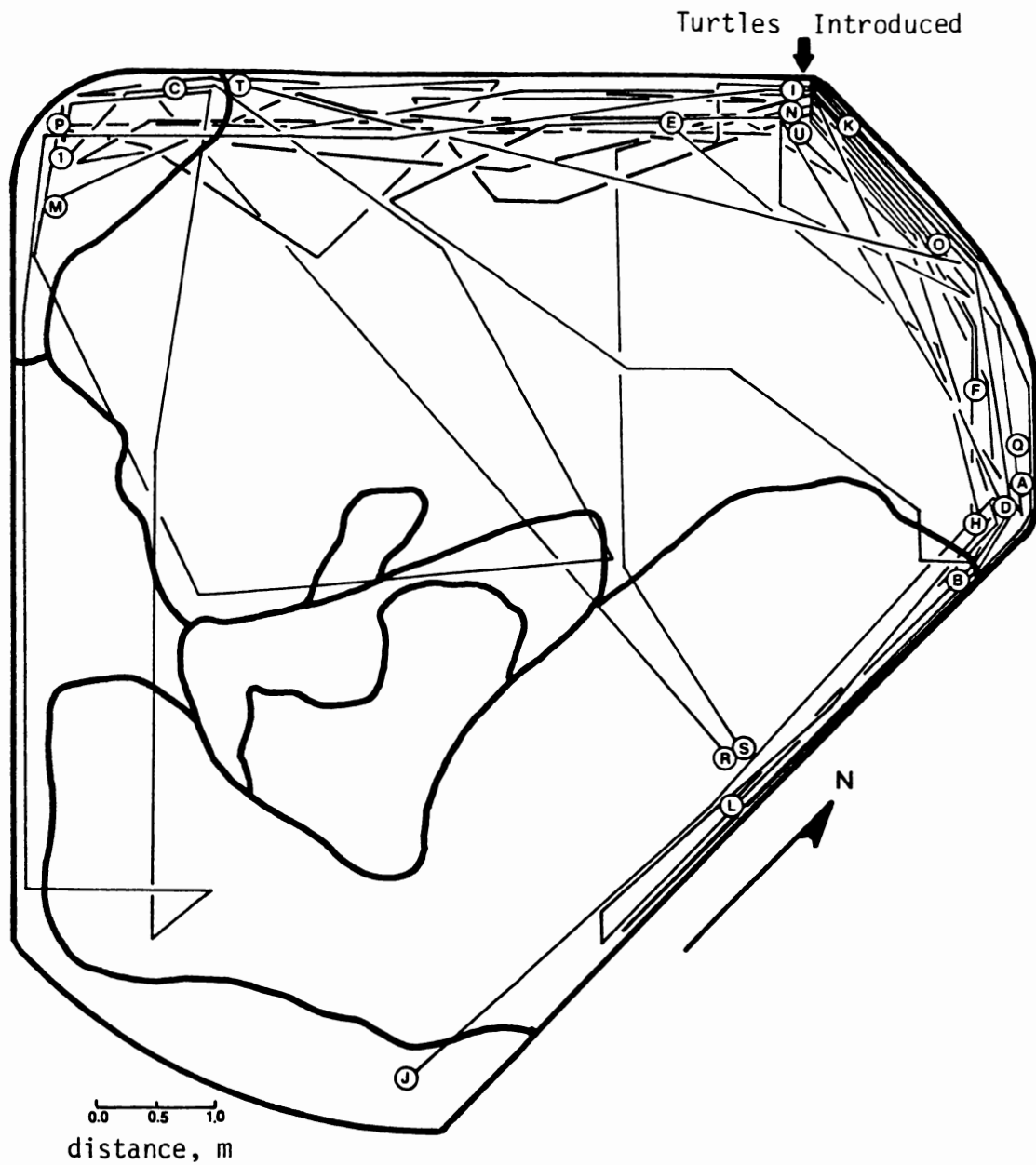


Figure 10. Composite map of the locations of all 21 box turtles during their first 45 minutes in the enclosure. Quadrat locations 1 minute apart are connected by straight lines. Turtles' initials indicate their location at the end of the 45 minutes.

from the 0.25 m^2 quadrat into which they had been placed. Most turtles simply turned right or left after being introduced into the enclosure and moved along the perimeter in one direction. Some moved back and forth.

These differences do not appear to be accounted for by environmental variables (see Table 10). No significant differences were found, using a Kruskal-Wallis one way analysis of variance, between turtles who crossed the center of the enclosure, those who moved along the perimeter, and those who remained in their initial quadrat, in air temperature ($H = 0.92$, NS), ground temperature ($H = 0.64$, NS), or relative humidity ($H = 1.16$, NS).

Turtles crossed the center of the enclosure on two sunny days, one hazy day, and one shady day. They moved along the perimeter on days which were sunny seven times, hazy three times, shady three times, and raining once. Turtles remained in their initial quadrat on a sunny, a shady, and a rainy day.

Most turtles stopped moving in one of the corners adjacent to the corner where they were introduced. Only Turtle J, an adult female, stopped in the diagonally opposite corner, after having moved extensively back and forth along the perimeter. Turtles' locations at the end of the 45 minute observation period are shown in Figure 10. By this time, 10 turtles had dug into the ground, eight had burrowed but had remained in the same quadrat for at least 15 minutes, and one had remained in the same quadrat for 8 minutes but was observed there after the end of the formal observation period until a full 15 minutes had elapsed. Only two turtles, A, an adult male, and E, an adult female, were still active at the end of the observation period. Turtle A, however, dug

Table 10. Median temperature and humidity for introductions to the zoo enclosure during which turtles crossed the center of the enclosure vs. moved along the perimeter vs. remained in the initial quadrat.*

Behavior	N	Temperature ($^{\circ}\text{C}$)		Relative Humidity(%)	Introduction	
		Air	Ground		Date	Time
Crossed center	4	21 (17-27)	24 (13-29)	64 (46-76)	(5/9-6/8)	(11:05am-6:20pm)
Moved along perimeter	14	22 (13-30)	20 (16-25)	71 (47-93)	(5/10-6/9)	(9:55am-6:40pm)
Remained in initial quadrat	3	23 (22-26)	20 (20-23)	66 (65-68)	(5/21-6/3)	(12:40pm-6:00pm)
Overall	21	22 (13-30)	20 (13-29)	71 (49-93)	(5/9-6/9)	(9:55am-6:40pm)

*Ranges of temperature, humidity, dates, and times are indicated in parentheses.

into the ground 13 minutes after the observation period formally terminated. Turtle E was still active 20 minutes after the official end of the observation period. Their initial resting locations were recorded for all turtles except E.

Subsequent daily locations revealed that corner areas continued to be favored by turtles as resting sites. The three areas in which turtles congregated are denoted in Figure 11 as Areas 1, 2, and 3. The rest of the enclosure was designated as Area 4. For each of the 18 relocated turtles, the proportion of its observed locations which were within each area was calculated. The means of these proportions were obtained for each area and compared with the proportion of the total square meters of the enclosure contained within that area (see Table 11). The mean proportion of locations in Areas 1, 2, and 3, combined, was 0.89, although together they encompassed a proportion of only 0.10 of the total area.

Within this overall pattern of area use, individual turtles showed their own area preferences. The 18 repeatedly located turtles spent a mean proportion of 0.69 (range, 0.43-1.00) of their observed daily locations within one preferred area of the enclosure, although which area this was varied from turtle to turtle. Turtles were found in their individually preferred areas a median of 6.0 times vs. 2.5 times in the other three areas combined. This includes two turtles who spent equal amounts of time in two areas, only one of which was included as preferred. This preference for one area vs. all others is statistically significant (Wilcoxon signed-rank test, two-tailed, $p < .01$). The number of times each turtle was found in each area, arranged by preference, is shown in Figure 12.

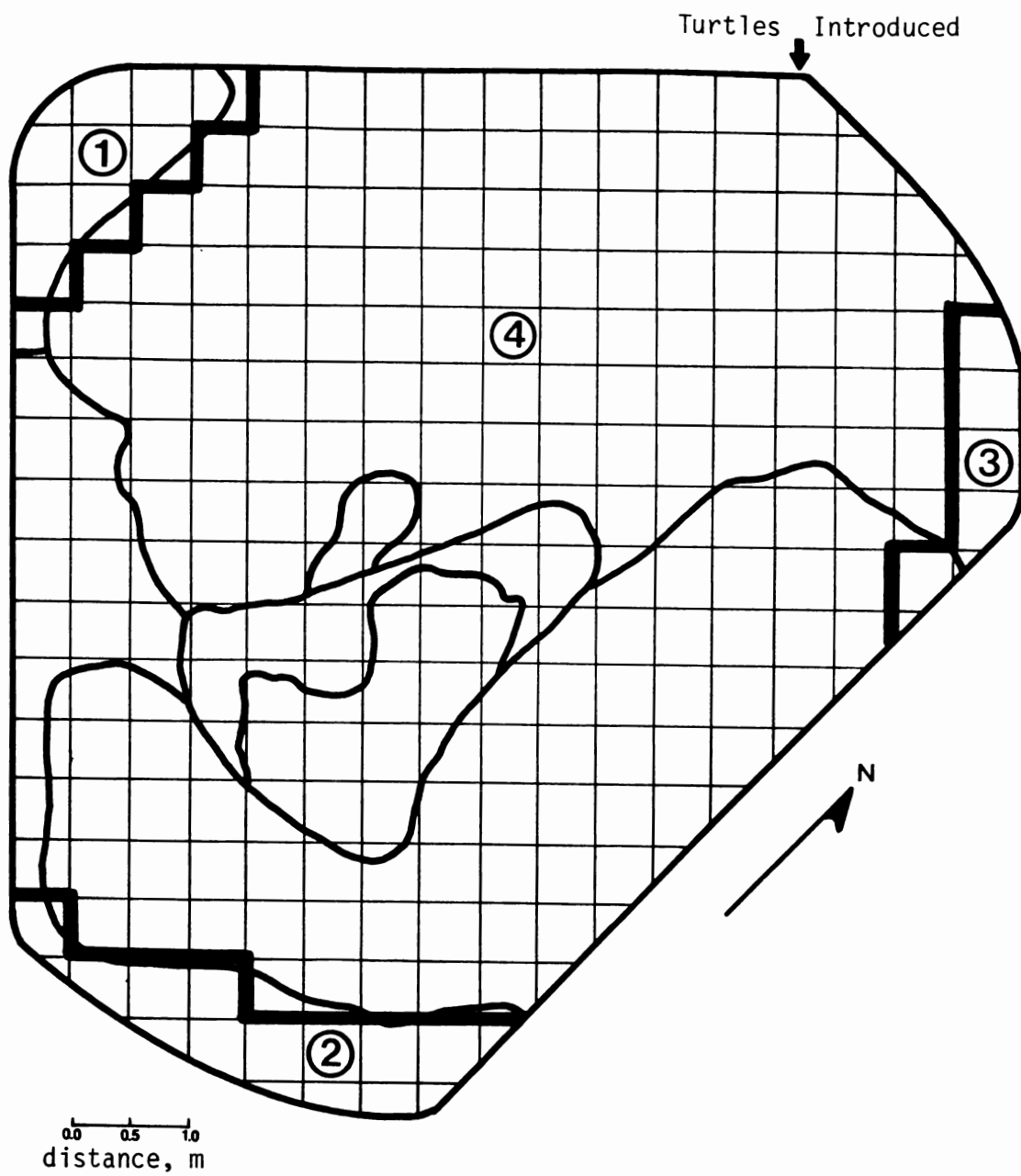


Figure 11. Four areas of the box turtle enclosure. Areas 1, 2, and 3 were preferred by turtles.

Table 11. Mean proportions of each turtle's locations within Areas 1, 2, 3, and 4 compared with the proportion of total square meters contained within each area.*

	Area			
	1	2	3	4
Mean proportion of each turtle's locations	0.36	0.37	0.16	0.11
Proportion of total square meters	0.04	0.04	0.02	0.90

*Based upon 179 locations of 18 repeatedly located turtles.

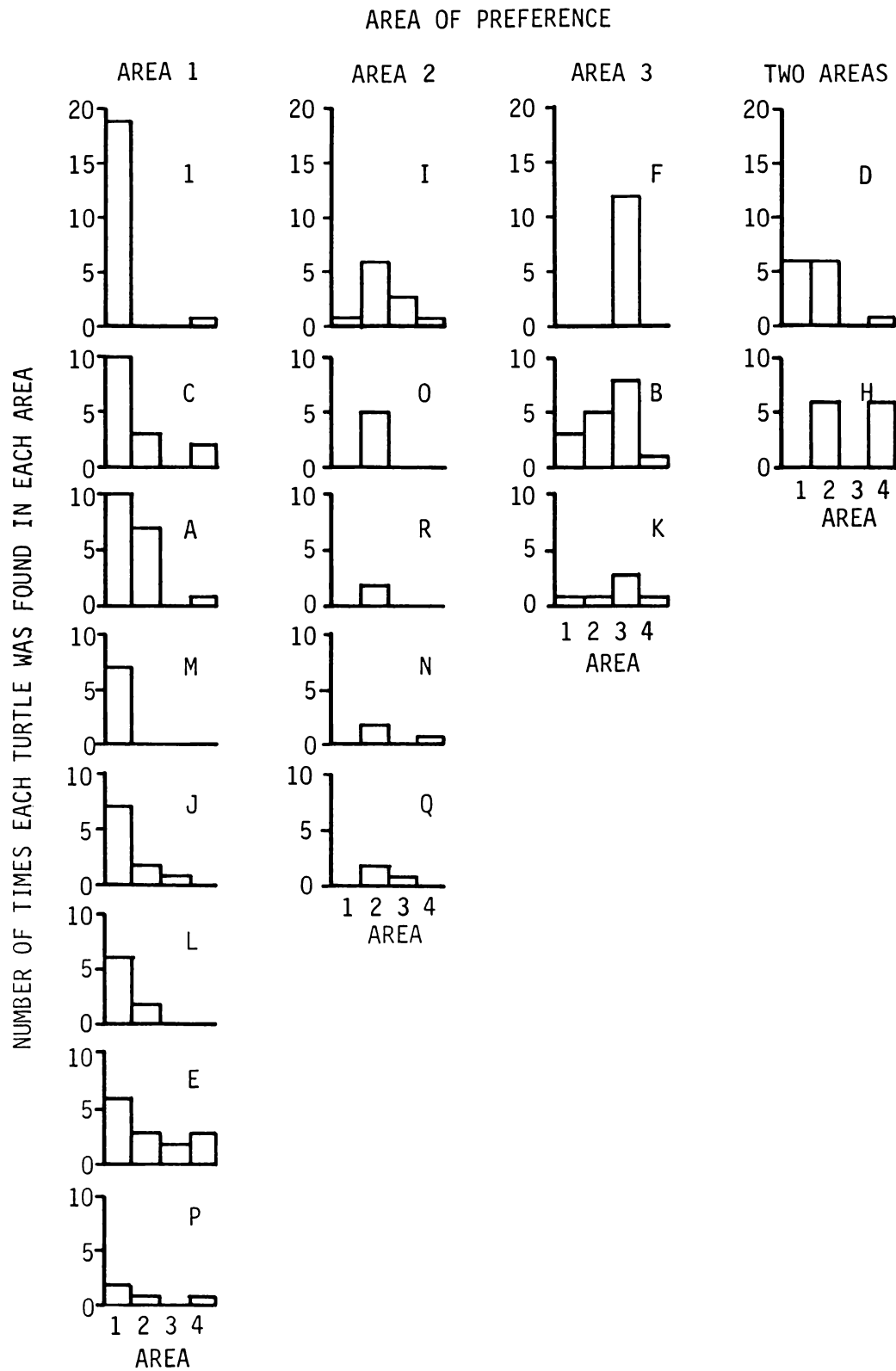


Figure 12. Number of times each turtle was found in each area of the enclosure.

The relationship between turtles' preferred areas, based upon their daily locations, and the areas of their first resting sites, as described on pp. 66-68, is shown in Table 12. Turtles S, T, and U, whose daily locations were not recorded more than once, and Turtle E, whose initial resting site was unknown, were excluded from this analysis. Areas 1 and 2 were eventually preferred by more turtles than initially rested there. The only turtle who initially rested in Area 2 was later found more frequently in Area 1. Area 3 was preferred by less turtles than originally rested there. All turtles who originally rested in Area 4 were later found more frequently in other areas. No turtle showed a sole preference for Area 4. This finding, combined with the numbers of turtles showing a preference for each area, may indicate that the desirability of the areas corresponded with the order in which they are numbered, but that Area 2, which was farthest from the point of introduction, was not immediately discovered. This area was used more by turtles who were introduced to the enclosure late. The median order of introduction of turtles preferring this area was 15, compared with 10 for Area 1 and 7 for Area 3. This suggests that Areas 1 and 3 may have "filled up" causing later turtles to seek farther for a resting site.

A clear differentiation in area use is evident when 19 of the original turtles are compared with 24 additional turtles, even though the original, "resident" turtles were removed from the enclosure following the last observation period and were reintroduced simultaneously with the new turtles. New shelters, in the form of bushes which had been planted in Area 4 while the turtles were absent, were used almost exclusively by the new turtles, while other, previously available,

Table 12. Daily area preference compared with initial choice of resting area.*

Initial Resting Area	Preferred Area				Total
	1	2	3	4	
1	4	0	0	0	4
2	1	0	0	0	1
3	0.5	2	2	0.5	5
4	2	4	1	0	7
Total	7.5	6	3	0.5	17

*Based upon 17 relocated turtles with known first resting sites.

resting sites were used by the reintroduced turtles (see Table 13). This difference is statistically significant ($\text{Chi}^2 = 6.72$, $p < .01$).

Discussion

Turtles showed marked individual preferences for areas of the enclosure despite the fact that the total enclosure was much smaller than one average home range. This was based largely upon observed resting sites. Boice (1970) also noted some individual preferences for areas of an enclosure on the basis of resting positions. A. Ross Kiester (pers. comm.) noted some tendency for box turtles to reuse their own resting sites in the field.

The significantly higher use of established resting sites by resident turtles and new resting sites by newly introduced turtles, although the resident turtles had been removed from the enclosure while the new resting sites were installed and then reintroduced simultaneously with the new turtles, raises questions regarding the mechanism of this segregation. Virtually exclusive use of a quadrat of an enclosure by the dominant male and one female was reported by Boice (1970). It is not known whether any defense of space was involved. Such defense might take the form of subtle, easily overlooked behavior. Fecal pellets, especially those laid by a dominant male, were sufficient to cause the dispersal of other desert tortoises, Gopherus agassizi, when deposited in their accustomed sleeping places (Patterson, 1971).

The box turtles also showed certain consistencies in their use of the enclosure. The most frequently used resting sites were in corner locations. Observations of turtles' movements revealed that most moved along the perimeter of the enclosure. Several factors which

Table 13. Differential use of new vs. established shelter sites by new vs. reintroduced turtles.

	New Shelters	Established Shelters	Total
New turtles	17	7	24
Reintroduced turtles	5	14	19
Total	22	21	43

Chi^2 (with Yates correction) = 6.72, $p < .01$.

may have been experienced as attractive by the turtles include shade, lower temperature, cover, vegetation and consequent soil characteristics, and tactile and visual proximity to objects. These factors are inter-related and confounded in this study. By carefully controlling the setting, one might establish which cues turtles used to guide their movements.

Study 3. Responses to Spatial Cues

Introduction

Little is known about the ways box turtles experience their environment. The cues that box turtles routinely use in their movements through the terrain are largely unknown.

Box turtles in an outdoor enclosure were most frequently found in areas which suggest that shade, cover, and proximity to objects may have been experienced as attractive. The specific cues which the turtles perceived, and even the sensory modes employed, have yet to be defined.

Personal observations of eastern and three-toed box turtles revealed that they consistently headed toward a border of woods when placed in an open grassy area. To a human observer, from turtle eye level, the line of woods appeared as a dark band which contrasted with the brighter open area.

Darkness is a possible cue in both situations, although other possibilities include temperature and olfactory stimuli. Turtles are believed to have well-developed vision, including color vision, on the basis of morphological, electrophysiological, and behavioral evidence (reviewed by Granda, 1979).

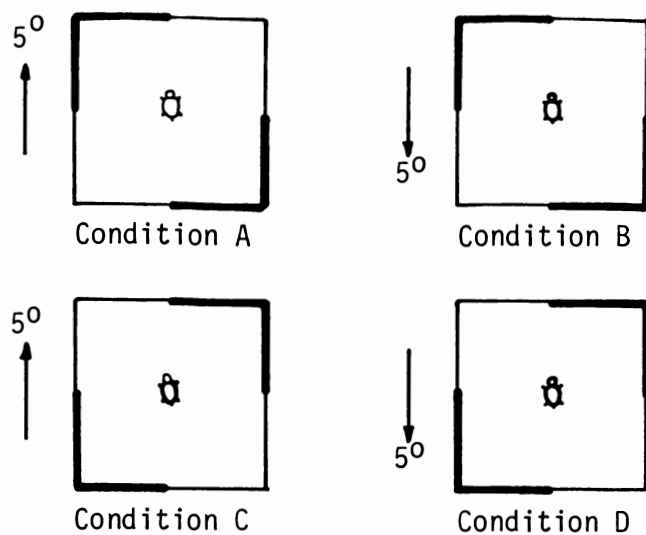
When released in an open area, box turtles also showed an apparent tendency to head uphill, although this was confounded with heading toward the woods in these personal observations. This relationship may often occur naturally. Dolbeer (1969) reported finding more eastern box turtles on wooded hillsides than level wooded areas, with the least preferred habitat being low, open, grassy areas.

In order to distinguish cues used by box turtles, darkness and slope were presented independently of each other and of other possible cues in laboratory tests. It was hypothesized that eastern box turtles, which inhabit wooded hills and utilize local cover, would move toward darkness and uphill.

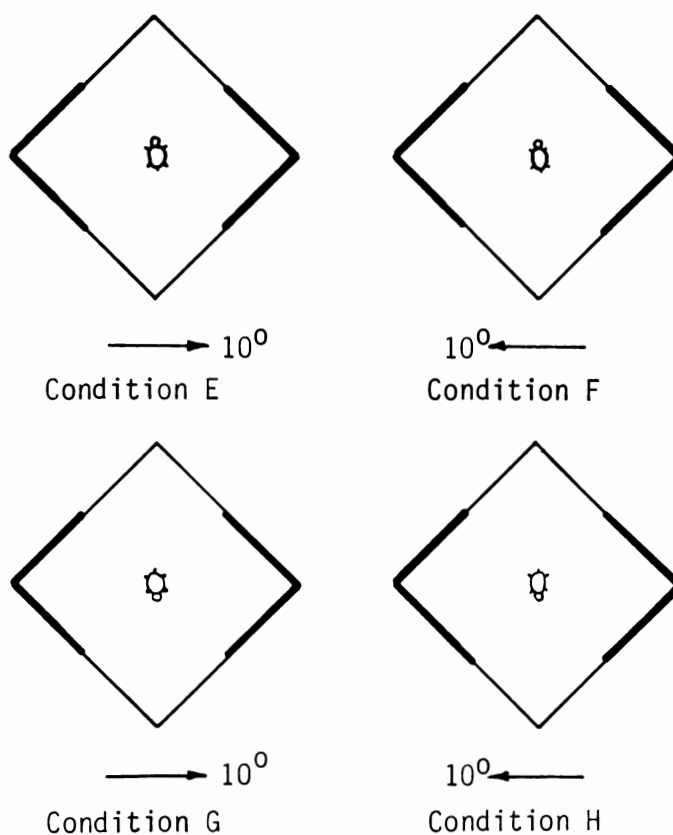
Methods

Subjects were 10 hatchling box turtles provided by the Knoxville Zoological Park. They varied between approximately 2-5 months of age when first tested and 8-11 months during the final testing. All hatchlings had been raised indoors in plastic trays, except for a brief exposure by some turtles to the open, relatively level box turtle enclosure (described on pp. 66-67) in which these turtles hatched.

Turtles were tested in an open-topped wooden chamber which measured 122 x 118 cm across and 61 cm deep. Alternate corners of the chamber were painted a dark "forest" green (Munsell value, 2). The other two corners and the floor were painted a light "grass" green (Munsell value, 8). One side of the chamber, containing a dark and a light corner, was raised 5° (see Figure 13 A). In a modification of this experiment, one corner, rather than a side, was raised with a slope of 10° (see Figure 13 B). The experiment was conducted in this condition



A. Original Experiments



B. Modified Experiments

Figure 13. Orientations of test chamber with slope and starting position as shown. Light lines indicate light walls; heavy lines indicate dark walls. Direction of arrows indicate direction of upward slope.

using the same two values of green and repeated using those values of grey and of violet.

Shadowless, moderately low illumination (usually 11-44 lux) was provided. This was accomplished by placing a partition between the test chamber and a window which was the only source of illumination. This permitted only light reflecting around the partition to illuminate the chamber. To a human observer, the illumination appeared subdued, although colors were clearly distinguishable.

A modal temperature of 26⁰ C (range, 23-29⁰C) was maintained during testing. The turtles were usually maintained at a higher level of illumination, similar temperature (26.5⁰ C) and higher humidity than the conditions presented in the test situation.

Subjects were placed in the center of the chamber oriented as shown in Figure 13. The chamber was systematically rotated between trials in a design which counterbalanced for possible cues inside or outside the chamber (including the position of the observer) and possible tendencies of turtles to move forward or to one side.

In the original experiment (shown in Figure 13 A), turtles faced a side of the chamber. Four conditions were required for complete counterbalancing. In condition A the left front corner and the one diagonally opposite it were dark and the forward side of the chamber was elevated. Condition B was the same except the rear side of the chamber was elevated. In condition C the right front corner and its diagonal opposite were dark and the front of the chamber was elevated. In condition D the rear of the chamber was elevated. The box was rotated so that the back corners in conditions A and B were the front corners in conditions C and D. The box was thoroughly cleaned with soap and

water between trials.

In the modified version of the experiment (shown in Figure 13 B), the turtles faced a light corner, with dark corners to their right and left. In condition E, the right corner was elevated 10^0 ; in condition F, the left corner was elevated. Conditions G and H were the same as E and F, respectively, except that the turtles were introduced facing in the opposite direction.

Choices were recorded only when turtles actually touched a wall of the chamber. A choice of dark or light was recorded depending upon the value of the wall which was touched. A choice of up or down was recorded on the basis of position relative to the center axis of the chamber. Trials were allowed to continue until turtles first touched a wall or to a maximum duration of 20 minutes. Some turtles were inactive when tested and remained where they had been placed in the center of the chamber. Such turtles were retested after at least one intervening test and given a maximum of three opportunities to perform under each condition.

Results

All seven turtles who moved at all went to the dark portion of the chamber during the original experiment, in which they were placed facing a wall which was half light and half dark (see Table 14). In the modified condition, turtles were placed facing a light corner. Despite having to turn aside to do so, most turtles again went to a dark portion of the chamber. The number choosing the dark side was fairly constant, regardless of color, as shown in Table 14. Across conditions, the turtles moved to a dark wall of the chamber significantly more often

Table 14. Turtles' choices of dark (D) vs. light (L) portions of the test chamber in each experimental condition.

Turtle	Original Condition		Modified Condition						Total*	
	Green, 5 ⁰		Green, 10 ⁰		Grey, 10 ⁰		Violet, 10 ⁰			
	D	L	D	L	D	L	D	L	D	L
1	1	0	1	0	0	1	1	0	3	1
2	0	0	1	0	0	1	0	1	1	2
3	1	0	1	0	1	0	1	0	4	0
4	0	0	1	0	1	0	1	0	3	0
5	1	0	0	1	1	0	1	0	3	1
A	1	0	1	0	1	0	1	0	4	0
B	1	0	1	0	1	0	1	0	4	0
C	0	0	1	0	1	0	1	0	3	0
D	1	0	0	0	0	1	0	0	1	1
E	1	0	0	1	1	0	0	1	2	2
Total	7	0	7	2	7	3	7	2	28	7

*Wilcoxon signed-ranks test on total dark vs. light choices by turtles, $T = 1$, one-tailed, $p < .01$.

than to a light wall (Wilcoxon signed-ranks test, one-tailed, $T = 1$, $p < .01$).

More turtles moved to the uphill rather than the downhill side of the chamber in all conditions, although this difference did not attain statistical significance (see Table 15). The difference was somewhat greater in the modified conditions, in which the slope was 10^0 rather than the original 5^0 . More turtles moved downhill than uphill regardless of color. Grey was omitted from this analysis due to an incomplete counterbalancing with respect to slope. No significant interaction between choice of slope and choice of value was obtained in any condition (see Table 16).

Discussion

The eastern box turtles tested in the present experiment apparently used the visual cue of darkness in determining their direction of movement. The darker of two values was selected significantly more often. Although the turtles showed a tendency to move forward, more turtles moved to a darker corner of the test chamber even when a lighter corner was directly in front of them. This occurred regardless of dimmer than usual illumination and despite widely differing hues. A "forest" green was no more effective than simply grey or even violet. The consistency of performance during trials spanning 6 months does not suggest ontogenetic changes in use of value or slope during this period.

The turtles moved uphill more often than down; this tendency was stronger when the slope was greater. This result is consistent with reports that certain gastropods and arthropods, as well as mammals, will move more directly up an inclined plane with greater slope (Croizier and

Table 15. Turtles' choices of uphill (U) vs. downhill (D) portion of the test chamber in each experimental condition.

Turtle	Original Condition		Modified Condition				Total*	
	Green, 5 ⁰		Green, 10 ⁰		Violet, 10 ⁰			
	U	D	U	D	U	D	U	D
1	1	0	0	1	1	0	2	1
2	0	0	1	0	0	1	1	1
3	1	0	1	0	1	0	3	0
4	0	0	1	0	1	0	2	0
5	0	1	1	0	1	0	2	1
A	0	1	0	1	0	1	0	3
B	1	0	0	1	1	0	2	1
C	0	0	1	0	1	0	2	0
D	1	0	0	0	0	0	1	0
E	0	1	1	0	0	1	1	2
Total	4	3	6	3	6	3	16	9

*Wilcoxon signed-ranks test on total up vs. down choices by turtles, $T = 11.5$, NS.

Table 16. Number of turtles choosing dark vs. light by uphill vs. downhill portions of the test chamber in three experimental conditions.

	Original Condition			Modified Condition					
	Green, 5 ⁰			Green, 10 ⁰			Grey, 10 ⁰		
	Dark	Light	Total	Dark	Light	Total	Dark	Light	Total
Uphill	4	0	4	4	2	6	6	0	6
Downhill	3	0	3	3	0	3	1	2	3
Total	7	0	7	7	2	9	7	2	9
	Fisher exact test, NS			Fisher exact test, NS			Fisher exact test, NS		

Navez, 1930; Croizier and Pincus, 1927-1928; Croizier and Stier, 1927-1928).

Hatchling sea turtles, which must normally move down the beach to the lower, open ocean, have been experimentally shown to move downhill and toward a bright or open horizon (see p. 20). Diamondback terrapins which inhabit swampy areas have been shown to move downhill but toward patches of vegetation (Burger, 1976). Vegetation generally appears dark against the horizon.

Movements toward darkness and uphill, as performed in the present study, would tend to keep box turtles in wooded areas providing cover and counteract the tendency to wander downhill due to gravitational attraction. Thus the results obtained in this study would seem to be related to the preference of eastern box turtles for wooded hills in contrast to low, open areas.

CHAPTER III

PREFERENCE FOR INDIVIDUALS AND RECOGNITION OF NEIGHBORS

Study 4. Preference for Individuals

Introduction

In order to learn about box turtles' experience of each other, their recognition of and preference for other individual turtles were investigated. The spacing patterns of captive box turtles were studied to discover whether the turtles showed discrimination among other turtles by consistently choosing to be near certain individuals. Effects of gender were also investigated, in the absence of any apparent courtship behavior, to determine whether turtles discriminated between certain classes of individuals.

The relative proximity of turtles' resting locations was chosen as a measure for several reasons: Choice of a resting location represented a commitment by the turtle, usually of at least several hours; use of resting positions also allowed the locations of all turtles to be recorded before any of them moved; finally, resting was a commonly observed behavior.

Methods

Differential proximity of resting turtles was recorded for two groups of five hatchlings, each housed indoors in 26 x 33 x 10 cm plastic trays, and for 19 turtles (eight adult females, eight adult males, and three juveniles) housed in an outdoor enclosure at the Knoxville Zoological Park. This enclosure and the turtles in it are described on pp. 60-61.

Positions of all turtles in the zoo enclosure were recorded relative to each other at least 1 day subsequent to the introduction of each turtle. These observations were conducted simultaneously with the observation of daily locations relative to areas of the enclosure discussed on pp. 60-76. Observation of relative locations was begun when there were two turtles in the enclosure and continued until 19 turtles had been introduced at a rate of slightly less than one per day. The maximum number of turtles in the enclosure was 18 due to the death of one subject. A total of 179 turtle locations was recorded during 18 days of observation. Most turtles were resting when these observations were made.

Positions of hatchlings housed indoors were recorded relative to each other on eight occasions between September 1, 1977 and March 21, 1978. These turtles had hatched the previous spring and had been housed in these units since July 7, 1977, almost 2 months prior to the first observation. Observations were made at night when turtles were inactive and appeared to be sleeping.

Turtles were recorded as "touching," if there was contact between them, or "close," if they were not touching but were less than about 10 cm apart for the zoo turtles and 4 cm for the hatchlings. In both cases this was roughly equivalent to one turtle-width. In order to avoid the redundancy which would have resulted if all the turtles close to or touching every other turtle were counted, the number of close or touching pairs of turtles was used in this analysis; a turtle could be a member of several pairs simultaneously.

Results

Zoo turtles. Twenty-seven different pairs of turtles were found close to or touching each other during the 18 daily observations. The number of potential pairs ranged from one on the first day, when there were two turtles in the enclosure, to 153 on the last day, when there were 18 turtles in the enclosure, with a median of 50 potential pairs. Obviously, the number of actual pairs which could occur simultaneously was much smaller. The median number of observed pairs per day was 1.5 (range, 0-8). A total of 41 pairs, including repeated pairs, was observed in 18 days. All 16 adult box turtles were observed in pairs at least once (median, 4; range, 1-12, with repeated pairs included). None of the three juvenile turtles was observed close to or touching another turtle; however, the median total number of observations per juvenile was only 3.0, compared with 11.5 for adults.

Twenty pairs of adult box turtles were observed together only once, three were observed together twice, three were observed together three times, and one pair was observed together on 6 days. The number of times pairs of turtles were observed together was not significantly, nor even positively, correlated with the product of the total number of times each turtle in the pair was observed ($r_{25df} = -0.31$, NS), indicating that it is unlikely the observed frequency of pairing was an artifact of order of introduction.

All repetitions of each pair occurred within the same or adjacent quadrats, although not in identical locations, making it difficult to distinguish between turtles' preferences for each other and their mutual preference for a portion of the enclosure. To minimize this problem,

the number of touching pairs which were repeated were compared only against the number of repeated close pairs, which were also found in the same area (less than 10 cm apart), rather than with all theoretically possible pairs. The comparison of the number of mixed-sex vs. same-sex pairs which were touching is obviously free of this issue.

Nine of the sixteen adult turtles (five females and four males) were members of a repeated pair. Five of these (three females and two males) were members of two different repeated pairs. All repeated pairs touched at some time. Pairs who touched did so every time they were observed with the exception of two occasions on which turtles observed close to each other were later found touching. These two pairs were excluded from the analysis. No turtles seen together only once touched each other (see Table 17). These differences between the number of touching vs. close pairs which were repeated are statistically significant (Fisher exact test, $p < .05$).

Touching pairs were comprised of turtles of opposite sexes twice as often as they were comprised of turtles of the same sex. Half as many same-sex pairs touched as did not (see Table 18). This difference, however, did not attain statistical significance using the Fisher exact test.

Female turtles touched each other more often than males. Of the eight male-male pairs, only one was ever observed touching, whereas three of the four female-female pairs touched.

Hatchlings. Two groups of hatchlings were observed on eight occasions. Because the two groups behaved virtually identically on every measure considered, their data were pooled. Eighteen of the

Table 17. Number of touching vs. close pairs which were observed together once vs. more than once.

Number of Occurrences	Touching	Close	Total
Once	7	13	20
More than once	5	0	5
Total	12	13	25

Fisher exact test, $p < .05$.

Table 18. Number of touching vs. close pairs which were of mixed vs. same sex.

	Touching	Close	Total
Mixed sex	8	5	13
Same sex	4	8	12
Total	12	13	25

Fisher exact test, NS.

twenty total possible pairs occurred at least once during the eight observations. The median number of pairs observed each day was 4.5 (range, 4-10). A total of 48 pairs, including repetitions of the same pairs, occurred over the eight observations. All hatchlings were found paired several times (median, 9.5; range, 6-14, including repetitions). The median frequency with which each of the eighteen different pairs occurred was 2.0 (range, 1-6). Fourteen of the eighteen observed pairs were repeated at least once.

As was true for the turtles in the enclosure, turtles who touched each other were found together more often than those who were merely close. Pairs were classified on the basis of whether they were observed touching or close more often. One pair which was found touching once and close once was excluded from the analysis. The 10 touching pairs were found together a median of 3.0 times (range, 1-6) whereas the seven close pairs were found together a median of 2.0 times (range, 1-4). This difference is statistically significant (Wilcoxon rank sum test, $T' = 45.5$, two-tailed, $p < .05$).

Discussion

Selective association between turtles is a subtle, potential form of sociality which has been neglected in previous investigations. Evidence of such discrimination is indicative of recognition and preference when other possible factors are taken into account; however, the differential frequencies with which turtles associated with each other was confounded with preference for areas. To reduce this problem certain types of observed pairs were compared with others, rather than with "possible" pairs which were not observed.

Significantly more turtles who touched each other were found together again than turtles who were merely close. This was true for

both zoo turtles and hatchlings. This would seem to indicate discrimination of and preference for nearby turtles which were touched as opposed to those which were not. Among adult zoo turtles, most of the touching pairs were comprised of turtles of opposite sexes; most of the close pairs were comprised of turtles of the same sex. It was not possible to determine the sex of the hatchlings.

These findings suggest that the turtles were selective of turtles whom they touched and that this may have been based upon awareness of certain attributes of those turtles, such as gender, outside of a mating situation. Thus, components of social experience rather than random aggregation are suggested by the observed patterns of differential proximity between turtles.

Discrimination between turtles or groups of turtles might be of importance in gender recognition, courtship, and dominance relations. Brumwell (1940) observed a female ornate box turtle snap at three males who were following her but mate with the fourth. Burghardt (1977b) mentioned that dominance hierarchies in snapping turtles appeared to be maintained through deference based on individual recognition rather than on frequent agonistic encounters. In such situations, recognition would prove efficient by allowing the other's characteristics to be assessed once and remembered rather than repeatedly tested.

The present study (see pp. 86-91) was based upon captive turtles for whom abnormally high population densities may have affected the recognition process. The following study (see pp. 93-108) was designed to test for discrimination between turtles who lived near each other in the natural habitat and those who lived far apart as inferred from interactions between pairs observed in captivity.

Study 5. Recognition of Neighbors

Introduction

To demonstrate that box turtles know their neighbors reveals something about their awareness; it also may suggest previous social interaction among these turtles. A study of neighbor recognition of box turtles was conducted using a technique with which Barash (1974) demonstrated neighbor recognition, as well as preestablished dominance relationships, among supposedly solitary mammals.

This technique consists of catching animals in the field at different distances from each other, then testing them in pairs in captivity. By noting systematic differences in their behavior, one may directly observe whether the animals discriminate between those caught nearby ("neighbors"), and those caught farther apart ("strangers").

This observable discrimination between classes of individuals exemplifies the behavioral approach to the study of experience advocated on pp. 1-5. It also has the advantage of allowing inferences to be drawn about sociality in the field on the basis of behavior observed in captivity.

In two parallel studies, wild-caught box turtles found at differing distances from each other and captive-reared hatchlings housed together vs. separately were tested for discrimination between neighbors and strangers. Behavior categories thought likely to manifest such discrimination were recorded during an observation period or subsequent food competition trial (see Table 19 and Figures 14-18).

It was hypothesized that strange turtles would elicit more investigatory behavior than would familiar turtles. To test this

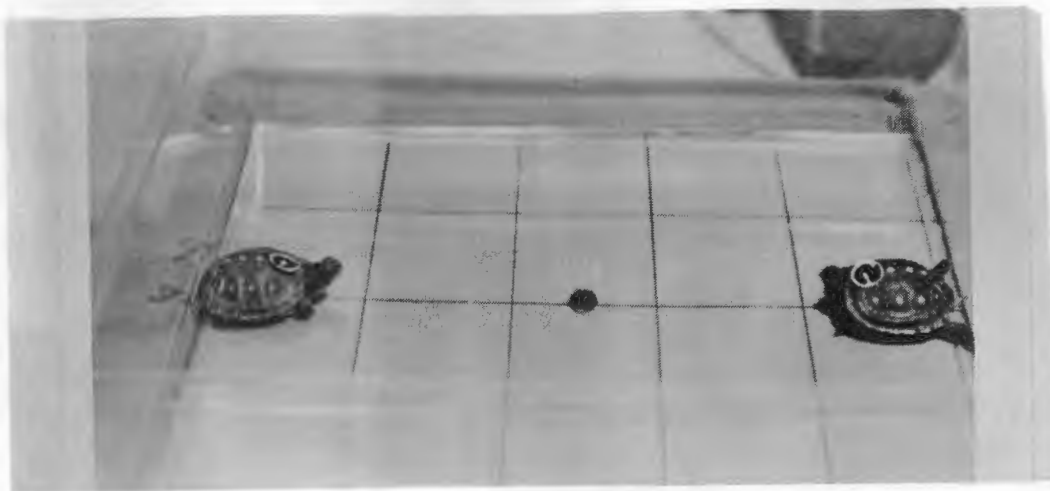


Figure 14. Food competition setting.

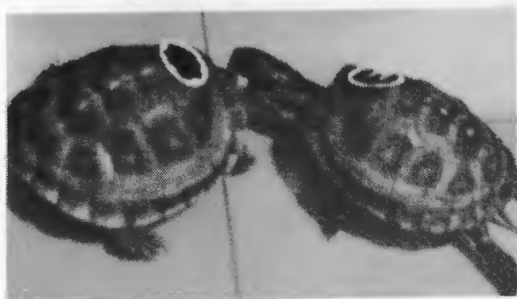


Figure 15. Head-ducking and biting.



Figure 16. Nosing.



Figure 17. Neck-arching and gaping.



Figure 18. Competing for food.

prediction, nosing the other turtle was recorded (see Figure 16). This behavior is often directed toward potential food objects as well as toward other individuals (personal observations) and is commonly identified as smelling in turtles (Allard, 1948; Auffenberg, 1965, 1977; Carpenter and Ferguson, 1977; Eglis, 1962; Legler, 1960; McCutcheon, 1943; Weaver, 1970).

Any existing dominance relationships would be expected to reduce agonistic encounters among neighbors. Familiarity itself may also reduce agonistic behavior (Marler, 1976). For these reasons, it was hypothesized that strangers would engage in more agonistic behavior than would neighbors. Biting and snapping at the other turtle was recorded, as was head-ducking (see Figure 15). Head-ducking often occurs in response to being bitten, but may also follow sudden movements or noises or the approach of another individual. It is considered a defensive behavior (personal observations).

Three other gestures, thought to have possible communicatory functions, were investigated. It was hoped that the differential occurrence of these behavior patterns would provide further evidence of discrimination between neighbors and strangers while at the same time revealing more about their own functions.

Two categories, gaping and neck-arching, were regarded as possible dominance or threat displays. In gaping, the mouth is held fully open as shown in Figure 17. A similar behavior was observed in Pacific pond turtles, Clemmys marmoranta (Emydidae), during competition for basking sites (Bury and Wolfheim, 1973). In 77 of 111 observed instances, the turtle at whom the gape was directed moved away or pulled into its shell. Of those who did not leave, six were bitten. Gaping by captive

box turtles was noted by Harless and Lambiotte (1971), who were unable to interpret it, but speculated that it might function as yawning.

Neck-arching sometimes accompanies gaping in box turtles as shown in Figure 17. It often occurs during competition and courtship (personal observations). Combat in Galapagos tortoises, Geochelone elephantopus (Testudinidae), was reported to be resolved in favor of the turtle who could reach its head the highest (MacFarland and MacFarland, 1972). In Gopherus sp. tortoises, holding the head high is reported as an indication of dominance, particularly in association with combat (Weaver, 1970). Neck-arching by courting male tortoises was also reported by Weaver (1970), who suggests that in this context it may function to inhibit interruptions by other less motivated, less dominant males. Rosenberger (1936) observed neck-arching by a courting male box turtle. Personal observations suggest that neck-arching in box turtles may be indicative of interest, or high arousal, in the absence of fear. It may be opposite in function as well as a form of head-ducking, in concordance with Darwin's (1872) principle of antithesis.

The third behavior investigated as having a possible communicatory function was mouthing, which was noticed by Irma Davis (pers. comm.). Mouthing has been observed in social situations and is often accompanied by a slight "chewing" noise in the absence of food. This is interesting in view of the absence of reported sound production by box turtles, except for the hiss produced during sudden retraction into the shell (Carpenter and Ferguson, 1977; Gans and Maderson, 1973).

The frequency with which each of the preceding behavior categories was emitted by each pair of box turtles was recorded during an observation period. The duration of contact between turtles and a measure of

activity (squares entered) were scored from video tapes of the observation period. In order to test the hypothesis that neighbors would have preestablished dominance relationships, the outcome of feeding competition and duration of feeding were recorded, live and from tape, respectively, during food competition trials.

Methods

Subjects. In one of the two parallel studies, 15 male wild-caught turtles from the study area near Knoxville, Tennessee (described on pp. 29-36) and from the vicinity of Oak Ridge, Tennessee served as subjects. Three turtles were located using a dog trained to hunt birds. In the other study, subjects were eight hatchling box turtles maintained indoors at the Knoxville Zoological Park.

Subjects were designated as "neighbors" or "strangers" on the basis of the proximity in which they had been living. Wild-caught turtles designated as strangers were caught more than 40 km apart; those designated as neighbors were found within 100 m of each other. This is well within the average home range length found in the present study for this area (see pp. 47-55) and is similar to home range "diameters" reported in other studies (see pp. 10-13). Since box turtles are known to have extensively overlapping home ranges and to maintain these ranges for many years (see pp. 13-15), it seems plausible to regard such turtles as potential neighbors.

Wild caught turtles were maintained in the laboratory in separate 28 x 56 x 26 cm cardboard boxes with plastic liners. They were visually isolated from each other. These turtles were found between August 31 and October 24, 1978 and were tested between September 25 and December 6.

Hatchling turtles were regarded as neighbors to other members of their housing unit and strangers to the members of the other unit. These housing units consisted of two plastic trays each of which measured 25.5 x 33 x 10 cm. Five turtles were maintained in each group. These groups were formed by random assignment on July 7, 1977. Prior to this, the turtles, which had hatched at the zoo between April and June, had been housed together. The two groups of turtles were maintained in visual isolation and kept non-adjacent to each other in an attempt to minimize other cues.

Testing was begun after turtles had been living in this arrangement more than 2 months. Tests were conducted from September 15 to November 20, 1977.

The turtles were fed twice a week and were never tested after having been fed the same day. Since all wild-caught turtles and all hatchlings were on the same feeding schedule, turtles being tested together had the same immediate feeding history. The wild-caught turtles were fed lettuce, various fruits, and earthworms. The hatchling box turtles were fed a diced mixture of vegetables, fruits, eggs, and beef heart. Wild-caught turtles were maintained at 24-25°C and tested at 27-28°C. Hatchling turtles were usually maintained at 27°C at the Reptile Complex of the Knoxville Zoological Park. Prior to testing they were transferred in their home containers to the Reptile Ethology Laboratory at The University of Tennessee, Knoxville. They were maintained there for the duration of testing at 27°C and tested at 28-29°C.

Apparatus. Turtles were tested in an "open field" box. Wild-caught turtles were tested in a wooden box, measuring 122 x 118 x 61 cm, and painted with enamel paint to facilitate cleaning. Lines painted on the floor divided it into twenty-five 24.4 x 23.6 cm rectangles.

Hatchling turtles were tested in a plastic tray, which measured 30 x 24 x 6 cm. Lines were drawn on a surface which was placed beneath the container and viewed through its floor. They divided the area into 20, 6 x 6 cm squares.

The test chambers were washed thoroughly between trials to minimize olfactory cues. Chlorine bleach was used to clean the plastic tray and an alcohol solution to clean the wooden chamber.

Hatchlings were watched by an observer seated quietly approximately 1 m away. Wild-caught turtles were viewed through a one-way mirror. Both groups were videotaped during testing.

Procedure. The order of testing was designed so that each hatchling was tested an equal number of times as a neighbor and as a stranger in an alternating pattern. Half were tested first as neighbors, half as strangers. The order in which the wild-caught turtles were tested was constrained by the order in which they and turtles from neighboring areas were caught.

Turtles were rinsed with tap water before and after testing. They were placed in the test chamber in pairs, with one turtle on each side of the chamber with its back against the wall, facing the other turtle. Hatchlings were allowed a 5-minute habituation period during which an opaque divider separated the turtles.

Testing consisted of an observation period followed by a food-competition trial. The observation period lasted 10 minutes for the hatchlings and 30 minutes for the wild-caught turtles. At the termination of the observation period, turtles were returned to their starting positions on opposite sides of the test chamber and a preferred food item was placed in the center of the chamber (see Figure 14, p. 95). This consisted of a 1 cm cube of beef heart for the hatchlings and an earth worm for the wild-caught turtles. Turtles were observed until the food was consumed or until an interval of time equal to the observation period had elapsed.

Results

The gestures recorded during the observation period occurred with low frequency and high variability. With the exception of neck-arching by wild-caught turtles, these gestures were performed by pairs of turtles with median frequencies of less than four times during a 10- or 30-minute observation period. Many turtles were generally inactive during testing. Despite this, neighbor and stranger pairs showed different patterns of behavior which were consistent for hatchling and wild-caught turtles.

Nosing, considered an investigatory olfactory gesture, was performed more by stranger than neighbor pairs for both hatchlings and wild-caught turtles, as shown in Table 20.

Biting or snapping and head-ducking were recorded in order to test the hypothesis that strangers would behave more agonistically toward each other than would neighbors. Significantly more head-ducking occurred between strangers than neighbors among both hatchling and

Table 20. Mean and median frequencies of nosing, biting or snapping, and head-ducking by neighbor vs. stranger pairs.*

Behavior	Hatchling				Wild-Caught			
	Neighbor Pairs n=12		Stranger Pairs n=12		Neighbor Pairs n=6		Stranger Pairs n=23	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Nosing	2.50 (0-8)	2	3.92 (0-11)	3.5	2.50 (0-6)	3	7.41 (0-31)	3
Biting or Snapping	0.33 (0-1)	0	3.67 (0-16)	1	0.16 (0-1)	0	14.91 (0-131)	0
Head Ducking	0.50 (0-1)	0.5	2.93 (0-9)	2**	0.00 (0-0)	0	2.04 (0-12)	0**

*Ranges are indicated in parentheses.

**Mann-Whitney test, one-tailed, $p < .05$.

wild-caught turtles (Mann-Whitney test, one-tailed, $p < .05$). More biting or snapping also occurred between strangers in both cases. This difference approached significance for the hatchlings (Mann-Whitney test, one-tailed, $p < .06$) (see Table 20).

Gaping, which was investigated as a possible threat display, occurred significantly more often among wild-caught strangers than neighbors (Mann-Whitney test, one-tailed, $p < .05$). This is consistent with the higher levels of biting or snapping and head-ducking observed in stranger pairs. Neck-arching, however, occurred somewhat more frequently among neighbors than strangers. It occurred much more frequently among wild-caught turtles than hatchlings. Wild-caught stranger pairs showed significantly more mouthing than neighbors (Mann-Whitney test, one-tailed, $p < .05$). These results are presented in Table 21.

Duration of contact between turtles did not yield consistent results for hatchlings and wild-caught turtles; it was a highly variable behavior as shown in Table 22.

There were no significant nor consistent differences in the number of squares entered by neighbors vs. strangers, indicating that differential frequencies noted in other types of behavior could not be attributed simply to a higher overall activity rate by one group (see Table 22).

Vigorous competition for food occurred between many turtles and included pulling, shoving, and carrying away the food. The time which elapsed from the second the first turtle bit the food until it was consumed, however, did not differ significantly between neighbors and strangers (see Table 22). The food was consumed by all hatchling pairs. Three wild-caught pairs (one neighbor and two stranger pairs)

Table 21. Mean and median frequencies of gaping, neck-arching, and mouthing by neighbor vs. stranger pairs.*

Behavior	Hatchling				Wild-Caught			
	Neighbor Pairs n=12		Stranger Pairs n=12		Neighbor Pairs n=6		Stranger Pairs n=23	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Gaping	1.08	1 (0-3)	0.50	0 (0-4)	0.33	0 (0-1)	0.95	1** (0-3)
Neck- arching	2.00	1.5 (0-5)	1.75	1 (0-5)	27.33	27.5 (17-37)	24.27	22 (8-54)
Mouthing	0.67	0 (0-3)	0.67	0 (0-3)	0.33	0 (0-2)	2.77	2** (0-11)

*Ranges are indicated in parentheses.

**Mann-Whitney test, one-tailed, $p < .05$.

Table 22. Mean and median duration of contact, number of squares entered, and duration of feeding for neighbor vs. stranger pairs.*

Behavior	Hatchling				Wild-Caught			
	Neighbor		Stranger		Neighbor		Stranger	
	Pairs n=12		Pairs n=12		Pairs n=6		Pairs n=23	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Contact Duration (seconds)	33	0	18	0	22	0	215	0
	(0-200)		(0-73)		(0-120)		(0-1776)	
Number of Squares Entered	15	12	14	12	52	22	36	31
	(4-38)		(0-29)		(8-138)		(5-122)	
Feeding Duration (seconds)	293	274	301	297	178	34	136	86
	(22-573)		(30-578)		(23-600)		(20-600)	

*Ranges are indicated in parentheses.

did not consume the food during the allotted interval. They were assigned a feeding duration of 600 seconds; the maximum duration in which consumption occurred was 573 seconds.

Neighbors and strangers did not differ significantly in the number of pairs in which one turtle ate the food vs. pairs in which the turtles split the food (see Table 23). Hatchling neighbors, however, showed a consistent pattern of feeding dominance, as discussed on pp. 109-116.

Discussion

This study addressed the question of neighbor recognition in box turtles by providing a controlled situation in which discrimination between neighbors and strangers could be observed. More investigation of strangers than neighbors was hypothesized. A consistent trend in this direction was shown by the greater frequency of nosing strangers.

A higher level of agonistic behavior with strangers than neighbors was also hypothesized. The significantly higher levels of head-ducking with strangers among both hatchlings and wild-caught turtles tend to support this hypothesis, as does the significantly greater frequency of gaping among wild-caught strangers vs. neighbors. The lack of consistent differences in number of squares entered makes it unlikely that these results are simply due to greater activity by strangers.

The hypothesis of preestablished dominance relationships among neighbors was not supported by the duration of feeding or by the number of wins vs. ties, although an orderly pattern was revealed by hatchlings' relative success in food competition (see pp. 110-112). Duration of feeding may not have been an adequate measure of competition because competition may have simultaneously prolonged feeding by interrupting

Table 23. Number of neighbor vs. stranger pairs in which the food was won by one turtle vs. divided.

	Hatchling			Wild-Caught		
	Neighbor Pairs	Stranger Pairs	Total	Neighbor Pairs	Stranger Pairs	Total
Win/Lose	8	7	15	4	19	23
Tie	4	5	9	2	4	6
Total	12	12	24	6	23	29

it but hastened feeding by dividing a fixed quantity of food between two turtles and through social effects such as those described by Overmann (1970).

CHAPTER IV

INDIVIDUAL STYLES OF INTERACTING

Study 6. Individual Consistencies in Social and Spatial Relations

Introduction

This aspect of the investigation integrated results obtained in earlier sections with additional observations in order to determine whether individual box turtles showed consistent individual styles in the ways they related to their social and spatial environments. Individual differences in success in feeding competition were assessed and then compared with differences in reactions to human handling. Reactions to human handling were in turn compared with use of space in order to identify individual styles which cut across different situations. Such general individual styles would indicate the active role played by the individual in structuring its interactions and thus emphasize the importance of the individual's way of experiencing its surroundings.

Methods

Individual feeding dominance was studied using eight hatchling box turtles. The results of the neighbor recognition food trials, described above (pp. 93-108) were analyzed in terms of individual turtles' successes. Each turtle engaged in a paired food competition trial with each of six other turtles, three from its own housing unit and three from the other group. Individual differences in numbers of wins, ties, and losses were recorded. Each turtle was assigned a food competition success score which was equal to the number of encounters

it won minus the number that it lost. The possible existence of dominance hierarchies was explored by diagramming the success of each turtle relative to the others with whom it interacted.

Turtles' reactions to human contact and close approach were observed and recorded. Contact consisted of a light touch on the carapace preparatory to measuring and paint-marking the turtle. Close approach consisted of holding a ruler a few centimeters directly above the turtle's shell as an initial phase of determining location in the field. An effort was made to avoid abrupt motions when approaching or contacting turtles.

Hatchlings' reactions to contact were recorded on eight occasions between July 7 and March 8, 1978. On each occasion they were assigned scores of 1, 2, or 3 based on whether they remained still, moved, or withdrew into their shells. These scores were averaged to provide a single reactivity score for each turtle.

Turtles found in the field were each touched once on the first day of observation and were closely approached on each subsequent observation. They were assigned Head Extension scores of: 1 (head withdrawn with eyes inside of shell); 2 (eyes to full head exposed); 3 (neck partially extended, skin folded); or 4 (neck fully extended, skin smooth). They were also assigned Activity Level scores of: 1 (motionless); 2 (shift in posture); or 3 (changed in position relative to the substrate). Each of these scores was averaged for each turtle.

Results

Diagrams of relative success in feeding encounters revealed no reversals when turtles were paired with members of their own living

groups. The pattern was less clear when turtles were paired with members of the other group (see Figure 19).

Hatchlings who were more successful in food competition reacted less to human contact ($r_s = -0.72$, NS) as shown in Table 24. The hatchlings most commonly were still, sometimes struggled, and only rarely withdrew into their shells when touched. They had been handled regularly by personnel at the Knoxville Zoological Park where they were housed.

In the field, turtles' neck extension scores subsequent to human contact or close approach were positively correlated with their mean daily displacements (distance between successive locations divided by intervening days). As shown in Table 25, the Spearman rank-order correlation was $r_s = 0.63$ (NS). Turtles usually had their heads withdrawn or the head but not the neck exposed. These turtles' activity levels in response to handling or close approach were negatively correlated ($r_s = -0.80$, NS) with their mean daily displacements (see Table 26). The turtles usually remained motionless or changed posture, usually by withdrawing their necks.

Discussion

Individual turtles differed in their success in food competition. A hierarchal pattern with no reversals was found within groups, whereas the pattern was less clear-cut between members of different groups, suggesting the existence of a dominance hierarchy within each group. Such hierarchies are suggestive of individual recognition and of individual differences among turtles.

The relation between success in feeding competition, lower reactivity to humans, and greater distances covered daily in the field

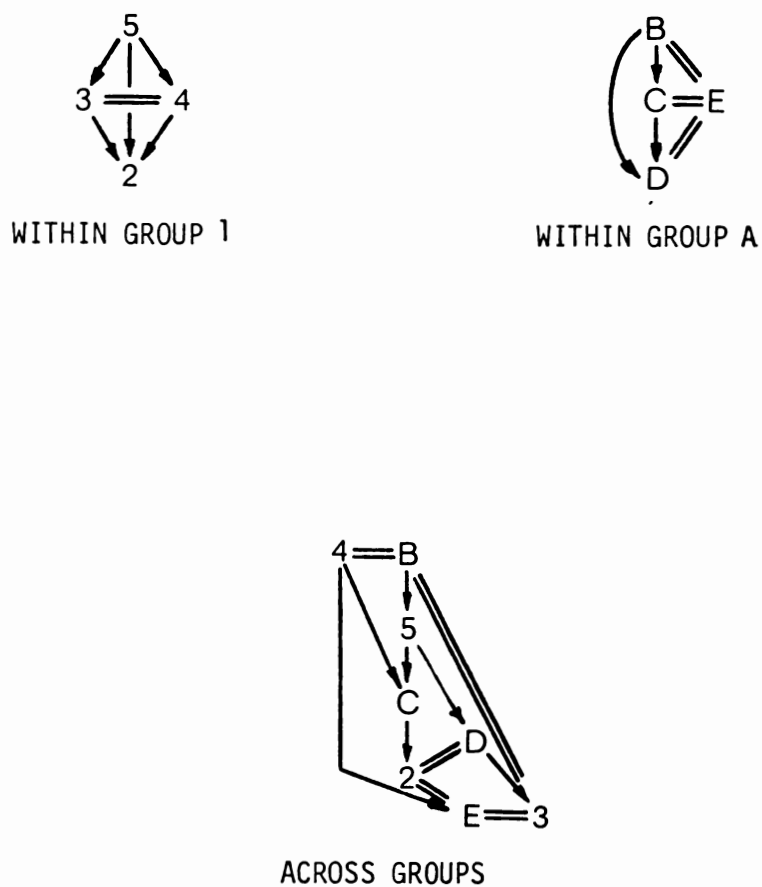


Figure 19. Food competition hierarchies based on single paired encounters with members of own group and other group.

Table 24. Correlation between hatchlings' reactions to human contact and their success in food competition against other hatchlings.

Turtle	Human Reaction Score*	Food Competition Wins minus Losses
2	1.62	-4
D	1.38	-2
4	1.38	2
E	1.25	-1
3	1.25	-1
C	1.12	-1
5	1.12	4
B	1.00	3

*1 = still
 2 = struggled
 3 = withdrew

r_s (corrected for ties) = -0.72, NS.

Table 25. Correlation between wild turtles' mean head extension subsequent to human contact or approach and mean displacement per day.

Turtle	Neck Extension*	Displacement per day (m)
F	2.00	21
A	1.55	15
C	1.00	17
E	1.00	13

*1 = head in
 2 = head out
 3 = neck partly extended
 4 = neck fully extended

r_s (corrected for ties) = 0.63, NS.

Table 26. Correlation between wild turtles' mean activity score subsequent to human contact or approach and mean displacement per day.

Turtle	Activity*	Displacement per day (m)
E	1.82	13
A	1.55	15
F	1.44	21
C	1.20	17

*1 = remained still
 2 = changed posture
 3 = changed position

r_s (corrected for ties) = -0.80, NS.

suggests consistent individual styles of interacting, with some turtles being more active, less subject to disturbance, and more dominant toward other turtles. Such turtles may be more successful. Data on reproductive success would be useful in evaluating this conjuncture. It is possible that this less cautious strategy would render the turtle more subject to injury or predation; however, predation pressure upon adult box turtles is thought to be low (see p. 8). Such general individual styles would seem to indicate the active role of the individual, and hence the importance of the individual's manner of experiencing its surroundings, in structuring its interactions with its social and spatial environment.

CHAPTER V

GENERAL DISCUSSION AND SUMMARY

The general question addressed in this investigation is how one may study the experience of another animal in an empirically rigorous fashion. The approach advocated is an integration of traditional ethological methods with a phenomenological orientation. These two fields are presented as mutually compatible and complementary. Their compatibility is manifest in their common endorsement of certain fundamental positions:

1. Both emphasize the need to adopt the viewpoint of the subject and to study phenomena of importance to the subject.

2. Both recognize that the subject exists in a dynamic relation to its surroundings and that the behavior of the subject can only be studied meaningfully within this context. This idea is expressed by the phenomenological concept of being-in-the-world and by the ethological concept of the adaptive relationship of an animal to its environment.

3. Both recognize that because the subject takes an active role in perceiving its environment, what constitutes its environment must be determined relative to the subject. Phenomenologists refer to the phenomenal field while ethologists refer to such concepts as sign stimuli in indicating those aspects of the world which have meaning for the subject. This view has been clearly expressed by the idea of the Umwelt (Von Uexküll, 1934).

Although similar in spirit, the fields of ethology and phenomenology have differences which make them complementary rather than

synonymous. Phenomenologists have directly addressed and articulated the issue of experience, which ethologists have often implicitly accepted but overtly avoided, as not objective, especially under the influence of American experimental psychology. Ethology, on the other hand, has a well-formulated scientific method (whose development was aided in part by American psychology) which is expressly suited to naturalistic, holistic inquiry; this method may provide an alternative to the "transcendental reflection" which sometimes characterizes phenomenological approaches (Thinès, 1977, p. 132).

A phenomenological ethology may extend the investigation of the study of experience to animals with whom we do not share language. It may do so by providing a new theoretical framework for ethological studies, both by integrating seemingly diverse findings and by posing new questions to be investigated using scientifically acceptable methods. Such a study may be conducted by attempting to identify components of the Umwelt, that is, by identifying those aspects of its world of which the animal is aware and which it recognizes. One may then investigate the meaning these have for the animal by identifying the functional significance of specific cues as manifest in the animal's behavior toward them.

Three interrelated topics seen as conducive to such investigation formed the subject matter of the present study. These topics were use of space, social behavior, and individual styles of interacting with both. Preference and other forms of discrimination between areas and between individuals were studied to establish recognition, and hence, inclusion in the Umwelt. Some of the specific cues and behavior patterns involved were then investigated in order to establish their significance

for the animal. Individual patterns of interacting with the spatial and social environment were investigated as evidence of the active role of the individual and the importance of the individual's experience. The research was performed in combination of naturalistic, semi-naturalistic, and laboratory settings. In all cases the issue of the subject's experience was addressed within the scope of accepted ethological methods. Six related studies were conducted.

In Study 1, individual recognition and preference for spatial areas was addressed by repeatedly locating box turtles in their natural habitat through the use of telemetry. Four turtles were located a total of 46 times. Most turtles were found to use only prescribed areas within a larger area of suitable habitat. The median home range area was estimated to be 0.336 ha with a longest axis of 202 m.

These results are consistent with those of other investigators, indicating that box turtles do discriminate between areas of suitable habitat. Difficulties in unobtrusively observing the turtles in the field made it impossible to assess directly the basis of this discrimination. Despite precautions to avoid disturbing the turtles, they moved during a total of only 10 minutes in the course of 24, 30-minute observation sessions conducted on six turtles. Prior activity was often indicated by direct observation, however, and successively located turtles showed a median daily displacement of 14 m. This points to the need for caution in drawing conclusions about turtles' limited repertoire on the basis of which behavior has not been observed in the field.

Study 2 consisted of direct observations of turtles' movements and more detailed information about their locations. This was possible with 21 turtles introduced to an outdoor enclosure. A total of 180

locations was recorded for 19 of these turtles. Turtles showed statistically significant individual preferences for different areas within the enclosure, even though the 58 m² enclosure was much smaller than the average home range size. These preferences were based primarily upon resting locations and might correspond with differential use of places within their home ranges. The persistent nature of such preferences was indicated when the turtles were removed from the enclosure for 11 days and then reintroduced to it simultaneously with 24 new turtles. New shelter sites, which had been created while the enclosure was empty, were used by more than three times as many new as old residents; formerly established shelter sites were used by twice as many original residents as new turtles. These differences were statistically significant.

The turtles also showed overall patterns of area use. Forty-five minute observation sessions on each of the 21 turtles originally introduced to the enclosure revealed that most turtles moved along the perimeter of the enclosure. They tended to rest in corner locations. This suggests several factors, such as shade, lower temperature, and tactile or visual proximity to objects, which may have been meaningful to the turtles as indications of suitable sites. Determination of which factors were actually used by the turtles was not possible in this situation.

In Study 3, the functional significance of two such potential cues was investigated by presenting them to 10 hatchling box turtles under controlled laboratory conditions. The turtles moved significantly more often to a dark rather than a light side of a chamber, regardless of color. They also showed a tendency to move uphill rather than downhill.

No interaction was found between these two factors. Personal observations have indicated that eastern box turtles will move from exposed grassy areas into wooded terrain, where they are usually encountered, and that even in wooded areas they often utilize cover extensively. In these situations, as in the outdoor enclosure described above, darkness is one of many potential cues. Results of the present study suggest that darkness is experienced as attractive by the turtles even when it is divorced from such factors as lower temperature and cover which would commonly be associated with darkness in the field.

In order to learn about box turtles' experience of each other, the basic question of recognition of other individuals or classes of individuals, was addressed within a spatial context. In Study 4, recognition and preference was investigated by recording the relative locations of 19 turtles in an outdoor enclosure and of 10 hatchlings housed indoors in two groups. Among both the hatchlings and the turtles in the enclosure, pairs which touched were significantly more likely to be found together again than those which were simply close. Among the adult turtles in the enclosure, most of the touching pairs were comprised of turtles of opposite sexes; most of those pairs found close but not touching were comprised of turtles of the same sex. These results suggest discrimination between turtles who touched and those who did not.

Discrimination between turtles who had lived nearby vs. farther away was explored in two parallel investigations of neighbor recognition which comprised Study 5. In the first investigation, captive-reared hatchlings were maintained in two groups then tested in pairs for discrimination between members of their own group vs. members of the

other group. In the second investigation, wild-caught turtles were maintained in isolation and tested in pairs for discrimination between turtles who had been trapped less than 100 m apart and those trapped many kilometers away.

This study went beyond the basic question of discrimination and investigated the significance of potentially communicatory patterns of behavior. More investigation of strangers than neighbors was hypothesized. The higher incidence of nosing strangers among both hatchlings and wild-caught turtles is consistent with this hypothesis. Higher levels of agonistic behavior with strangers than neighbors was also hypothesized. The significantly higher levels of head-ducking with strangers in both experiments and the significantly greater frequency of gaping among wild-caught strangers tend to support this hypothesis. Duration of feeding encounters and the incidence of ties vs. decisive food competitions did not provide evidence to support the hypothesis of a preestablished dominance hierarchy among neighbors. Diagrams of relative success in food competition did, however, reveal a clear hierarchial pattern with no reversals within housing groups of hatchlings; the pattern was less clear-cut between members of different groups.

In Study 6, hatchlings who were more successful in feeding competition were found to react less strongly to human contact. In the field, repeatedly located turtles who reacted with less head retraction and movement to human contact and close approach traversed a greater distance between successive locations, with the number of days between locations taken into account. These results suggest individual styles which are valid across contexts, thus indicating the importance of an

individual's experience in structuring its interactions with both its social and spatial environment.

Taken in totality, the results of the overall investigation indicate that it is possible to study meaningfully an animal's experience by empirical observation of behavior in context. This suggests that a synthesis of ethology and phenomenology is possible and may contribute to the further development of both fields. In the present study, aspects of the social and spatial experience of eastern box turtles were explored through behavioral observations. The focus was upon discrimination as an indication of what is experienced and, thus, included in the Umwelt. The investigation was extended to the nature of this experience by determining the significance of the cues and gestures involved in such discrimination. Thus, this investigation demonstrates that the phenomenological issue of experience may be addressed in a non-human animal using an ethological approach.

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VITA

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