To the Graduate Council:

I am submitting herewith a dissertation written by Arnold David Froese entitled "Aspects of Space Use in the Common Snapping Turtle, *Chelydra s. serpentina*." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Gordon M. Burghardt, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

ASPECTS OF SPACE USE IN THE COMMON SNAPPING TURTLE, *CHELYDRA S. SERPENTINA*

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee

Arnold David Froese

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ABSTRACT

Descriptions of social organization patterns between and within various species are required to answer evolutionary questions about social behavior. Social organization is often expressed in patterns of spatial distribution such as habitat preferences, activity cycles, and habitat utilization. These distribution patterns were investigated in the common snapping turtle, *Chelydra s. serpentina*, in the laboratory and in the field.

The first experiments evaluated juvenile substrate preferences in two-choice tests. The substrates used were equal areas of sand and pea gravel. Turtle positions on either substrate were recorded at various temperatures. A slight preference for sand could not be replicated, and temperature had no apparent effect on substrate choice. Young turtles in the field were found on various substrates. While soft sand may be preferred, young turtles adapt to a range of suitable substrates.

Juvenile turtles in a 1 m diameter pool, clustered around rocks. Therefore, preferences for open versus obstructed areas were tested with five hatchling and nine juvenile turtles. One-half of the pool contained rock obstructions, and the other half was open. Photographic records indicated that both groups preferred the obstructed area at night. During daylight the larger turtles did not prefer either half of the pool. However, the hatchlings still preferred the obstructed half. In the field, turtles were found around obstructing or camouflaging objects. Possible functions of these preferences could have been increased protection and food availability.

Diurnal cycles were measured during area preference tests. Both groups of young turtles showed significantly different heightened daytime activity and lowered nightime activity.

Adult turtles in a 0.8 ha pond were tracked by radio telemetry in fall and spring. Nighttime activity was significantly greater than for other time blocks. However, some turtles were active at all hours of the day.

The differences between laboratory and field diurnal cycles may have been due to specific habitat conditions in the laboratory, developmental differences between the groups of turtles, or artifacts of captivity. The extent of confounding due to captivity requires further evaluation.

Fall and spring activity rates for the field turtles were not directly comparable due to differences in location techniques. Activity rates were quite variable between turtles. Spring activity rates were negatively correlated with turtle size. Activity rates showed little correlation with ambient temperature, probably because an attenuated range of temperatures was sampled.

Cycles of activity and inactivity were different in two size classes of turtles. Large adults had long inactive periods interrupted by short range movement. Smaller adults had short durations of inactivity and frequent periods of long range movement.

The turtles in the pond extensively used one or more home sites. These sites resembled the "forms" described for box turtles. Turtles spent inactive periods at home sites, and repeatedly returned to these following activity. Home sites were heavily concentrated in obstructed areas.

Adult turtles had home ranges which included an average of 38% of the pond area. This estimate was probably low because of the limited time during which movements were sampled. Home range estimates were considerably variable between turtles. The extensive habitat utilization supports earlier reports that home ranges for aquatic reptiles are highly habitat determined. While the home range sizes and overlap suggested considerable conspecific tolerance, the specificity of home sites and withdrawal responses of a juvenile when an adult approached provided indirect evidence for competition between conspecifics.

The results suggested organizational patterns and conspecific responses permitting adaptive differential utilization of space within a microhabitat. Only lack of description on hard-to-observe species support biases against social complexity in reptiles. The flexibility of organizational and behavioral patterns in a range of habitats should be further investigated.

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INTRODUCTION

Box (1973) and Brattstrom (1974) have recently referred to the gap in our knowledge of reptilian social behavior. Brattstrom characterized turtles as ". . . dislay(ing) limited interaction with other individuals and tend(ing) to aggregate only for mating, basking, and egg-laying." While this latter view is probably accepted by many reptilian behavior researchers, several recent reformulations of the nature of social behavior encourage further social behavioral investigation on "solitary" and "non-gregarious" species.

In contrast to these recent reformulations, the traditional approach to social behavior is typified in Etkin's (1964) simple dichotomy between social groups and aggregations. Mutual conspecific responses maintained the group in the former case, while limited environmental features produced fortuitous groupings in the latter. While this distinction may indicate differences in the stimuli leading to the response of grouping (conspecifics or environmental features), the dichotomy imposes two limitations on social behavior. First, social behavior is assumed to occur only in the social group. However, just as social behavior may occur between people in an "aggregation" watching a fireworks display, so 20 turtles basking on one of the few logs in a pond may exhibit social behavior. In fact, Bury (1973) has described social behavior between turtles in such situations. Second, social behavior is assumed to occur only in group situations. Leyhausen (1965) attacked this assumption in his evaluation of social behavior in the solitary domestic cat. To maintain a solitary existence requires complexity in

social organization, and responsiveness to distant conspecific stimuli, rather than to immediate stimuli. The emphasis for solitary species, as contrasted with "social" species, is on distance maintenance rather than distance reduction. Social and solitary are, therefore, not dichotomous classes indicating anything about social behavior or complexity. Rather, they only indicate something about density and overlap of activity ranges of the species in question.

Researchers, therefore, must undertake new tasks in the evaluation of questions of social behavior in various species. "Solitary" species must not be assumed to be non-social, and typical aggregations may be ripe grounds for preliminary descriptions of social behavior.

The literature suggests certain types of social responses in turtles. In courtship sequences, Auffenberg (1966) described head bobbing by a male gopher tortoise which apparently attracted females. Weaver (1970) described other aspects of tortoise behavior which were important in sex and species discrimination. Behavioral differences between species included frequency and location of biting and ramming, and active or passive female responsiveness. *Chrysemys* courtship behaviors apparently serve similar functions as those listed for *Gopherus* (Davis and Jackson, 1970, 1973; Jackson and Davis, 1972a, 1972b). The male approaches a female, turns his fore claws in a characteristic manner, an vibrates his claws against the head of the female. Because of its unusual nature and complexity Grant (1936) and Marchand (1944) had earlier characterized this behavior as similar to mesmerism. Conclusions about lack of complexity in social responses, therefore, seem unwarranted, at least for some turtle species.

There are other indications of social responses in turtles besides courtship sequences. Turtles aggregate in large numbers to bask. According to more traditional criteria mentioned earlier, such groups might be omitted from considerations of social behavior. However, conspecific responses have been observed in such aggregations (Bury, 1973).

Social organization patterns are related to population density and use of space. Turtles have home ranges which last for extended time periods. Home ranges of the common box turtle, *Terrapene c. carolina* have been intensively investigated. Stickel (1950) indicated that these turtles had small, extensively overlapping home ranges. Yahner (1974) recently reported great stability of home ranges for box turtles originally studied four years previously by Dolbeer (1969). While home range overlap suggests tolerance for conspecifics, stability of ranges suggests both habitat familiarity, and certain recurring conspecific interactions.

Special problems arise in investigating social behavior and space use in aquatic turtles. Turtles move quickly in water, and disappear from sight by diving or hiding around obstructions. Many researchers, therefore, have evaluated space use on the basis of trapping records. Ream and Ream (1966) have shown how various trap types differentially sample subclasses of the population. Animals may also become trap shy, making relocation difficult, and confounding inferences about space use. Trapping records, therefore, can provide only limited information on how the animals use space.

Field research on aquatic turtles is more feasible with biotelemetry. Moll and Legler (1971) conducted such research, and concluded that:

> Biotelemetry devices are not to be regarded as a panacea for ecological problems. The sonic tags used in this study fully justified the difficulties of instrumentation since they provided some of the most valuable, complete, and accurate data which have ever been obtained on the movements of individual aquatic turtles. (59)

An integration of field techniques using biotelemetry and laboratory manipulations, therefore, seems appropriate for investigating how turtles utilize space and respond to conspecifics within the structure of particular habitats.

It is the purpose of this dissertation to provide descriptive data on space use, activity cycles, and habitat preferences within the context of closely manipulated or described populations of snapping turtles. Such data should indicate aspects of population social structure, thereby clarifying some contradictions in the literature. In addition, new questions about more specific aspects of control of such organizational patterns will be raised.

CHAPTER I

HABITAT PREFERENCES

Competition between conspecifics can be greatly influenced by the habitat in which the animals live. Kruuk (1972) described hyena dens in which cubs usually dig narrow tunnels at the end of the larger dens. The narrow channels effectively isolate the young from intra- and interspecific predation. The habitat preference of the young for the den area is obviously adapted to the life history of the hyena.

The snapping turtle, *Chelydra s. serpentina*, reportedly prefers soft mud bottom areas (Newman, 1906; Cahn, 1937; Lagler, 1943; Carr, 1952; Wood, 1953) and obstructions (Pope, 1939; Lagler, 1943; Clark and Southall, 1920). These preferences appear strong during hibernation (Clark and Southall, 1920; Pope, 1939; Anderson, 1965), as well as in warm weather (Lagler, 1943). Pope (1939) found snappers in mud under submerged logs. Clark and Southall (1920) reported that turtles hibernated in muskrat holes and under old fallen logs. During the warm season Lagler (1943) found snapping turtles in shallow water beside logs and stumps, sometimes in the mud. Wood (1953) recorded turtle positions in relationship to light intensity, and reported that they were more dense around posts supporting gates into various light zones. He commented that this clustering permitted the turtles to remain in a dimly lit area, with good visual access to an illuminated area.

Mud substrates and obstructed areas appear to be preferable areas for snapping turtles. However, all of the previous literature is anecdotal. There have been no quantitative tests of the strength or

variability of either substrate or obstruction preferences. The following data, therefore, provide some quantitative measures of such habitat preferences. In addition, field observations are reported which suggest adaptive functions of such preferences.

Substrate Preferences

The first experiments are an evaluation of preferences for sand or gravel substrates as tested in a two-choice situation.

Experiment I: Sand and Gravel Test

Materials and Methods

Nine 18 month old common snapping turtles, *C. s. serpentina*, which hatched in the laboratory, were used in this test. These turtles are described in the Appendix. Turtles were tested 16-27 January, 1973. Since hatching, they had been individually housed in small glass aquariums except for periods of food competition testing (see Froese and Burghardt, 1974). The only substrate available to the turtles prior to the substrate test was glass.

The test chambers were opaque plastic cages with floor dimensions of 21.7 X 43.4 cm. A 3.7 X 1.9 cm. lead weighted wooden block divided the floor space in half.

The substrate for one side of the test chamber was pea gravel. Sample diameter measurements on 20 pieces of gravel averaged 9.8 mm. The other side had a substrate of fine, washed, river sand less than 1 mm in diameter. The substrate on both sides was about 2.6 cm in depth, and water extended about 5 cm above the substrate. Fluorescent bulbs were

placed about 1 m above the substrate surface. A timer controlled a 12 hour day/night cycle. All times mentioned are Eastern Standard Time.

To eliminate position bias due to differences in room structure, the nine test chambers were placed alternately with gravel, and then sand, facing the observation position. One turtle was placed on the center divider of each test chamber. The direction the head faced was alternated to control for left or right turning preferences. Except for feeding days, the turtles remained in the test chamber for the duration of the experiment. The turtles were moved to their home aquariums at 1000 hours on feeding days. They were fed at 1100 hours and placed back in the test chambers at 1600 hours. The turtles were tested on Tuesday, Thursday and Saturday, and fed on Monday, Wednesday and Friday.

The substrate on which each turtle was located was recorded hourly from 900 to 1700 hours. Every four hours (800, 1200, 1600 hours) the turtles were placed on the center divider facing the opposite direction of the prior placement. Four complete testing days were thus recorded. Maximum and minimum air temperatures were recorded each day. Beginning on the second complete testing day, air temperatures were recorded hourly at the time of position observation. Temperatures ranged from 22°-29° C.

Results

After moving to one side, a turtle could have remained there until replaced on the divider for another choice. For this reason, only the first hourly positions after placement on the divider could be considered independent choices. A total of 14 independent choices was made by each

turtle. In one instance each, Turtles 1 and 3 failed to move from the center divider prior to the hourly position recording. Their position at the next hourly recording was, therefore, used as their initial choice. Duration of time a turtle remained in any one area was measured by the frequency of initial choices plus subsequent positions on sand or gravel. These data, for initial choices and initial choices plus subsequent positions are shown in Table 1.

Table 1. Total Initial Choices and Initial Choices plus Subsequent Positions to Sand or Gravel

Turtle #	1	2	3	4	5	6	7	8	9	Totals
Initial Choice										
Sand	10	8	4	11[a]	8	6	9	8	9	73
Gravel	4	6	10	3	6	8	5	6	5	53
Initial Choice plus Subsequent Positions										
Sand	32	20	17	30	24	18	32	25	25	223
Gravel	9	22	24	12	18	23	10	17	17	152

[a] $p < .05$ (one-tail binomial probability test)

Differences between sand and gravel choice frequencies were obtained for the initial choice plus subsequent position scores for each turtle. A Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) indicated a significant preference for the sand side ($T = 7$, one-tailed $p < .05$).

While seven of the nine turtles had initial sand scores which were higher than gravel scores, this ratio does not differ significantly from chance (.10 > p > .05; one-tailed binomial probability test). Only one of the seven turtles which did have higher sand scores, showed a significant preference for the sand (see Table 1).

Discussion

The juvenile turtles preferred sand over gravel under the described testing conditions. The lack of significance of initial choice data indicate that the preference for sand is not absolute. It is possible that the substrates used during testing were not sufficiently different in size to reveal preferences on initial choices which might, in fact, exist for various ranges of substrates found in the field. Observations of burrowing behavior in both the sand and the gravel substrates support the idea that the substrates may not have been sufficiently different.

Although the recorded temperatures varied only 7° C during testing, there appeared to be some relationship between temperature and substrate choice. The product moment correlation coefficient between temperature and frequency of sand choice was, however, not significant (r = -.36, p > .05).

Experiment II: Effect of Different Temperatures on Sand and Gravel Preferences

Substrate preferences are probably dependent on several interacting environmental features. I have already reviewed literature which suggests that snapping turtles hibernate in fine substrates. Turtles can probably burrow in fine substrates more easily than in coarse ones. If burrowing

is a response to a drop in temperature, sand substrate preferences might be greater at lower than at higher temperatures. The slight negative correlation in Experiment 1 under restricted temperature variation, also suggested that preferences to sand might be enhanced at lower temperatures. In Experiment II, substrate preferences were tested at controlled temperatures.

Materials and Methods

Eight of the turtles from Experiment I were also used in Experiment II. This experiment was conducted between 17-27 June, 1973. During the time period between Experiments I and II the turtles were individually housed in visually isolated 23 X 14 X 17 cm glass aquariums, maintained on an alternating 12 hour day/night cycle, and fed approximately three times per week.

The same test chambers and substrates as in Experiment I were used. Seven liters of water and .875 liters of each substrate were placed in the test chambers.

The test chambers were placed inside an environmentally controlled chamber. Temperature was regulated within ± 1° C, and fluorescent lighting was on an alternate 12 hour day/night cycle.

In this experiment, I employed the same controls for position bias and turning preferences as in Experiment I. The animals were fed outside of the test chamber, and testing resumed the day following feeding.

Substrate choices were tested at three temperatures: 10°, 20° and 30° C. These temperatures represent moderately cold to moderately warm normal temperatures for field habitats. Half of the turtles were tested in the order 10°, 20° and 30° C; and half were tested in the reverse order.

Two days prior to onset of data collection, turtles were fed, and then placed in the test chambers. The substrate on which each turtle was located was recorded three times per day, at four hour intervals: 700, 1100, and 1500 hours. After locating each turtle, I placed it on the center divider, thereby insuring that all observed locations were independent.

Six locations for each temperature for each turtle were recorded. Turtles were tested for two days, fed the next day, and replaced in the test chamber. Temperatures were changed, to the next level on feeding days. I allowed at least one additional day following feeding for temperature stabilization.

Results and Discussion

The turtles showed no significant preference for sand in this test (Wilcoxon matched-pairs signed-ranks $T = 10$, $p > .05$). The choices of the turtles to either substrate in six trials are shown in Table 2. The ratio of sand/gravel preferences was used to rank each turtle's sand

Table 2. Preference for Sand/Gravel at Various Temperatures

Temperature	Turtle # 1	2	3	4	5	6	7	8	Totals
10° C	0/6	5/1	6/0	2/4	2/4	4/2	3/3	3/3	25/23
20° C	3/3	5/1	2/4	3/3	5/1	4/2	4/2	4/2	30/18
30° C	3/3	5/1	5/1	1/5	5/1	3/3	3/3	4/2	29/19
Totals	6/12	15/3	13/5	6/12	12/6	11/7	10/8	11/7	84/60

preference under various temperature conditions. A Friedman two-way analysis of variance (Siegel, 1956) indicated no significant differences in preference to sand at the various temperature levels ($X^2_r = 1.75$, $p > .05$).

The failure to confirm overall sand preferences casts doubt on the conclusions of Experiment I. It also appears that temperature was not a significant factor influencing substrate preference. It should be recalled, however, that seasonal variation includes other factors beside temperature change. Day length changes, and possible hormonal changes may contribute to hibernation phenomenon. However, sand substrate preferences in the juvenile snapping turtles are not enhanced by a simple temperature reduction.

General Discussion and Field Data

Laboratory tests minimally supported the general notion that juvenile snapping turtles prefer mud bottoms. These juvenile turtles occur in small streams and tributaries to larger water bodies (Pell, 1941). It is possible that the lack of clear preference for the finer substrate indicates an adaptive response to moving stream water which would have an exposed rocky substrate. However, Newman (1906) reported young snapping turtles in small pools, and at the margins of swamps. This suggests use of habitats with finer substrates than rocky streams.

In August 1973, I captured 43 hatchling common snapping turtles along 75 m of a narrow, fast moving stream which had a clay and pebble substrate. This stream was in Knox County, Tennessee. I have also captured and seen many hatchling and juvenile snapping turtles in a mud-

bottom pond on University of Tennessee property (to be described in Chapter II). It appears that hatchling and young snapping turtles may be found on a range of substrates. While adults are also found in almost all fresh water habitats throughout their geographic range (Conant, 1958), the reported preference for soft mud substrates may reflect a developmental shift from more universal substrate preferences of the young.

In both experiments, sand was chosen more often than gravel. While the data were equivocal, the results may typify the situation in the field. A statement that mud bottoms are "preferred" may indicate a more restrictive relationship of the animal to its habitat than actually exists, since several substrate types are utilized. The preceding experiments emphasize the need for quantitative verification of qualitative field observations.

Open versus Obstructed Area Preferences

The literature suggests that snapping turtles prefer obstructed to open areas. Several experiments were conducted to quantitatively demonstrate the preferences of juvenile turtles for open or rock obstructed areas.

Experiment III: Positions of Turtles in a Pool with Obstructions

The first experiment in this series was a pilot attempt to determine general aspects of distribution of turtles with regard to space.

Materials and Methods

The same turtles used in Experiment I were used in this experiment.

They were individually housed under conditions described in Experiment II for 20 days prior to testing. Testing was conducted between 24 September and 19 October, 1973.

Testing was conducted in a 1 m plastic swimming pool. The sand and pea gravel substrate was about 3.5 cm deep. Water above the substrate was about 6 cm deep. Rocks of various shapes and sizes were anchored in the substrate in the positions shown in Figure 1. Prior to testing, the turtles shifted these rocks to approximately the positions shown in Figure 2. I could observe the turtles through one-way glass in a 2 m high partition. In addition, a video monitor system (Olson Mini Camera TMC 2A0) was used to plot turtle positions on a data sheet. The monitor permitted more accurate determinations of turtle positions from a fixed camera point. So they could be individually identified, numbers were painted on each turtle's carapace.

Location of each turtle was recorded three times daily three times a week on non-feeding days. Morning, noon and evening locations were thus recorded for 11 2.3 days.

Prior to this testing, I fed the turtles by flushing finely chopped fish through two rubber tubes which opened into the pool. However, such feeding proved unsatisfactory for several reasons: 1) the turtles bit the rubber tubing, thus dislodging it, 2) the food had to be chopped finely to permit passage through the tubing, and 3) such finely chopped food was not readily detected by the turtles. Therefore, I later threw pieces of fish over the partition and into the pool. Food was randomly scattered throughout the pool.

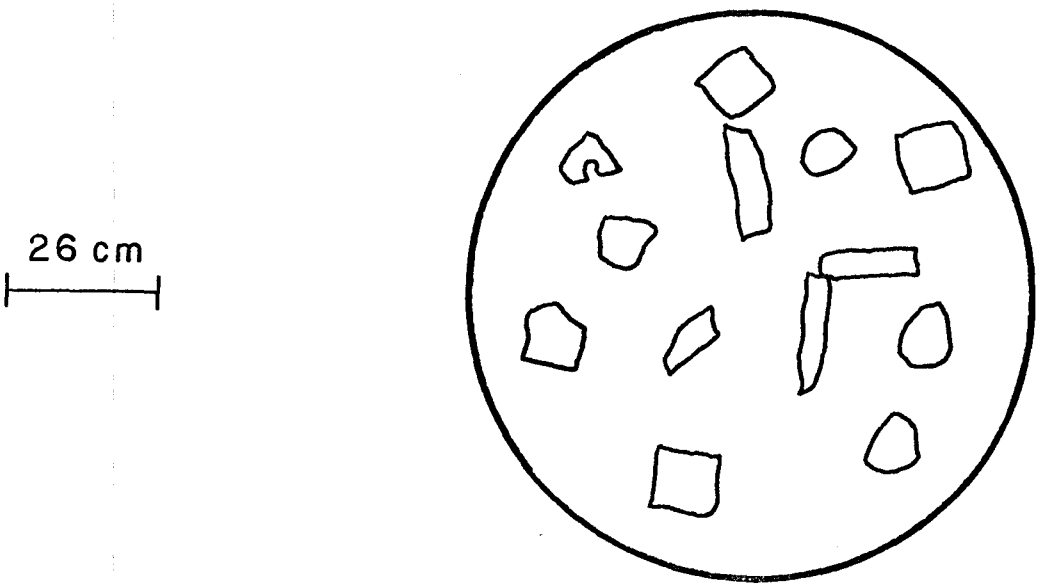


Figure 1. Original Rock Positions in Pool.

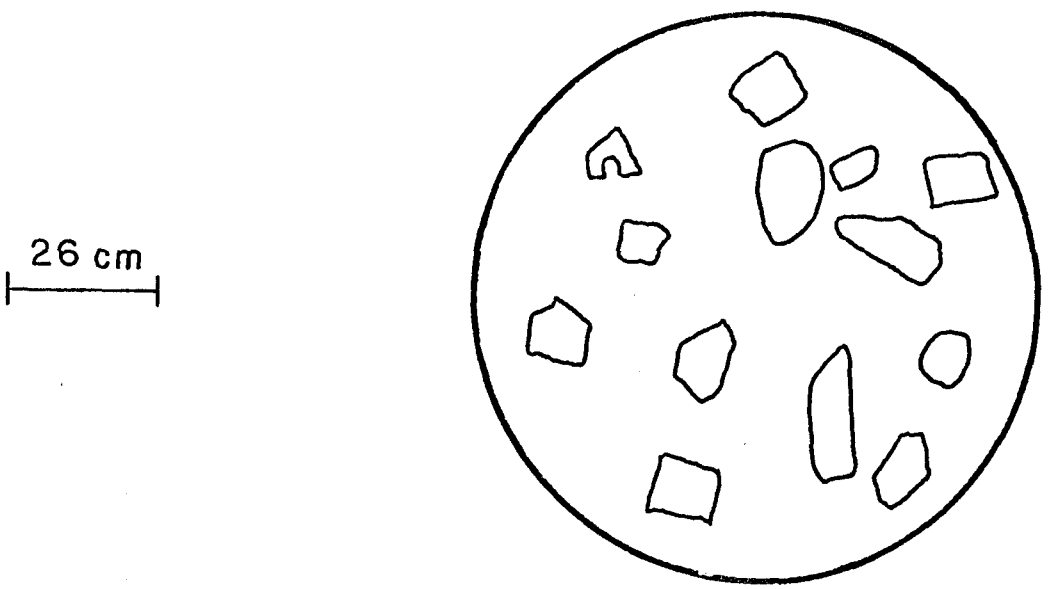


Figure 2. Shifted Rock Positions in Pool.

Results

The locations of the turtles suggested that they remained close to the obstructions. Turtles were clustered around rocks, and around the edge of the pool. Figure 3 shows total positions for all nine turtles across all testing days. Separate positions for morning, noon and evening recordings are shown In Figure 4a, 4b, and 4c. The only apparent differences across times of the day were that fewer turtles were in the relatively less obstructed half of the pool in the morning.

Experiment IV: Two-Choice Open versus Obstructed Area Test with Juveniles

This experiment quantitatively evaluated the choices of turtles for open versus obstructed areas of a pool.

Materials and Methods

The same turtles used in Experiment I were also used in this experiment. The plastic pool used in Experiment III was divided into an open half which was free of rocks, and an obstructed half which had 12 rocks. The substrate was the same as in Experiment III. A diagram of the pool is shown in Figure 5. The rocks were glued to the pool with rubber silicone cement. A 35 mm camera was mounted above the pool, and I tripped the shutter with a remote cable release. In addition to ceiling fluorescent fixtures, a 150 w flood lamp illuminated the pool. Both light sources were controlled by a timer on an alternating 12 hour day/night cycle. An electronic flash provided light for night recording. Testing was conducted between 20 February and 29 March, 1974.

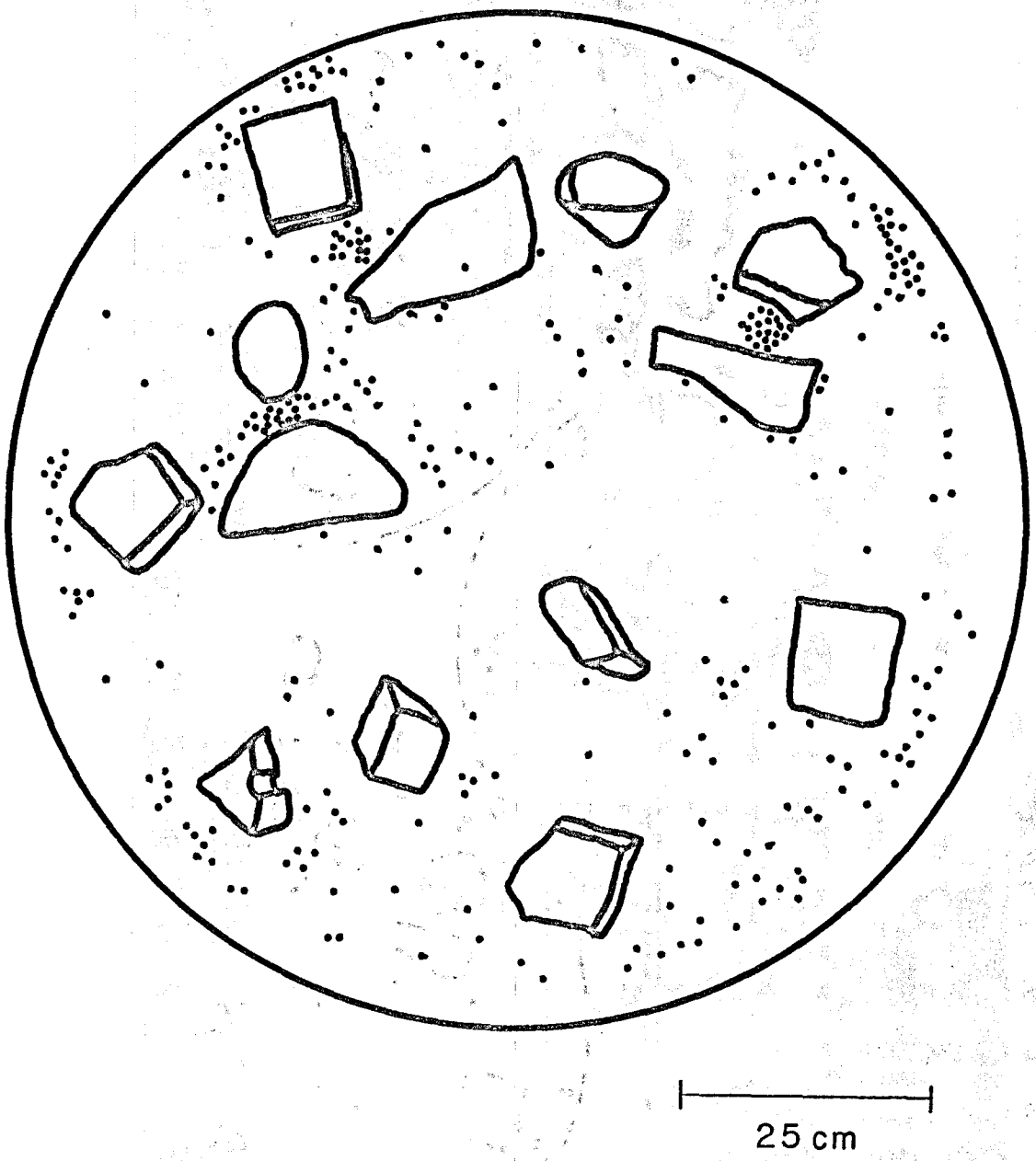


Figure 3. Total Turtle Positions Relative to Obstructions. One dot represents one turtle at one time of one day. Each turtle is represented 35 times in the figure.

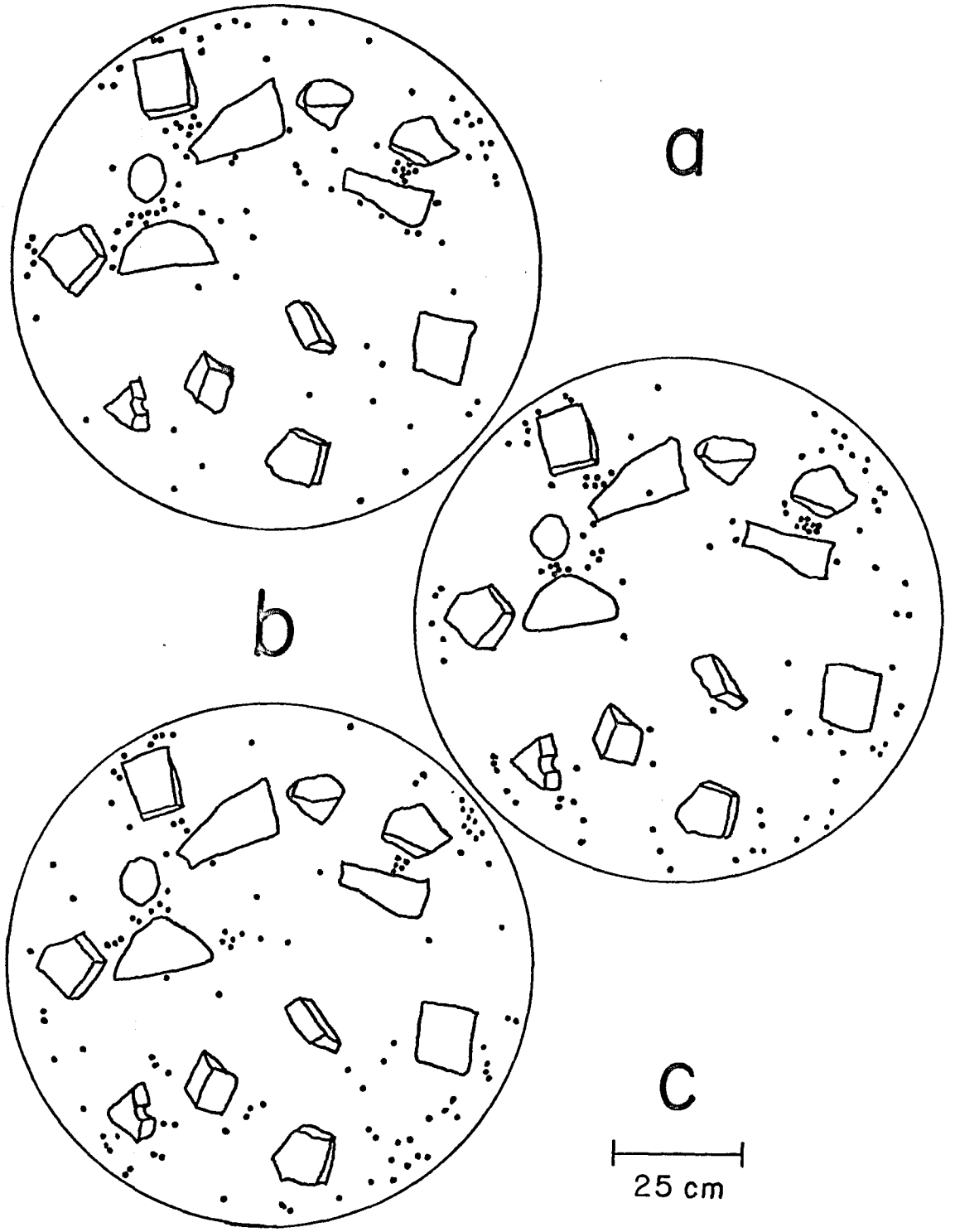


Figure 4. Total Positions at Various Times of Day: (a) Morning; (b) Noon; (c) Evening. One dot represents one turtle in one day. Each turtle is represented 11 times in Figure 4a and 12 times each in Figures 4b and 4c.

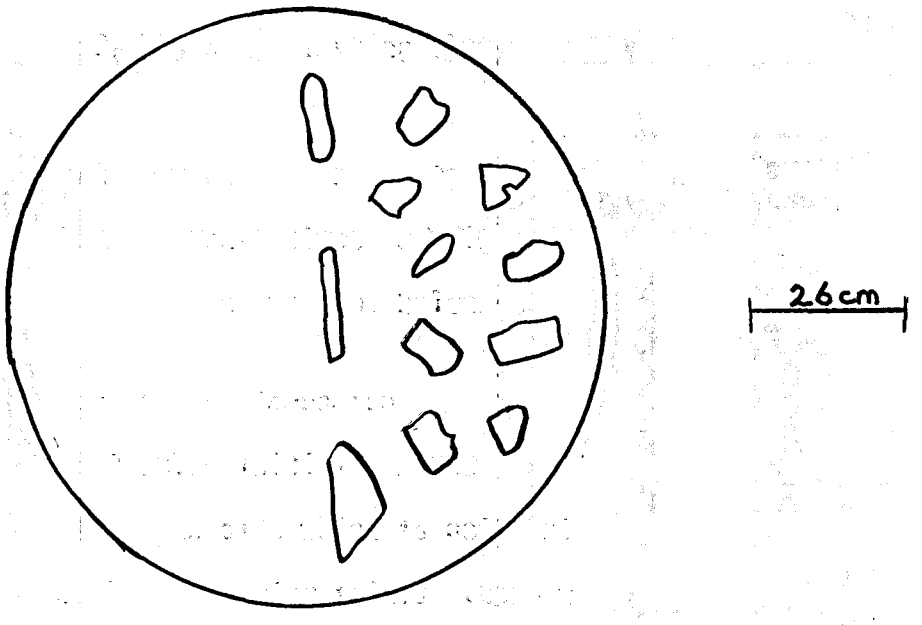


Figure 5. Open and Obstructed Pool Areas.

Each turtle was placed in the center of the pool, parallel to the line dividing the two halves. The direction the head of the turtle faced was altered 180° on successive introductions to balance left or right turning preference. The half of the pool each turtle first entered was recorded.

One week following introduction, I began photographing positions on non-feeding days (Monday, Wednesday and Friday). Pictures were taken at 830, 1130, 1430, 2030 hours. The only photograph taken during the night portion of the light cycle was at 2030 hours. After six filming days, the pool was emptied and the substrate was rinsed, stirred and replaced. The pool was turned 180° to control for position preferences due to structural

features of the room. Testing then resumed for another six filming days.

Turtles were fed in the test pool three times per week on non-testing days. Twenty pieces of fish (about 30 g total) were divided equally between the two pool halves.

Results and Discussion

Six turtles initially moved to the obstructed side, and three moved to the open side which is not a significant difference.

Of the 48 testing trials, there were more turtles on the obstructed side than the open side on 29 trials, and more on the open side on 19 trials. This difference was also not significant (one-tailed binomial probability test $p > .05$). In fact, there was a stronger preference for the side of the pool towards the one way glass, regardless of whether that was the open or obstructed side, than there was for the obstructed side itself (window side preferred 33 times, wall sides preferred 15 times; one-tailed binomial probability test $p < .05$).

Total choices for each turtle were separated into the four time periods used during testing. Choices to the obstructed side out of 12 possible choices per cell are shown in Table 3. For each turtle, the four times of the day were ranked from highest to lowest (1-4) according to number of choices to the obstructed side. A Friedman two-way analysis of variance (Siegel, 1956) indicated significant dependence of ranks on time ($\chi^2_r = 8.78$; $df = 3$; $p < .05$). This significant difference was due to the 2030 hours testing time. The Friedman analysis was not significant without the 2030 hours data, and 2030 hours was the only time during which a

Table 3. Number of Choices to Obstructed Side as a Function of Time

Turtle #	Hours				
	830	1130	1430	2030	Total[b]
1	4[a]	5	6	7	22
2	9	8	9	7	33
3	4	3	8	10	25
4	7	8	4	8	27
5	8	6	6	11	31
6	4	5	5	6	20
7	7	5	6	11	29
8	8	5	6	10	29
9	5	4	5	7	21
Total[c]	56/52	49/59	55/53	77/31	
	5/9	2/9	2/9	8/9	

[a]12 choices possible per cell.

[b]48 choices possible per row.

[c]Turtles with obstructed side > open side/total turtles.

significant number of turtles preferred the rock side over the open side (one-tailed binomial probability test $p < .05$). Since 2030 hours was the only night observation time, the results suggested that juvenile snapping turtles prefer obstructed areas during periods of darkness.

Experiment V: Two-Choice Open versus Obstructed Area Test with Recent Hatchlings

The generality of the findings in Experiment IV could be questioned on several grounds. Having been reared under conditions of captivity for over two years, the turtles were not naive. They were fed only during light hours, and seasonal variability was practically eliminated via

controlled temperature and artificial light cycles. It seemed advantageous, therefore, to replicate the obstructed/open habitat preference tests using a different group of turtles.

Materials and Methods

Five snapping turtles, *C. s. serpentina*, captured as hatchlings in September 1973, were used for this experiment. They are described in the Appendix. They were from the group captured in a small stream and mentioned in Experiment II (General Discussion and Field Data section, page 12). So they could be individually identified numbers were painted on each turtle's carapace. They were kept in the laboratory, under an alternating 12 hour day/night cycle, and room temperatures until testing. The turtles were seven months old when testing began on 9 April, 1974. Testing was concluded on 23 April, 1974.

The pool used in Experiment IV (Figure 5, page 19) was cleaned and used in this experiment. Water was filled to about 30 mm above the substrate. The turtles were placed on the midline of the pool.

A Nizo model S-80 time lapse super-8 mm movie camera provided a continuous record of the turtles' positions. An electronic flash was used for both day and night photography. The camera exposed about 1 frame every 80 seconds. Turtles were fed in the pool every other day as filming continued. All lights except the electronic flash were set on an alternating 12 hour day/night cycle. The camera automatically activated the electronic flash. Distractions caused by the flash were partially held constant by continuous day and night flash use.

Results

A sample of one frame from every 50 frames of film provided a total of 550 sampled positions for each turtle across six days and five nights. All five hatchlings preferred the obstructed side of the pool. A total of 76.5% of the sampled positions were on the obstructed side. During darkness, turtles were in the obstructed side during 84.7% of 255 recorded positions. During light, 69.4% of the recorded positions were on the obstructed side. Table 4 indicates day and night position frequencies for each turtle.

The turtles who remained in the open at night chose three basic portions of the pool. Most positions were adjacent to the edge of the pool (23/39 or 59%). In five cases (13%) the turtles were adjacent to a rock, but on the open side. One turtle (nine position recordings) was located away from any obstructions for almost an entire 12 hour night period. This turtle, however, burrowed in the substrate, and did not reappear until daylight. Therefore, hatchlings were found in the open at night in only two instances.

In contrast, of 90 positions recorded on the open side in the daytime, 30 (33%) were adjacent to the edge, 9 (10%) were adjacent to a rock, but on the open side, none were buried, and the remaining 61 (57%) were located away from any adjacent obstructions. While the obstructed side was preferred day and night, turtles moved in the open almost exclusively during the daytime. The ratio of turtles away from obstructions and in the open area (Table 4) was adjusted to equate for unequal total observation times. Even after this adjustment, the ratio was 22:1 for day position:night position in the open area.

Table 4. Number of Hatchlings on Open and Obstructed Sides of a Pool

	Turtle #												
	1		2		3		4		5		Total		Open Area Away From Cover
	Rock	Open	Rock	Open	Rock	Open	Rock	Open	Rock	Open	Rock	Open	
Day	39	20	45	14	41	18	39	20	41	18	205	90	51
Night	39	12	45	6	46	5	50	1	36	15	216	39	2
Total	78	32	90	20	87	23	89	21	77	33	421	129	53

Field Observations of Habitat Preferences

Small turtles were captured in habitats which had different kinds of obstructions. The 43 hatchlings described following Experiment II (see page 9) were caught on top of moss, under moss, under branches, and in open water on a rock, pebble, and detritus substrate. In open water, the turtles often resembled the substrate. The flat, cerrated body and long tail resembled a dead leaf and stem. Motionlessness enhanced the cryptic effect. Camouflaging substrates may be preferred by hatchlings following emergence from the nest and movement to water.

In the study pond, hatchlings were captured on large rocks, in and under moss, and in heavily overgrown swamp areas. Juveniles were captured in shallow spring areas, under moss, buried in mud, moving on top of mud, and adjacent to emergent vegetation.

Discussion

Observations of escape behavior by turtles which I approached suggested that obstructions serve a protective function. A turtle in the water with its head up first responded to approach by orienting its head toward me. On further approach, the turtle generally withdrew its head quickly. In open water, the turtle swam rapidly towards deeper water or towards cover. In moss or adjacent to other obstructions, the turtle moved slowly if at all. I confirmed this slow movement by hand capturing most such hidden turtles at the spot where their heads disappeared.

Most young turtles in the stream and at the pond were close to, if not in, some obstructing or camouflaging portion of the habitat. Besides

protection, obstructed areas may provide other advantages. The moss may be a direct and an indirect food source, as many aquatic invertebrates inhabited these moss areas. On sunny days, moss absorbed light and increased the water temperature considerably. The warm temperature could directly and indirectly benefit the turtles by increasing metabolism and attracting other food sources.

Slow movement under cover was a general phenomenon across various age groups of turtles. Table 5 illustrates responses observed for various

Table 5. Responses of Various Classes of Turtles to Disturbances under Various Conditions

Classes	Location of Turtle	Open or Cover	Behavior
Hatchling	on pebbles around leaves	open	motionless
	under moss	cover	motionless
	on top of moss	open	motionless, some swimming
Yearling and up	under moss	cover	slow movement or motionless
	buried in mud	cover	motionless
	no cover	open	escape
Adult	buried in mud	cover	motionless
	in burrows or under rocks	cover	motionless
	open water	open	dive, escape

sizes of turtles under different conditions of cover. Snapping turtles under cover do not respond to visual or other disturbances by rapid escape, but rather remain relatively motionless until physically touched.

Responses to visual or auditory disturbances appear highly moderated by habitat positioning. Habitat selection seems important, therefore, in placing the animal in a position providing cover and, thereby, protection.

The laboratory tests also indicated that obstructed habitats were preferable to open areas. In the juvenile turtles, this preference was related to the day/night cycle. Turtles significantly preferred obstructed areas during periods of darkness. The younger turtles preferred the obstructed area during day and night. However, the preference was stronger during dark periods, and one turtle in the open during the dark even buried in the substrate until morning.

Habitat selection, and concomitant behavior, therefore, appear to be important adaptations of these snapping turtles. How habitat selection relates to activity cycles will be further discussed in Chapter II.

CHAPTER II

ACTIVITY CYCLES

There exist several unsubstantiated accounts of nocturnal activity in snappers. Pope (1939) suggested that snapping turtles have nocturnal tendencies. Wood (1953) indicated that they were "light shy." Brown (1969) and Ernst and Hamilton (1970) have repeated statements of these supposed nocturnal patterns.

Several researchers have successfully trapped turtles at night (Lagler, 1943; Hammer, 1969). White and Murphy (1973) hunted snapping turtles at night with a spotlight. These reports support accounts of nocturnal activity in snapping turtles.

Several other authors have directly observed aspects of activity cycles in captive or wild snapping turtles. Norris-Elye (1949) watched hatchlings just after emergence, and noticed much activity when turtles were in the sunlight. A cloud cover was accompanied by reduction in activity. Norris-Elye attributed the activity change to temperature differences. However, in view of other work on hatchling behavior (Noble and Breslau, 1938; Wood, 1953; Lehman, 1966), the activity reduction may have followed illumination intensity changes. Lehman (1966) reported light avoidance (nocturnal activity inferred) in adults which was unlike the positive phototaxis of the hatchlings. Kiviat (personal communication), observed early morning and late afternoon activity peaks. He did not report the times sampled, and his observations may have included only two sides (beginning and end) of a continuous nocturnal activity cycle.

Murphy and Sharber (1973) relocated three radio-marked turtles 600 times between July and November. They reported no nocturnal/diurnal differences in activity, but did not state how many day/night readings they took. In view of this conflicting data, a systematic attempt to evaluate activity cycles was undertaken.

Besides diurnal cycles in turtles, two accounts suggested long inactive periods following feeding. Baldwin (1926) reported that following feeding, snapping turtles remained inactive for unspecified long periods. While studying the effects of initial feeding of hatchlings on phototaxis, Wood (1953) observed that hatchlings went to dark places and burrowed in the substrate following feeding. These reports suggest that movement (activity) is related to food requirements. Activity cycles may not only follow diurnal patterns, but may be more flexible depending on amount of food obtained at the last meal, metabolic rate (variable with temperature) and other interacting factors. Documentation of the long range activity patterns is needed.

Laboratory Tests

Experiment VI: Hatchling Activity Cycles

The literature on hatchling snapping turtles indicates positive phototaxis and increased activity during daylight (Norris-Elye, 1949; Noble and Breslau, 1938; Lehman, 1966). On the other hand, the few anecdotal accounts of adult snapping turtle activity suggest a reversal in phototaxic orientation, and a depression of activity during daylight (Pope, 1939; Wood, 1953; Lehman, 1966). Since these effects are not clearly established (Murphy and Sharber, 1973) activity cycles in a

variety of sizes of snapping turtles were observed. This experiment reports activity in turtles less than one year of age.

Materials and Methods

Activity cycles were evaluated in the film used in Experiment V. Movement between adjacent film exposures was measured for each turtle. Adjacent frame samples were taken every 50 frames of film. A total of 180 adjacent frame samples representing almost nine days were used. One frame of film was exposed every 80 seconds. Movement rates, therefore, are distance moved per inter-frame interval (IFI = 80 seconds).

Results

The film indicated clear cyclic activity highly dependent on light. Movement almost ceased when the light was turned off, and abruptly resumed when the light came on. Statistical analysis of one film showed total movement by turtles to be significantly different under nocturnal and diurnal conditions (dependent $t = 7.91$, $df = 4$, $p < .05$). The diurnal rythm is shown in Figure 6. Turtles were more active in the daytime, and their activity was bimodally peaked in the morning and in the evening. After darkness, activity dropped to almost zero within four hours, and remained negligible until the abrupt rise and peak at daybreak.

Experiment VII: Juvenile Activity Cycles

Materials and Methods

The nine juvenile turtles used in prior experiments (I, II, III, IV) were also used in this study. The turtles had been individually housed since last testing.

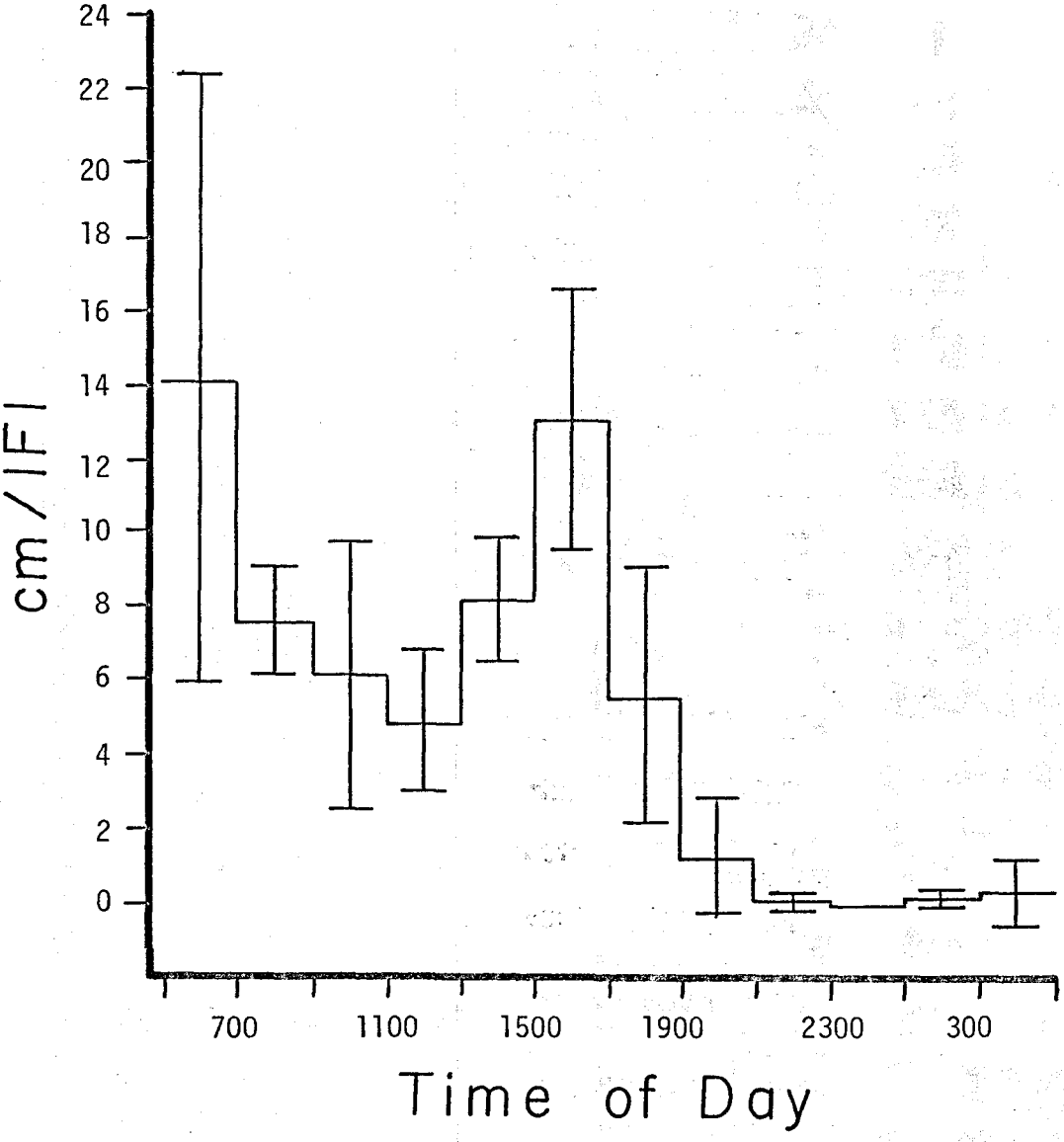


Figure 6. Hatchling Movement at Various Times of the Day. Each turtle's movement between inter-frame intervals (IFI's) was summed for all IFI's falling between the two-hour time blocks. Movement per IFI was calculated by dividing each turtle's sum for each time block by the number of IFI's sampled in each time block. The long horizontal bars represent mean movement per IFI for all turtles. The vertical bars represent $\pm 1\sigma$.

The pool used in Experiment IV (see Figure 5, page 19) was cleaned and filled with water to a level of about 6 cm above the substrate. Water temperature ranged from 21°-25° C. The Nizo model S-80 time-lapse super-8 mm movie camera was used to provide a continuous record of turtle movement. An electronic flash was used for day and night photography. Since these larger turtles moved faster than the hatchlings, a check of reliability of intervals between measurements was conducted. The camera exposed one frame every 30 seconds for two films and then was switched to one frame every 80 seconds for one additional film. Activity rates are expressed in distance moved/time interval used. Lighting, except for the electronic flash, was on an alternating 12 hour day/night cycle. Movement was measured between two adjacent frames every 50 frames of film.

Results

The IFI used to record movement appeared irrelevant for activity rate did not increase proportionally on the 80 second interval. However, the relative periods of activity and inactivity remained similar. The 80 and 30 second IFI data, measured across various times of the day were highly correlated (r = + .78, p < .05). The total of all observations at 30 second and at 80 second IFIs was, therefore, used for further analysis.

Figure 7a and 7b indicates mean movement of all turtles per two frame sample across two hour time blocks. As in the previous experiment, movement was closely related to the light cycle. Turtles total movement scores for day and night were significantly different (dependent t = 9.03; df = 8, p < .05).

Figure 7. Juvenile Movement at Various Times of the Day: (a) 30 Second IFI (Inter-Frame Interval); (b) 80 second IFI. Each turtle's movement between inter-frame intervals (IFI's) was summed for all IFI's falling between the two-hour time blocks. Movement per IFI was calculated by dividing each turtle's sum for each time block by the number of IFI's sampled in each time block. The long horizontal bars represent mean movement per IFI for all turtles. The vertical bars represent $\pm 1\sigma$.

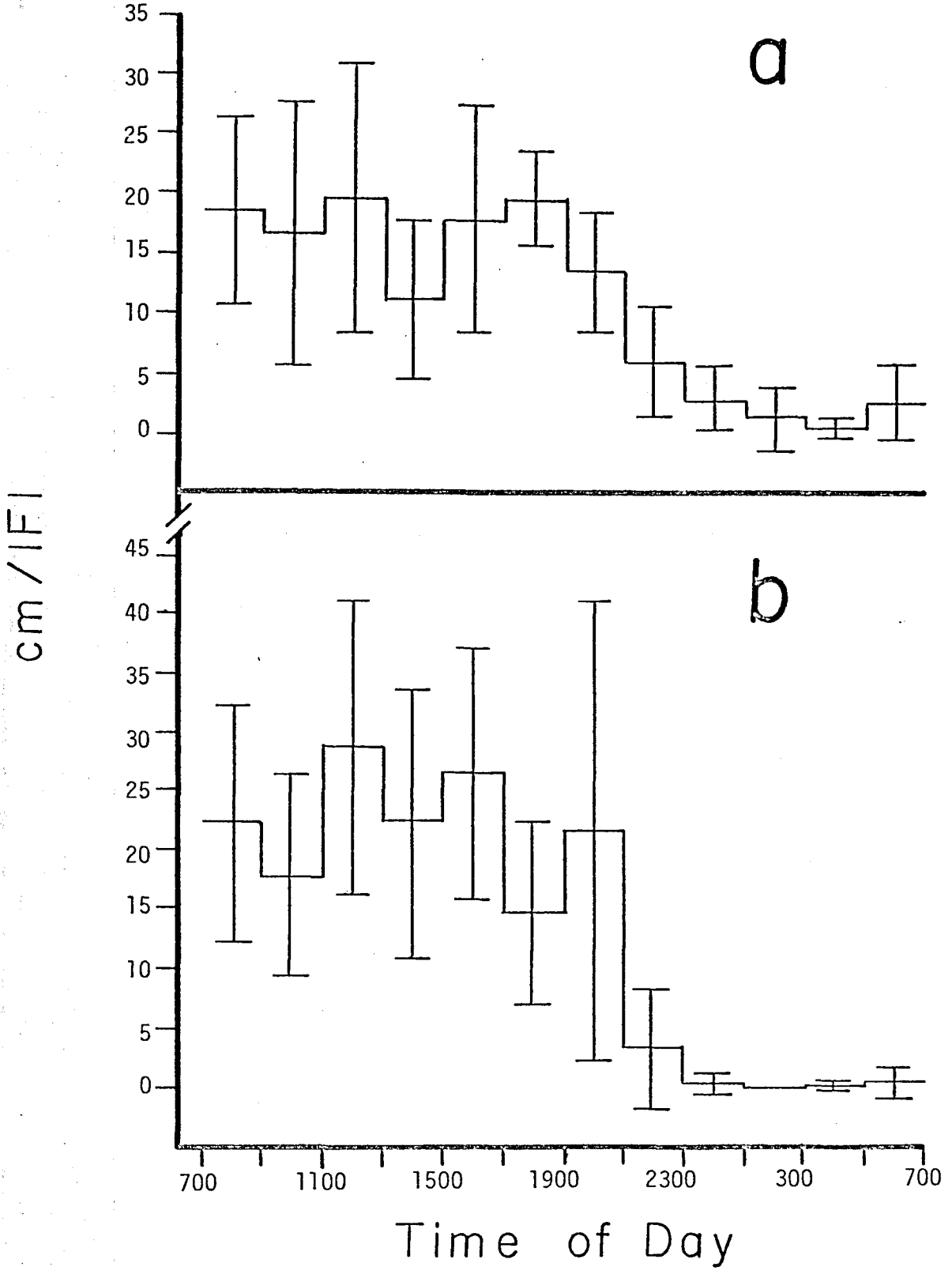

a
b
35
30
25
20
15
10
5
0
45
40
35
30
25
20
15
10
5
0
cm/IFI
700
1100
1500
1900
2300
300
700
Time of Day

Figure 7

Discussion

The conspicuous bimodal daytime distribution of activity seen in Experiment VI was absent in Experiment VII. Daytime activity for these juvenile turtles appeared to be more randomly distributed throughout the daylight hours.

Both groups of young turtles in the laboratory showed marked reduction of activity, during night hours. The night decrease was paralleled by positioning of the turtles in the obstructed areas (see Chapter I). This lends further support to the idea that habitat positioning is an important protective adaptation. Less active turtles are probably also less alert, and positioning in obstructed areas reduces their exposure to possible predation or conspecific aggression.

Field Observations of Activity Cycles

The only account of snapping turtle activity cycles in the field is a brief abstract by Murphy and Sharber (1973). They did not report their methodology or any data. I studied activity cycles in a field population of turtles to provide comparative data for the laboratory studies, and to clarify contradictory reports in the literature.

Study Site

Activity cycles were studied at a small pond about 0.8 ha in surface area, located directly south of the University of Tennessee Memorial Research Hospital. The pond's history has been briefly described elsewhere (Froese and Burghardt, In Press). A map of the pond is shown in Figure 8. The pond was shallow, maximum depth not exceeding 1.5 m, and

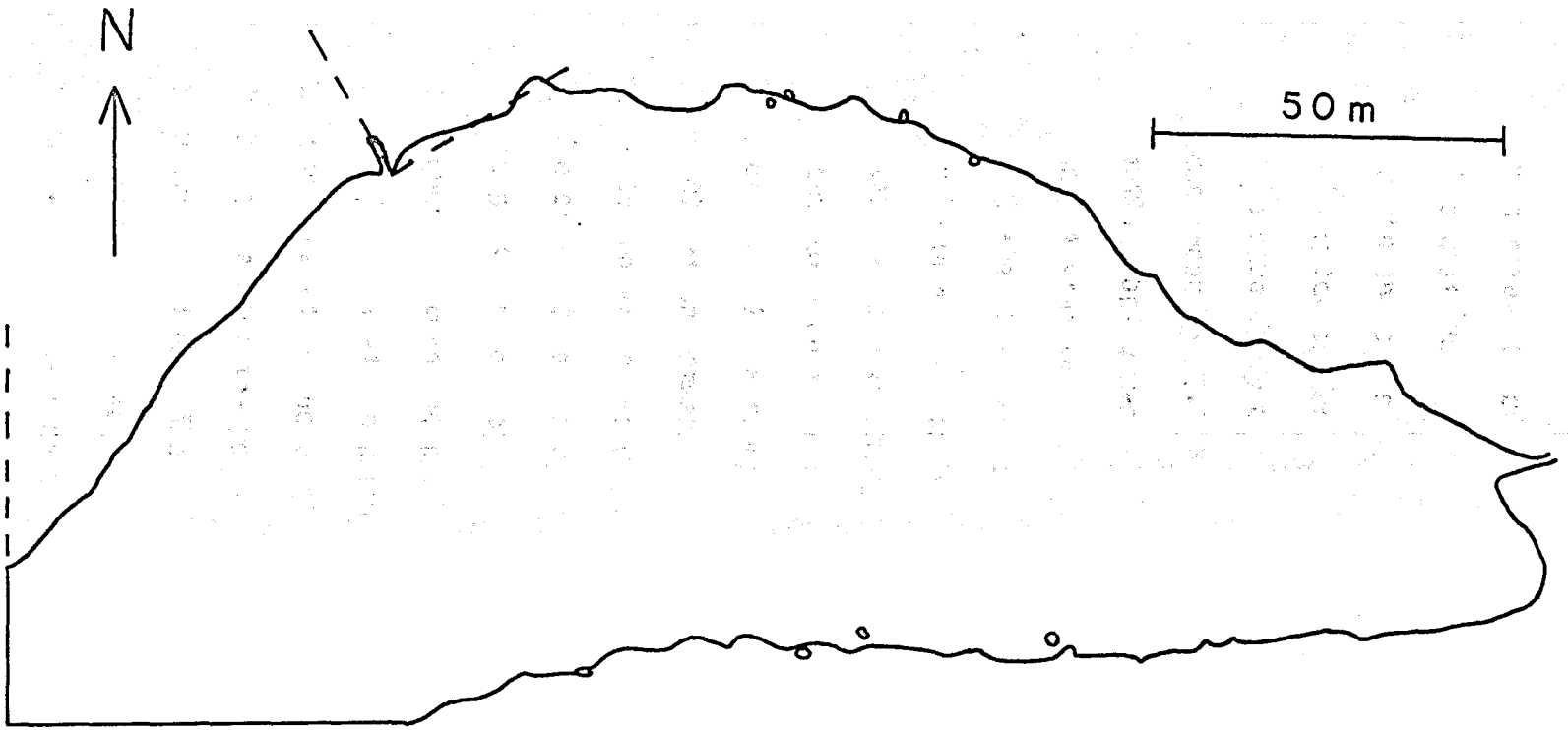


Figure 8. Study Pond Map.

had a thick mud substrate. Water entered the pond in a spring area on the east side. This east shore was shallow, and contained much aquatic vegetation. The south shore was a sharply cut bank, parts of which were undercut beneath the water surface. Several trees grew along the bank, and many large rocks were fully or partly submerged along the shore. The southwest shore was recently filled with rocks for road construction purposes. The gently sloping west and northwest shores supported much aquatic vegetation. A steeply sloping land-fill area with large boulders, brush, and logs dominated the north shore. The central portion of the pond was uniformly between 1-1.5 m in depth, and contained few submerged obstructions. I sank between 20 and 30 cm into the mud substrate when crossing this central area on foot.

The pond was about 250 m from Fort Loudon Lake, a portion of the Tennessee River. Migration between the river and the pond was, however, treacherous. The two water bodies were separated on one side by a four-lane highway. The other closest approach to the river contained a steep uphill bank at the pond, as well as a cliff at the river. Migration must not have been frequent between the pond and the river. Frequent migration would have undoubtedly reduced the population due to road kills.

The pond was located on the University of Tennessee Cherokee Farm. Cattle grazed the land around the pond until 1973, prior to the initiation of these movement studies. The cattle were removed from the area to allow road construction. The roadbed was adjacent to the pond's south bank. The extreme southwest section of the pond was covered by the road. Road construction included dynamite blasting, land fill, and heavy machinery. All of these variables could have considerably influenced the

turtles. Dynamiting, however, was completed in spring 1973, and did not occur during the time I studied the turtles.

The pond was a favorite fishing spot for several people and occasionally, they hooked turtles. Signs were posted around the pond indicating that the turtles were under study and should not be disturbed. In spring 1974, following some vandalism, "No Trespassing" signs were erected, and the policy was enforced by University police. At the same time, a fence was erected along the new highway, further limiting access to the pond.

Study Population

The adult snapping turtle population had been previously estimated at 48 turtles (Froese and Burghardt, In Press). Capture data from spring 1974 confirmed the dense population of adults in the pond. Twenty adult turtles were marked prior to spring trapping. A total of 12 adults were captured in spring, 6 of which had been previously marked. The revised estimate, therefore, was 20 X 12/6 = 40 adult turtles.

Half of the six turtles first captured in spring 1974 were males and half were females. The total male:female sex ratio (1: .65) represented a reduction of the difference of an earlier estimate (Froese and Burghardt, In Press). While migration and mortality may have altered the population structure since fall 1973, the combined data are probably a good estimate of these population parameters.

Materials and Methods

A telemetry system purchased from Mini-Mitter Corporation was used to monitor turtle movement. Model L transmitters were prepared and mounted

on adult turtle carapaces. Modified Lafayette Model HA 420 walkie-talkies received the signals from the transmitters. Modifications included fine tuning to transmitter frequencies, and installation of a beat frequency oscillator which made the pulsing signal more audible.

Each transmitter emitted a pulse at a different frequency, thus enabling location of individual turtles. Frequencies varied, in no less than .005 Hz intervals, between 26.880 and 27.615 Hz. The ambient temperature determined the pulse rate of each transmitter. The pulse rate of each transmitter was calibrated at various temperatures prior to attachment.

Two hand held directional antennas (Mini-Mitter Model AF) were used to triangulate turtle positions. In spring 1974, hand antenna use was discontinued in favor of a more accurate technique of locating the turtles. I rowed around the pond in an aluminum Jon boat and listened for signal intensity changes. I rowed in the direction indicated by increased signal strength until the most intense signal was located.

A stopwatch was used to record rate of transmitter pulsing. A secchi disk was also used to record water turbidity.

Animal Capture

Bait (fish market carp) was tied to the live animal traps previously described by Froese and Burghardt (In Press). Tying was necessary to keep the bait from floating out of the trap, and to prevent turtles from taking bait without tripping the trap. One float attached to the trap handle marked the location of the trap. After repeatedly checking empty traps, I attached another float to the trap door. When the

door closed, this second float was pulled under water, thus marking a capture. Traps were set under water and away from the shoreline. Several traps were stolen when they were accessible from shore.

Since the traps were under water, they had to be checked periodically to avoid drowning captured turtles. Intervals between checking the traps ranged from two to ten hours, largely depending on temperature. During hot weather, oxygen starved animals were sometimes found in traps which had not been checked for several hours. An oxygen starved turtle extended its neck to the top of the trap, and rapidly inhaled when removed from the water. No more than three of the trapped turtles showed signs of oxygen starvation. All of these turtles recovered after a short time out of water.

Captured turtles were weighed, measured, and marked at the laboratory. Turtles were individually marked by inserting small plastic buttoneers through drilled holes in the posterior marginal scutes (Pough, 1970). Froese and Burghardt (In Press) have described the numbering system. A transmitter was then attached to the turtle's carapace. A restraining board (Figure 9) facilitated work with the turtles.

Transmitter Preparation and Attachment

The transmitter and two 1.5 v power cells were sealed with silicone lubricant. Two stainless steel wires, about 1.5 mm in diameter and about 18 cm in length were wrapped around the unit. This unit was then dipped in a 50:50 mixture of beeswax and paraffin. After drying, the unit was next dipped in cranioplastic cement. The transmitter was then complete with four attachment wires firmly embedded in a hard plastic casing.

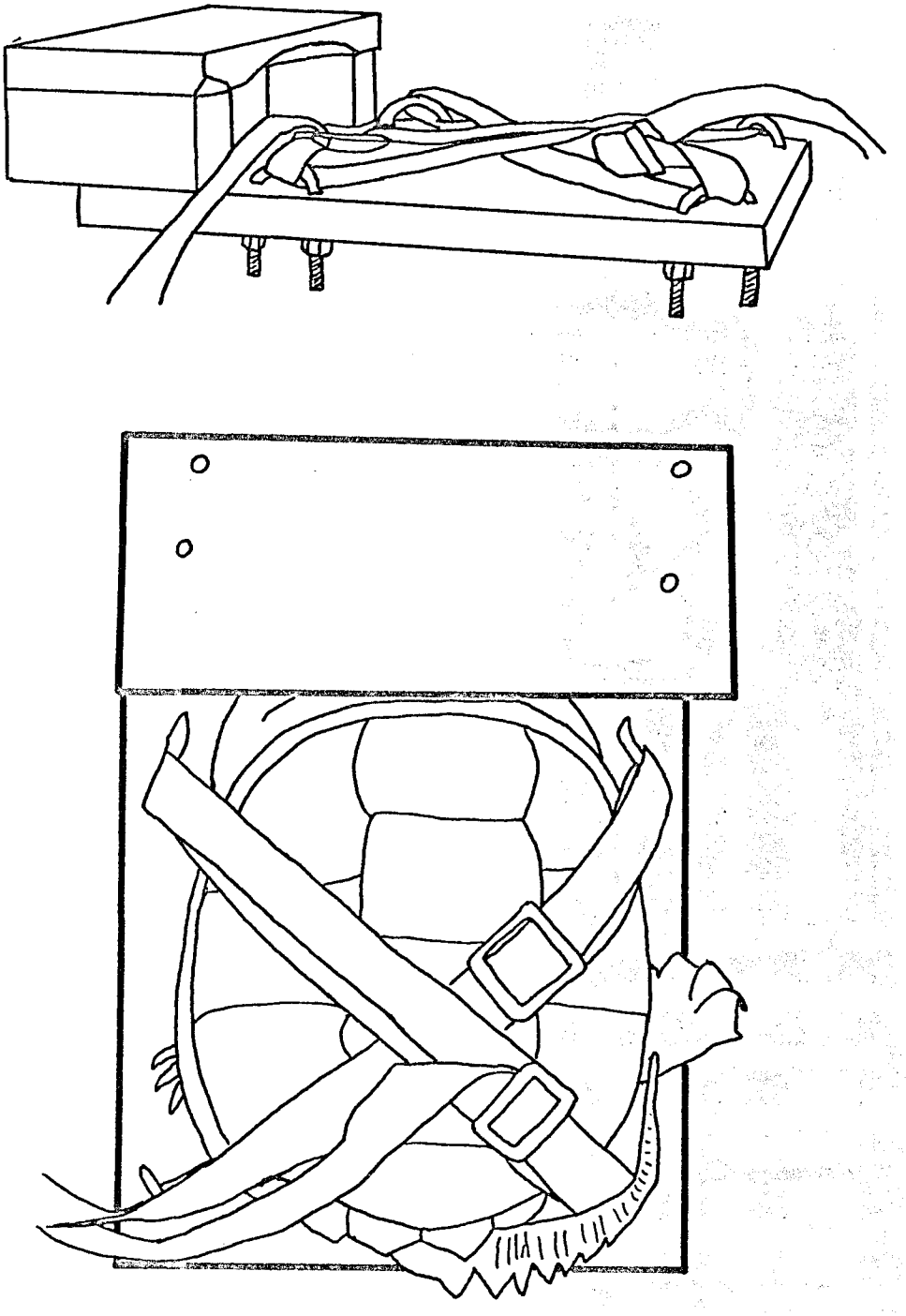


Figure 9. Turtle Restraining Board.

Depending on the neatness of the applications, these units measured about 4 cm in length, and 2 cm in diameter, and weighed about 20 g. A diagram of a complete unit is shown in Figure 10.

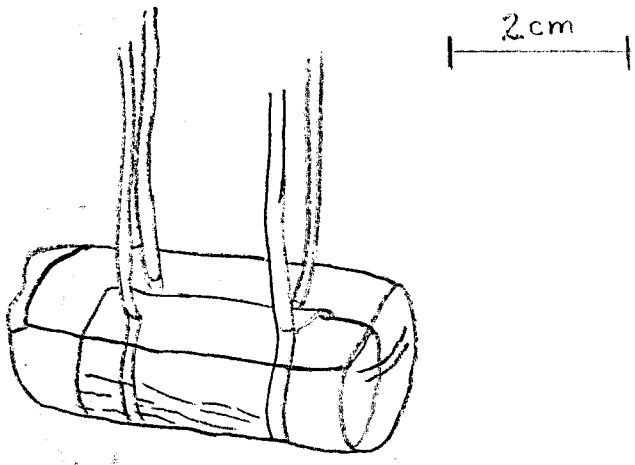


Figure 10. Completed Transmitter.

The unit was then dipped in a water bath, and pulse rate was calibrated at various temperatures. The latency to an asymptotic rate varied between transmitters, probably as a direct function of differential thickness of the cranioplastic cement. Maximum time to asymptote over 10° C changes, however, never exceeded 8 minutes.

The transmitters were attached to the posterior carapace of adult (> 200 mm carapace length) turtles. Four holes, about 2 mm in diameter, matching the distance between attachment wires at the base of the transmitter, were drilled into the marginal scutes of the turtle. On females, I attempted to position the transmitters away from the posterior midline

to reduce interference with mating. The attachment wires were diagonally fastened together beneath the carapace. The ends of the wires were clipped, and turned posteriorally until they lay under the carapace. They were then covered with either rubber silicone cement, or additional cranioplastic cement, to reduce the possibility of injury from the sharp edges. A completed attachment is shown in Figure 11. The turtle was then

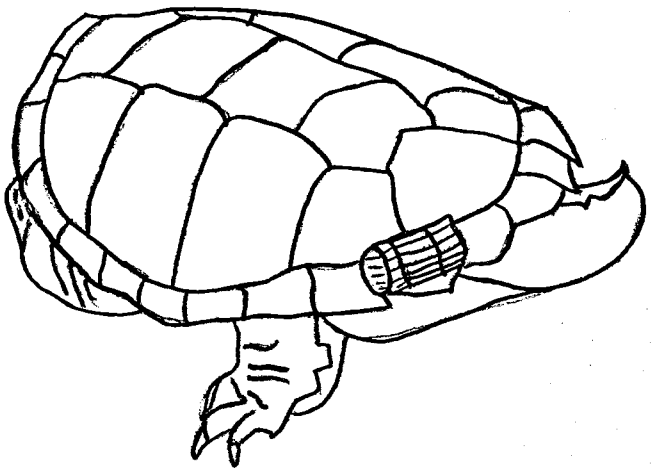


Figure 11. Transmitter Attachment on Posterior Carapace of Turtle.

released at its capture point.

Batteries lasted between one and three months. They were replaced after cutting the outer casing and removing the small transmitter unit. The outer casing was rebuilt each time the batteries were replaced. Turtles with weak or dead batteries were not all recaptured. Therefore, few batteries were changed.

Animal Location

Two people could triangulate the position of a turtle from different points along the shore. A protractor was glued to a board through which the handle of the directional antenna was then inserted. The base board was rotated so that a marked point on the opposite shore was fixed at an angle of 0°. Rotating the directional antenna produced changes in signal intensity which were then used to determine the direction of the transmitter. When the transmitter direction had been determined, the angle from the 0° line was read directly from the protractor.

The receivers had only three channels which could be switched without changing crystals. When more than three turtles were recorded, crystals had to be changed after every third turtle was located. A diagram of the receiver, protractor, and antenna system is shown in Figure 12.

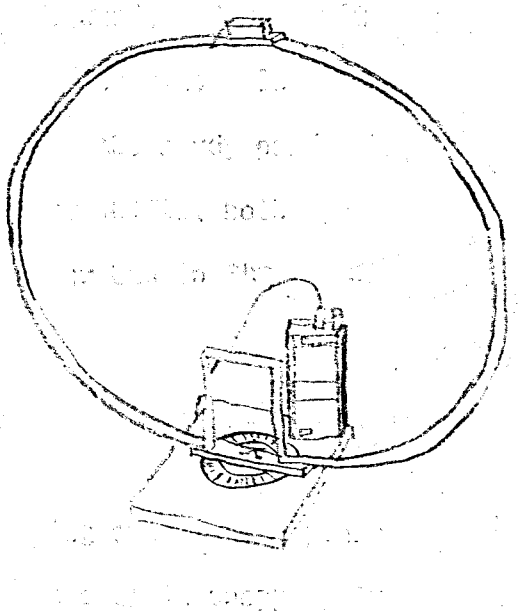


Figure 12. Receiver, Protractor and Antenna System.

Transmitters were accurately located by rowing around the pond while listening to the signal. Movement toward the transmitter caused an increase in signal intensity. Within 3 m of the transmitter, the signal changed to a dull, toneless thud. Manual location was more accurate in locating turtles than triangulation (see pages 54 and 59), and could be accomplished with only one person. When turtles were in the center of the pond, their position was estimated by sighting two imaginary lines across the pond, which intersected on the boat. The four points where these lines intersected the shoreline were then recorded. Manual location was exclusively used in 1974.

Preceding and following each daily set of recordings in fall, the pulse rate for each turtle was counted for one minute, and surface water temperature was recorded. In spring, pulse rate was counted for one minute for each turtle at each position recording.

In fall 1973, a total of five turtles was followed for various lengths of time. In spring 1974, two recaptured telemetered turtles from fall were again followed, and transmitters were placed on an additional eight newly captured turtles. In all, I have data on movements of 13 different turtles in the study pond. In spring 1974, I followed six turtles in four-hour shifts, both day and night, for a total of 72 hours. The turtles are described in the Appendix.

Results

Trap Data

Since trapping success as a function of time of day has been used to infer activity cycles in snapping turtles, results of trapping are

included here. Most of the 47 turtles trapped were trapped in the evening between 1600 and 2200 hours. In four equal time periods, morning, day, evening and night, the percentages of total turtles trapped were 16%, 29%, 44% and 11%. These data suggest that activity, as indicated by trapping success, was greatest in the evening hours. However, such a conclusion is unwarranted without evaluation of the number of trap hours during each time interval. Figure 13 indicates number of turtles captured and the corresponding number of trap hours. Number of captures in the evening was higher than would be expected on the basis of hours the traps were set. The difference across six hour time blocks was not significant ($X^2 = 4.6$, $df = 3$, $p > .05$). While turtles can be trapped at all hours, inference of activity cycles requires extensive sampling of all hourly intervals, and many trapped animals. Also, such an inference is based on the assumption that activity is equally likely to lead to trapping during light and dark hours.

Fall 1973 Telemetry Data

At each visit to the pond, I recorded each turtle's position at least twice. Movement rates were calculated from these successive locations. The distance each turtle moved between successive recordings was summed across separate observation times. The time in minutes between successive locations of each turtle was also summed across separate observation periods. Total distance was divided by total minutes, and the quotient was then divided by 60 to obtain the activity rate (m/hour).

Rates varied considerably for the five turtles (see Table 6). The relative state of hibernation of the animals may have influenced the rate

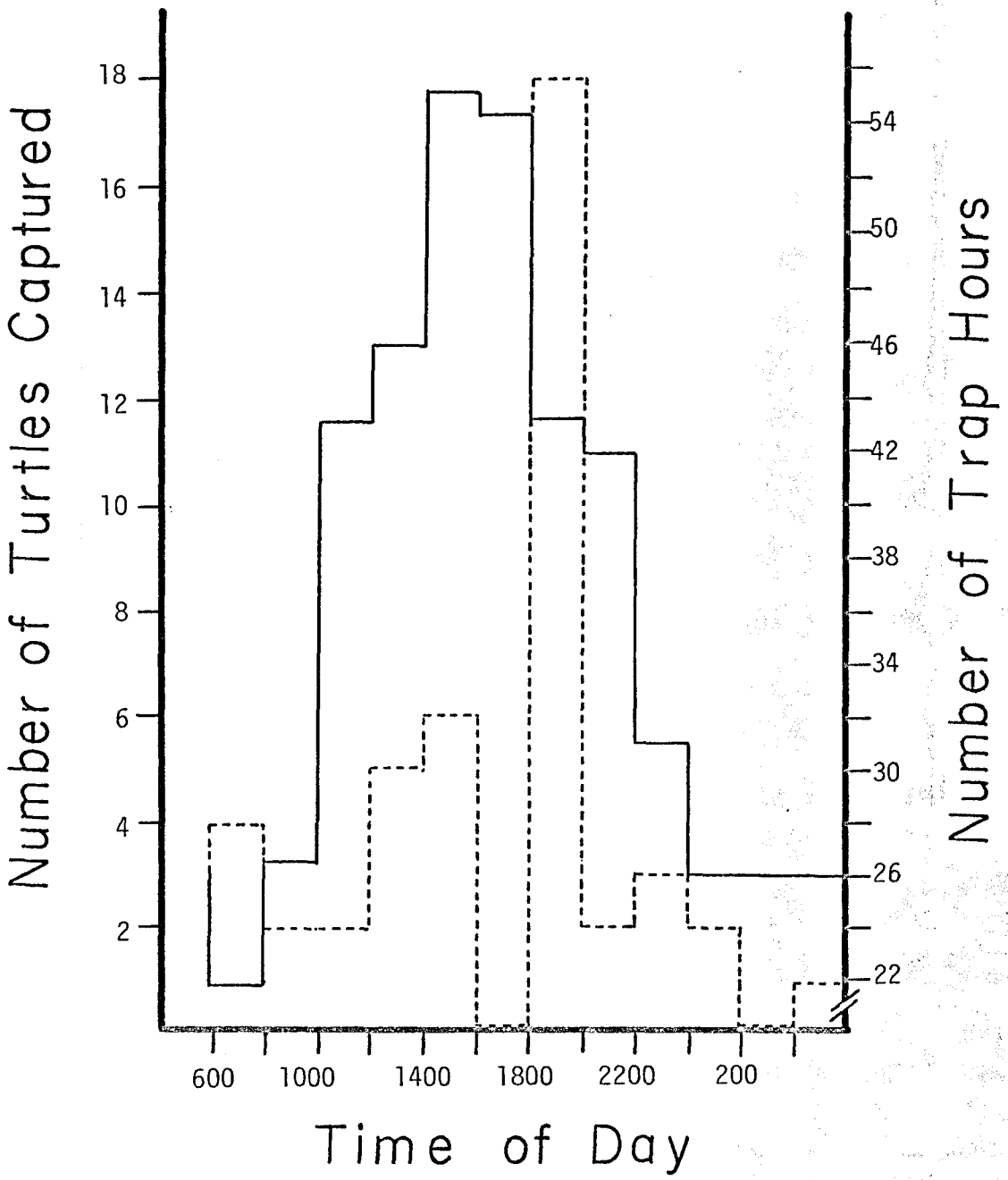


Figure 13. Trap Hours and Captures by Time of Day. The solid line represents trap hours, and the broken line represents number of turtles captured.

Table 6. Movement Rates for Fall 1973 Turtles

Turtle #	Date of First Tracking	Mean Minutes Between Recordings	Total Meters Moved	Total Hours Between Recordings	Average m/hour (Rate)
37	9/15	17	620	19.6	31.6
13	9/25	18	746	12.2	61.1
18	10/16	31	335	6.2	54.0
43	9/25	25	196	9.9	19.8
50	10/16	27	78	4.5	17.3

variability. I tracked turtles from September through October, 1973. However, not all five turtles were followed for this entire period. If hibernation contributed to the variability between turtles, those turtles which I began following later in the season should have had lower rates than those I began tracking earlier in the fall. The rates shown in Table 6 do not support the idea that a movement decrement due to hibernation accounted for much of the variability between turtles. If error in triangulation was randomly distributed across turtles, they showed considerable variation in movement rates. Larger turtles generally had faster rates than smaller turtles. This correlation was, however, not significantly different from zero (r = + .61, p > .05).

Differential activity as a function of time of day was evaluated across four six-hour time blocks. Mean activity rates were slower during midday periods than during morning, evening, or night (see Table 7). However, no consistent cessation of activity occurred during any time of day.

Table 7. Movement Rates[a] by Time Blocks for Fall Turtles

Turtle	Morning	Midday	Evening	Night
37	7.6	23.3	40.3	46.3
13	46.7	38.2	67.0	71.5
18	121.8	6.2	46.2	60.1
43	0.0	64.0	24.2	9.5
50	8.4	18.3	12.2	24.5
Average rate ($\Sigma X/N$) for five turtles	36.9	30.0	38.0	42.4

[a]m/hour duration between successive recordings

Activity rates for various times of the day were ranked from highest to lowest rate (1-4) for each turtle. These ranks were independent of the time blocks ($X_r^2 = 4.2$, $df = 3$, $p > .05$).

Movement rates corresponded with average daily temperature ($r = + .43$, $p < .05$). Since colder temperatures were recorded later in the season, the temperature movement correlation may merely reflect seasonal changes related to hibernation.

Spring 1974 Telemetry Data

During spring 1974, ten turtles were trapped and fitted with transmitters. Three transmitters failed just prior to an intensive week of tracking, and one turtle was found dead. Therefore, I intensively tracked the remaining six turtles from 13-20 May, 1974.

Movement rates were calculated for each turtle from mapped positions

and time records as in the fall 1973 data (see page 46). The only deviation from the fall procedure was that I obtained at least four successive relocations, at almost hourly intervals, during each visit to the pond. The spring turtles again showed considerable variability of activity rates (Table 8), but rates were much lower than for the fall 1973 turtles. There was, in fact, no overlap in the distribution of movement rates for the two groups of turtles, and the means for fall and spring were significantly different (t = 3.74, df = 9, p < .05. Since I employed different techniques for locating animals (see pages 54 and 59) during these two observation periods, the different rates do not

Table 8. Movement Rates for Spring 1974 Turtles

Turtle #	Mean Minutes Between Recordings	Total Meters Moved ÷	Total Hours Between Recordings =	Average m/hour (Rate)
3	56.8	31	57.7	0.5
13	57.3	113	58.3	1.9
51	56.4	616	57.4	10.7
59	57.5	344	58.4	5.9
70	58.1	59	59.1	1.0
71	57.0	681	57.9	11.8

necessarily indicate that turtles move less in the spring. Rather, the difference in rates probably indicates the inaccuracy of the triangulation technique. Movement rates may have differed during the two periods, but they are confounded by the change in technique. I am confident that the

spring 1974 technique was an accurate method for locating the animals (see pages 54 and 59).

Movement rates were more variable in spring than in fall. While the technique difference mentioned above could have attenuated fall variability, the ratio of highest to lowest rate was about 3.5:1 in fall, and 25:1 in spring.

In contrast to the fall data, activity rates in spring were negatively correlated with size of the turtle. This tendency for larger turtles to move less was significant (r = -.84, p < .05).

Differential activity as a function of time of day was evaluated across equal six-hour time blocks. Mean activity rates of all six turtles were greater at night than for morning, evening and midday periods. As in fall, midday activity was lowest (Table 9). Activity rates for various

Table 9. Movement Rates[a] by Time Blocks for Spring Turtles

Turtle #	Morning	Midday	Evening	Night
3	0.0	0.3	0.0	1.9
13	0.4	0.0	0.0	7.6
51	5.2	11.3	11.0	15.5
59	1.6	0.6	3.9	16.6
70	2.2	0.7	0.3	1.0
71	19.2	5.9	11.0	11.8
Average rate ($\Sigma X/N$) for six turtles	4.8	3.1	4.4	9.1

[a]m/hour duration between successive recordings.

times of the day were ranked from highest to lowest rate (1-4) for each turtle. The ranks suggested differences in activity rates between time blocks ($X_r^2 = 7.75$, $df = 3$, $.10 > p > .05$).

A combined analysis for 11 turtles in fall and spring indicated significant differences in activity rates across time blocks ($X_r^2 = 9.74$, $df = 3$, $p < .05$). Nighttime movement was highest and midday movement was lowest across all turtles. Morning and evening ranks were similar and slightly greater than midday ranks.

The pulse rate was counted at each position recording for spring animals. These data provided a continuous record of water temperature around the turtle. Water temperature varied as a function of water depth and amount of sun. The transcribed temperatures would be expected, therefore, to show some variability. Transmitter unreliability may also have produced excess variability in temperature records. For each four-hour time block, therefore, an average of temperature records from all turtles and the total movement rates of all turtles were calculated. These data are shown in Figure 14. Activity rate and temperature were not significantly correlated ($r_s = + .268$, $N = 18$, $p > .05$). The correlation was for nightime activity and temperature. However, neither were significantly different from zero (night $r = + .34$, $N = 9$, $p > .05$; day $r = + .09$, $N = 9$, $p > .05$).

Two distinguishable cyclic patterns of activity were evident for two groups of turtles. Three large adult turtles had an average of 2.4 days ($\sigma = .74$) of no recorded activity between activity peaks. A total of eight activity peaks was recorded for these turtles. Three small adult turtles had an average of .5 days ($\sigma = .27$) between activity peaks,

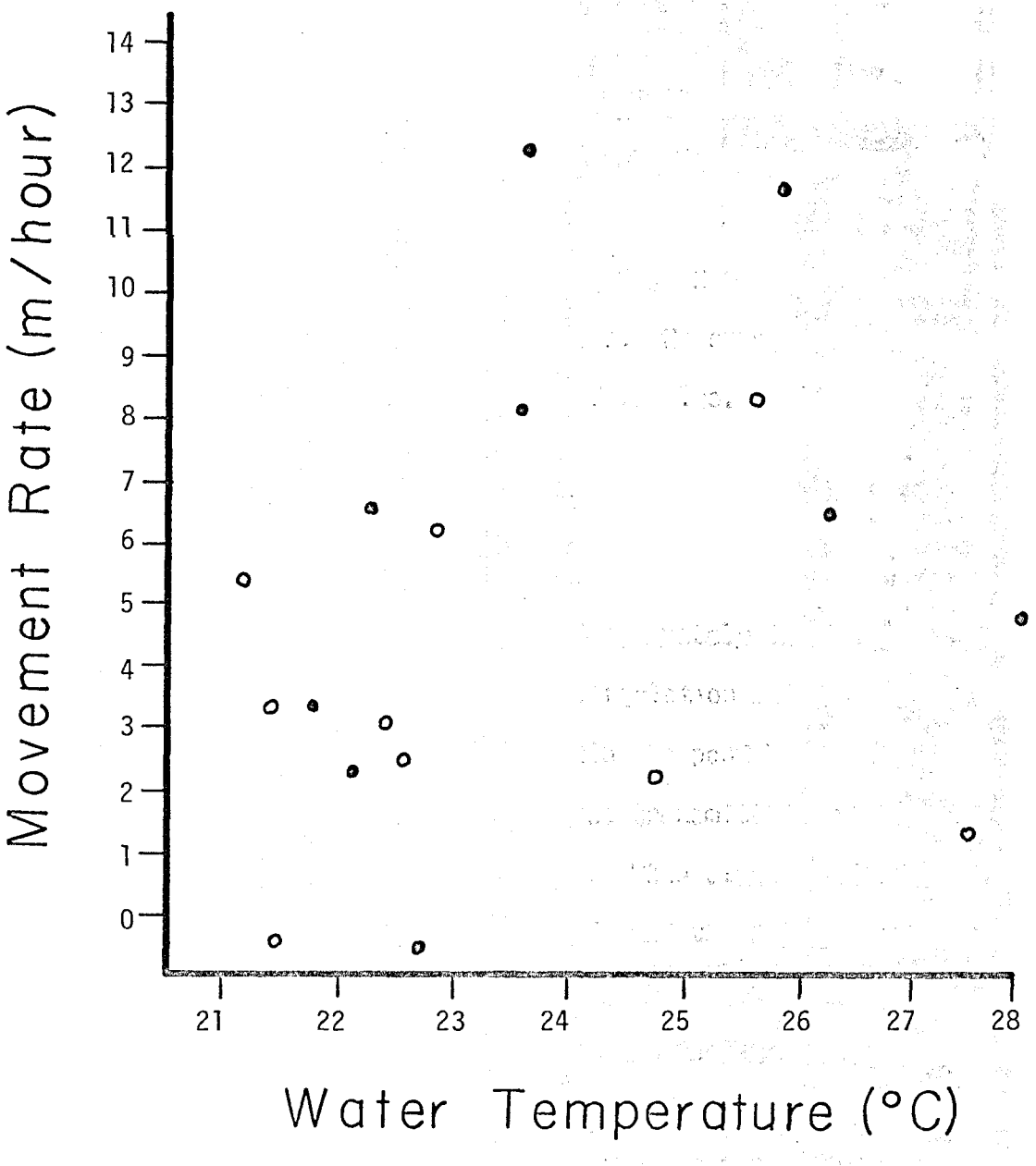


Figure 14. Movement Rates by Temperature. The open circles represent day recordings, and the closed circles represent night recordings.

and a total of 16 such peaks was recorded. Figures 15 and 16 illustrate the two types of activity cycles.

The large animals demonstrating the long periods between activity peaks were all males and had low overall activity rates. The negative correlation between activity rate and size described earlier, is probably produced by less movement during activity bouts and by fewer activity bouts.

One of the small adults was a female. Her activity cycle was similar to those of the two smaller males. No sexual differences could be inferred because of the low number of females.

Discussion

Technique

While the transmitters performed adequately in the pond, locating the animals was inaccurate with the triangulation method. Often triangulated positions failed to fall within the pond boundaries.

Late in fall 1973, I recovered one transmitter by rowing in the direction indicated by the hand antenna. When close to the transmitter, the directional antenna was disconnected, and the receiver was moved above the water surface until the strongest signal was received. After brief probing, I felt the transmitter on the turtle's carapace. The manual location technique was used exclusively following this recovery.

As previously mentioned, the greatly reduced activity rates for spring support the accuracy of the manual location technique. Recovery of the dead turtle, as well as three other accessible turtles, in May 1974 also supported the accuracy of this location technique. All of these

Figure 15. Activity Cycles of Small Adults. The solid blocks in the horizontal broken bar across the bottom indicate times during which all turtle movements were recorded. Each thick, short horizontal bar throughout the graph represents mean movement rates for a four-hour time block for one turtle. Each turtle is identified by different types of lines connecting the bars. M = midnight.

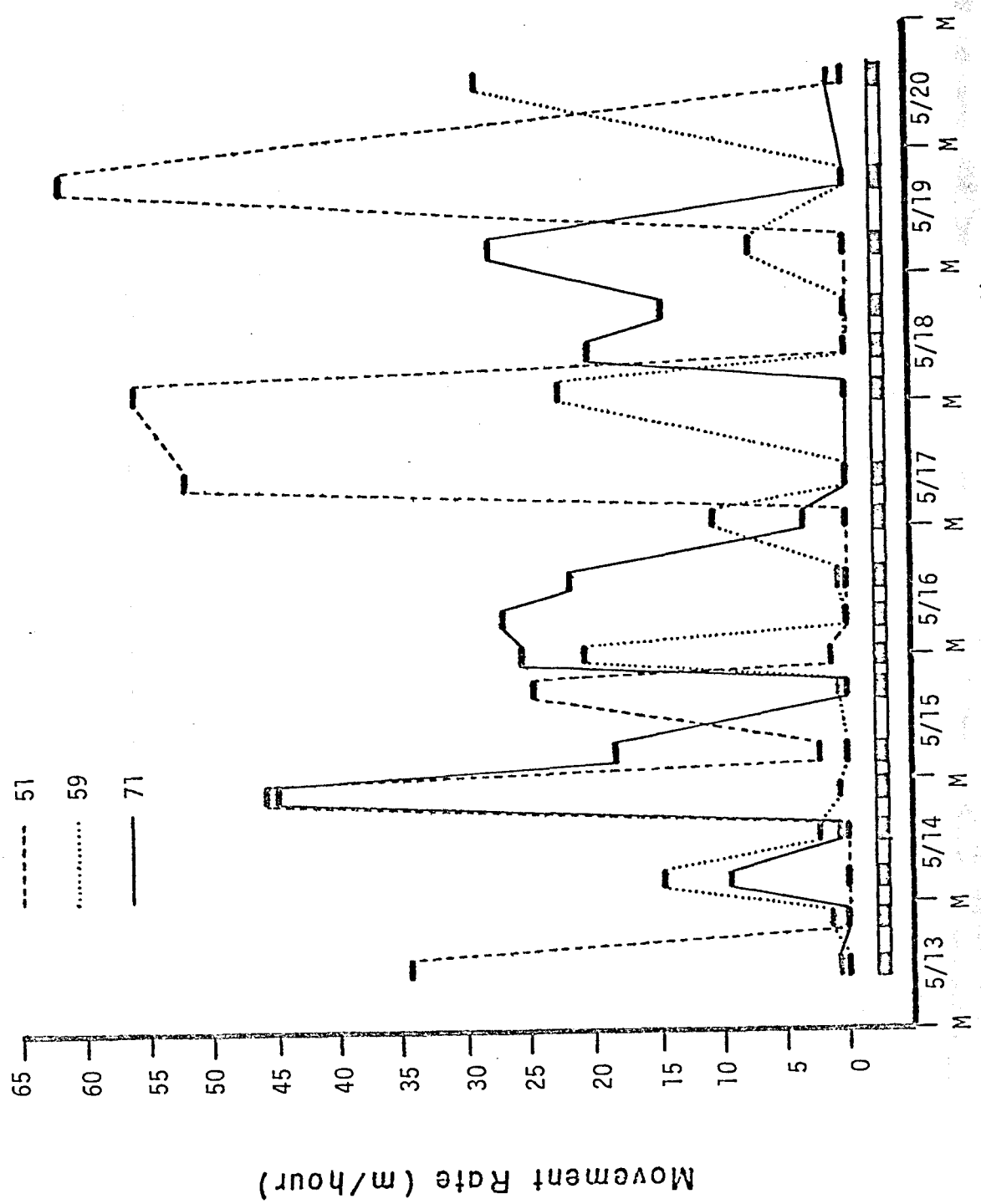

51
59
71
Movement Rate (m/hour)
65
60
55
50
45
40
35
30
25
20
15
10
5
0
5/13 M
5/14 M
5/15 M
5/16 M
5/17 M
5/18 M
5/19 M
5/20 M
Date and Time of Observation

Figure 15

Figure 16. Activity Cycles of Large Adults. The solid blocks in the horizontal broken bar across the bottom indicate times during which all turtle movements were recorded. Each thick, short horizontal bar throughout the graph represents mean movement rates for a four-hour time block for one turtle. Each turtle is identified by different types of lines connecting the bars. M = midnight.

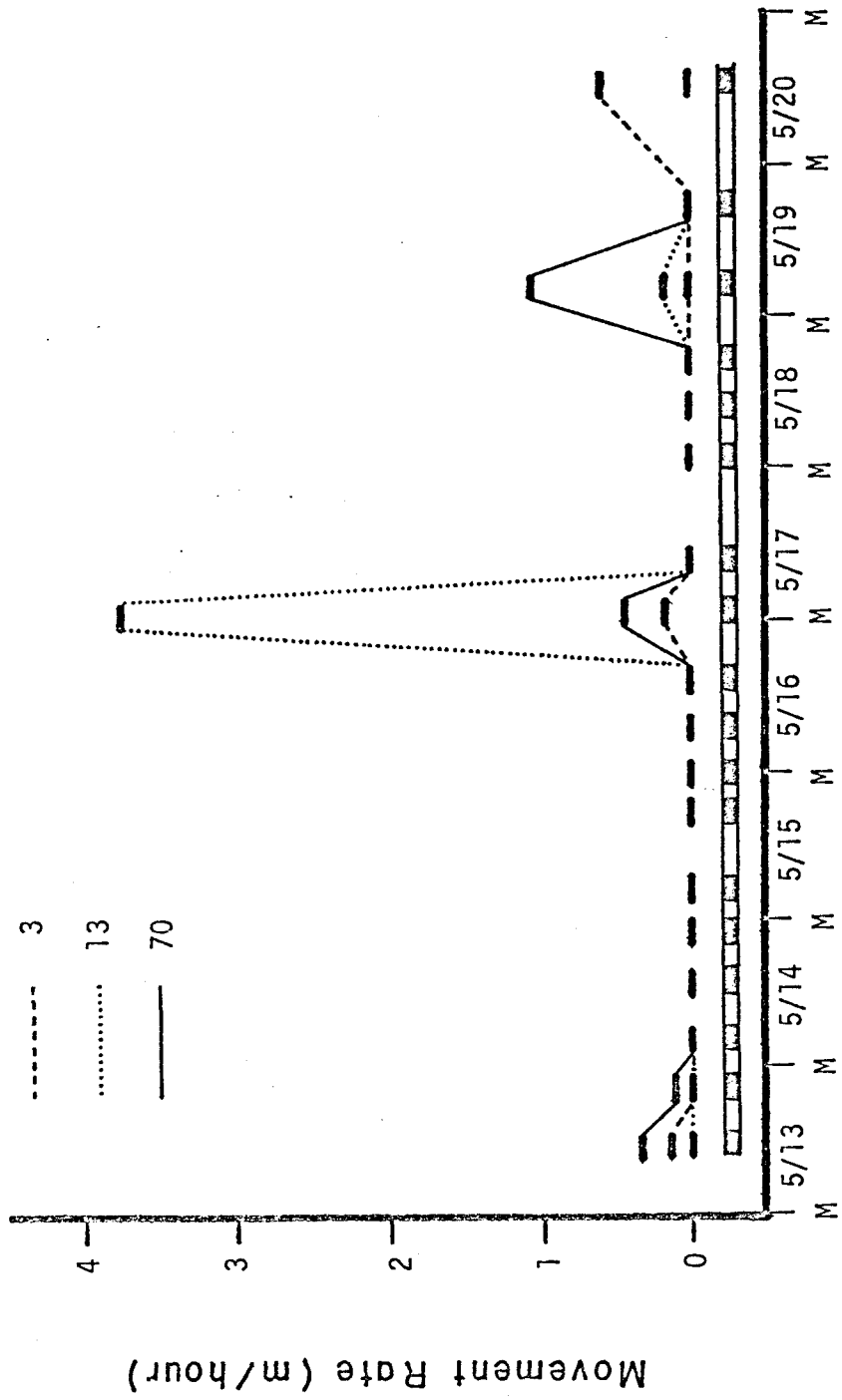

Movement Rate (m/hour)
4
3
2
1
0
3
13
70
5/13 M
5/14 M
5/15 M
5/16 M
5/17 M
5/18 M
5/19 M
5/20 M
Date and Time of Observation

Figure 16

recoveries were made within 1 m of the positions previously recorded on the maps.

These methodological differences indicate that fall and spring activity rates are not directly comparable. However, relative rate differences under various conditions may be compared, provided that recording error was randomly distributed among the turtles. The fall data however, should be considered tentative.

One possible problem with the manual location technique was that I assumed that rowing the boat over a turtle did not alter its normal activity. While this assumption seems reasonable in view of pond depth and turbidity, I cannot guarantee that it is valid.

Activity Rates

As noted above, the differences in mean activity rates between fall and spring have, at most an obscure relationship to seasonal differences in activity. If these rates were indicative of actual movement, the increased fall movement (a season when turtles begin hibernating) and decreased spring movement (a season of emergence and onset of sexual activity) are incongruous. No estimate of error of the telemetry equipment under the conditions of the study was available. Therefore, there was no way of adjusting rates for recording error. If fall movement was lower than spring movement, mean error for fall recordings would be at least seven times greater than actual movement rates (fall $\overline{X}$ = 36.8, spring $\overline{X}$ = 5.3, 36/5.3 = 6.9). This discrepancy suggests the degree of inaccuracy in the triangulation technique with the described equipment.

Turtle activity rates in fall varied from 17.3 to 61.1 m/hour while the range for spring activity rates was .5 to 11.8 m/hour. It is

obvious from the spring data that the turtles did not move excessively. The only other accounts of snapping turtle activity are anecdotal descriptions of the animal as slow, bottom walkers and sluggish (Newman, 1906; Cahn, 1937).

The correlations of size with movement rate for fall and spring are interesting. The fall correlation, however unreliable, is distinctly different from the spring correlation. Turtles followed in fall ranged from 216-310 mm carapace length. This range was greater than for turtles followed in spring (200-273 mm carapace length). The mean size of fall turtles was also greater than for spring turtles. If high activity rates are characteristic of recently matured turtles, those followed in fall may have been a more homogeneous sample than those followed in spring. The difference in range of activity rates, although a weak comparison because of the triangulation problems mentioned earlier, support this hypothesis. Pell (1941) suggested that immature turtles were responsible for dispersion and population of new areas. Hammer (1969) reported immigration of recently matured turtles into his study area. Recent immigration might be accompanied by lack of stability. According to this hypothesis, the longer a turtle remains in a body of water, the more stable that turtle becomes in that habitat. Stability, in this sense, refers to lowered activity rates and greater restriction of movement to specified pond areas. Movement restriction will be discussed further in Chapter III.

White and Murphy (1973) reported differences in the onset of reproductive cycles in different sized snapping turtles. Smaller males become reproductively active later in the season than do larger males.

While the spring recordings in this study may have been relatively early in the season, it is interesting that activity rates did not correspond with presumed activation of the reproductive cycle in males. If reproductive activity is correlated with general activity, larger turtles would be more active than smaller ones. White and Murphy's data suggest that the higher spring activity rates for the smaller turtles in this study were unrelated to sexual activity. Rather, the activity rates may indicate that a larger foraging area is required for the smaller turtles.

While fall and spring correlations of activity rate and temperature were both positive, neither of the correlations were very high. Even during the more active night periods in spring, the correlation accounted for little of the activity rate variability across time. An obvious reason for the low correlations was the attenuated temperature ranges in the samples in relationship to annual temperature fluctuations. However, the spring data indicated that activity remains relatively constant across a range of acceptable ambient temperatures.

Activity Time Preferences

The significant nocturnal increase in activity of fall and spring turtles is in contrast with Murphy and Sharber's (1973) account of no nocturnal/diurnal differences. Murphy and Sharber followed only three turtles, and activity differences would not be clear with such a small sample. My data support earlier anecdotal accounts (Pope, 1939; Brown, 1969) of nocturnal tendencies in the common snapping turtle. The data also support Kiviat's (personal communication) observation of increased activity in the morning and late afternoon. However, contrary to Kiviat's

implication of a bimodal cycle, the present data suggest continued increase in activity in the night, and a decrease towards morning.

The present data extend the accounts of light avoidance in captive adults (Wood, 1953; Lehman, 1966) to field animals. The data also suggest a developmental shift from positive to negative photic orientation sometime following hatching. Noble and Breslau (1938) found positive phototaxis in hatchlings just emerging from the nest. Lehman (1966) replicated this finding, and Wood (1953) related early feeding to the phototaxic shift. Foraging activity induced by hunger could have produced the diurnal activity in my turtles. The pond's extreme turbidity (Froese and Burghardt, In Press) undoubtedly reduced light penetration. Whether bright light plays some role in controlling the activity cycle could be determined by examining field habitats with varying depths and turbidities.

Activity Cycles

Baldwin (1926) and Wood (1953) reported cessation of activity following food ingestion. The large spring turtles demonstrated activity cycles which matched Baldwin's description. Short periods of activity were alternated with long inactive periods. Activity may not be highly correlated with feeding. However, location of several animals facing head first into rock or other dead end "forms" (see Chapter III) indicated that inactive periods may have been incompatible with feeding. The long range activity cycle between turtles may be related to the size and stability differences mentioned earlier. Other factors, like food availability, and dietary differences could have also produced the long range cyclic differences. While no quantitative data were recorded, turtles

inhabited areas of the pond close to aquatic vegetation, places also frequented by the abundant sunfish population. The vegetation, the fish, and other vertebrates and invertebrates are potential food for the turtle (Pell, 1940, 1941; Lagler, 1943; Self, 1938; Coulter, 1957; Hammer, 1969). Food in the pond, therefore, appeared abundant. However, differences in ability to obtain that food, as demonstrated by Froese and Burghardt (1974), may have made different diets available to turtles of various sizes. Depending on bulk of food, available nutrients, ease of digestion, and differential nutritional requirements for growth, such dietary differences could have readily influenced cycles of activity and inactivity. While nutritional requirements for turtles are lower than for warm-blooded and more active animals, this dietary factor could be of significance and should be further investigated.

Summary

Activity rates appear quite variable between turtles. Much of the rate variability, at least for the spring animals, was related to size differences. Larger turtles had lower activity rates, and fewer activity bouts per unit time than did smaller adults. Activity rates were higher during nocturnal than during midday hours. These data support earlier accounts of nocturnal tendencies but continued daytime activity raises further questions concerning light avoidance. Developmental differences in activity cycles between recently matured and larger adults are indicated. However, many correlating factors make a simple developmental interpretation of activity differences difficult. Changes in nutritional requirements with growth, as well as changes in available food may influence both

the nature and duration of activity. Such changes still need documentation.

Discussion of Laboratory and Field Data

Laboratory versus Field

Activity cycles in the laboratory differed markedly from those in the field. Clear diurnal cycles were observed in the laboratory. Onset of darkness corresponded closely with cessation of activity.

The laboratory and field activity cycles appear contradictory. There are, however, several possible explanations for the differences. Turtles from less than one year to almost three years of age were used in the laboratory. This range does not approach that of adult turtles. Therefore, the laboratory and field samples represent distinctly different populations. The laboratory turtles had also been under controlled conditions almost since hatching. Constant alternating 12 hour day/night cycles omitted dawn and dusk gradations of light intensity. Although an attempt was made to approximate natural habitat conditions, major differences included lack of temperature stratification of the water, no living prey, either plant or animal, no cover under which the turtles could hide and a diurnal feeding schedule. Any combination of these, and probably other factors could have altered the activity cycles.

Similarity of the cycles in the recent hatchlings and the juveniles indicated reliability of the effect. The activity cycles were highly dependent on light. This finding is similar to Evans (1940) report of less nocturnal activity in *Chrysemys picta* under laboratory conditions.

Boyer (1965) also indicated that *Chrysemys scripta* basking behavior was highly dependent on light. However, both of these species are diurnal in the field, (Moll and Legler, 1971; Evans, 1940) and their laboratory behavior corresponds with field behavior. In contrast, the snapping turtles showed clear diurnal preferences in the laboratory, while adults in the field were active around the clock, but significantly more active at night.

There are several possible explanations for the above reversal. The laboratory animals could be demonstrating normal activity cycles for their particular age/size class. In this case, some shift in cyclic pattern between juveniles and adults would have to occur. The positive phototaxis of hatchlings (Noble and Breslau, 1938; Lehman, 1966; Norris-Elye, 1949) apparently shifts quickly (Wood, 1953). It is doubtful, therefore, that the laboratory data present an accurate account of daily activity cycles of young snappers.

Captivity may have influenced the activity cycles. The turtles may have habituated to a diurnal feeding cycle. If most activity is for foraging, and if foraging is subject to feedback from time and place cues, a diurnal cycle could have been easily learned.

As suggested in the literature and by the present study, adult snapping turtles, to some extent, avoid light. Bright light could be an aversive stimulus which activates withdrawal. The lack of cover in the laboratory test apparatus may have produced continuous activity of turtles attempting to avoid the light. A preliminary test with the juvenile subjects produced no noticeable activity reversals when a portion of the pool was covered.

The laboratory data definitely indicated the dependence of activity on light conditions. The same appeared to be true of field adults, although the relative periods of activity and inactivity were reversed. Field data on young turtles would assist in clarification of these results.

Activity Estimates from Trap Data

Estimates of activity based on success of trapping appear notoriously poor in view of the results presented above. While evidence for diurnal activity cycles might be obtained through trapping, such a technique assumes a high correlation of activity and the motivational state of hunger. Activity may be more diversely motivated than allowed by this assumption. Also, no trapping techniques could demonstrate the differences in activity rates and cycles between small and large turtles which I observed.

Summary

The laboratory data and the trapping records were of limited usefulness in evaluating activity cycles. Laboratory techniques may be appropriate for evaluation of specific factors controlling the activity cycles. However, such evaluation depends on a clear description of the nature of activity cycles in the field.

Trapping records are not very sensitive to differences in the form of activity cycles between turtles. Use of such records to infer total activity cycles also requires assumptions which are probably not valid. Telemetry techniques have proven most useful in evaluation of activity cycles in snapping turtles.

CHAPTER III

HABITAT UTILIZATION

Differential utilization of various habitats by individuals within a population can spread resources according to requirements and reduce intraspecific competition. Snapping turtles of various sizes are divided into various acceptable microhabitats which may not extensively overlap (Froese and Burghardt, In Press). Moll and Legler (1971) described similar partitioning in *Chrysemys scripta* in Panama.

Utilization and division of space within various age/size classes of turtles is less clear. Lardie (1964) found softshell turtles in separate pools of a stream. He observed that captive specimens were aggressive towards conspecifics. The field spacing and laboratory aggression suggested that these turtles were territorial. Pell (1941) only trapped one turtle in any one area, and he suggested that snapping turtles were territorial. As previously suggested, trapping only provides limited information concerning population parameters. Only extensive trapping could adequately sample population sizes, and spacing would be more difficult to determine than population size. Hammer (1969) captured six turtles in one trap in one night. While refuting Pell's argument, Hammer's data could be consistent with snapping turtle territoriality. The captured turtles could have entered a single trap at different times.

Aquatic turtle home ranges are likely affected by size and shape of the habitat (Moll and Legler, 1971). Hammer (1969) estimated that snapping turtles had home ranges which encompassed most of a single large pool. These pools were waterfowl management areas with about 100 to 250 acres (40 to 101 ha) of turtle habitat (Hammer, 1972). Turtles which were

moved from one pool to another did not tend to remain in the new pool (Hammer, 1972). Ernst (1968) estimated the home range of *C. serpentina* at 4.55 acres (1.88 ha). Ernst did not compare the size of this home range with the acceptable habitat area.

Capture data may be useful for preliminary estimates of turtle movement. However, more information is available by systematically monitoring telemetered subjects (Moll and Legler, 1971). Therefore, I monitored turtle movements to obtain information on space utilization.

Home Sites

Since triangulation was inaccurate, fall data on home sites and home ranges were not analyzed. Turtles repeatedly returned to home sites after periods of activity. They also spent most of their inactive time at home sites.

Home sites were clearly defined for each of the six turtles intensively followed in spring. In addition to these six turtle, four more turtles were tracked between 9 April, 1974 and 13 May, 1974 for varying lengths of time. Therefore, home site data were available for ten turtles. One of these (Turtle 57), however, died shortly after release, and very limited data are available for her. The other three had transmitters which failed just prior to the 13 May, 1974 observation.

Home sites were very small, specific areas along the perimeter of the pond. These home sites are shown for 9 of the 10 turtles in Figure 17. Turtles 12, 13, and 19 used more than one home site.

Time spent at these home sites is shown in Table 10. Percentage of time at the home site was the ratio of relocations at home site/total

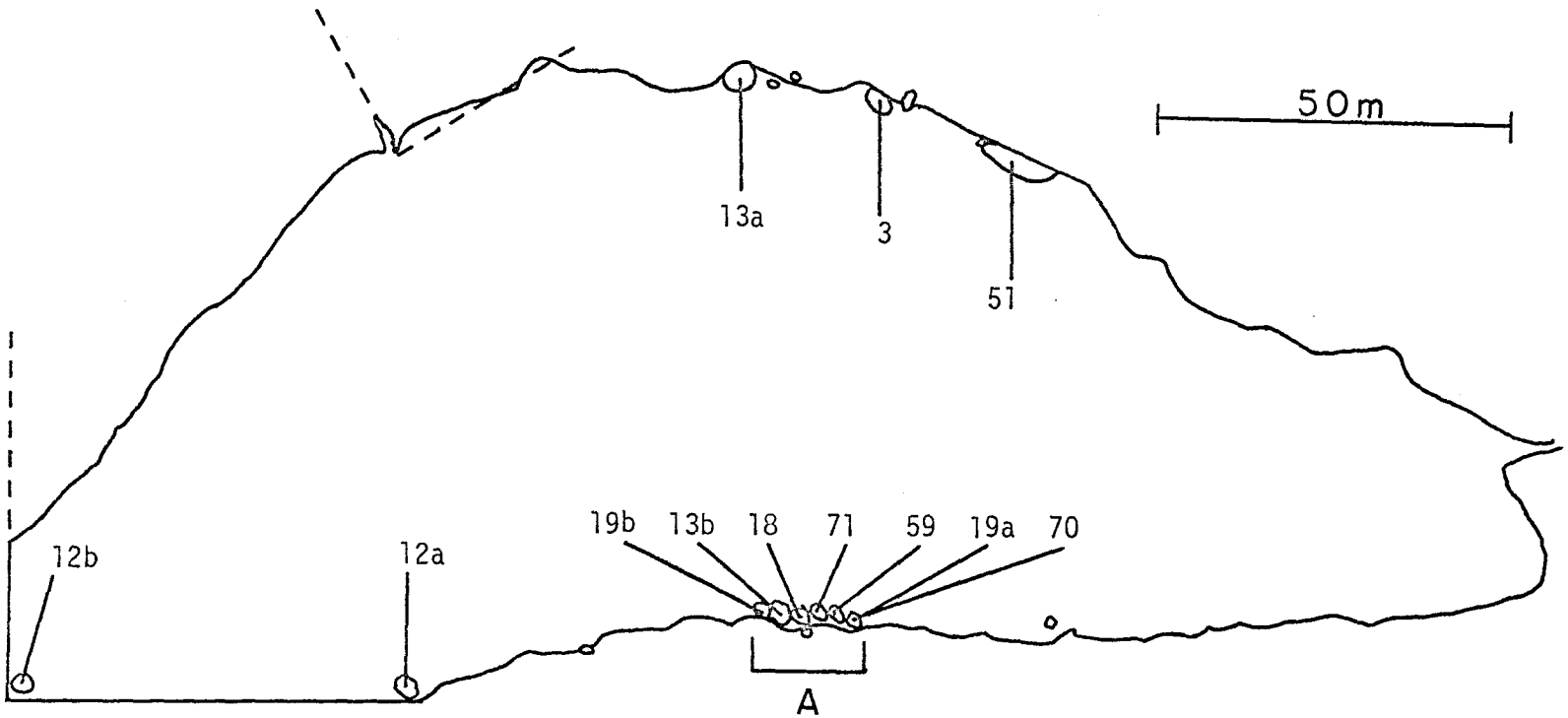


Figure 17. Home Sites for Nine Spring Turtles.

Table 10. Percent of Time at Home Site

Turtle Number	Home Site	Number of Relocations	Number at Home Site	Percent
3		77	68	.88
12	a	7	3	.43
	b		2	.28
13	a	98	62	.63
	b		27	.28
18		21	17	.81
19	a	11	4	.36
	b		4	.36
51		79	48	.61
57	died: no determination of home site possible			
59		86	71	.83
70		79	60	.76
71		74	32	.43

number of relocations. Turtles were relocated at their home sites a mean of 74% of their total relocations. Percentage of time spent at home site was positively correlated with size of the turtle, but the correlation was not significant (r = + .53, N = 9, p > .05).

As already mentioned, home sites were along the perimeter of the pond. These perimeter areas contained boulders, tree roots and bullrushes. A dense concentration of home sites (area A, Figure 17) was found along a portion of the shoreline which contained boulders, large tree roots, and a sharply undercut bank. The underwater cave was supported by large solid

rocks and extended more than 1 m under the bank. A diagram of this bank is shown in Figure 18. Turtles 3 and 51 were recovered from home sites

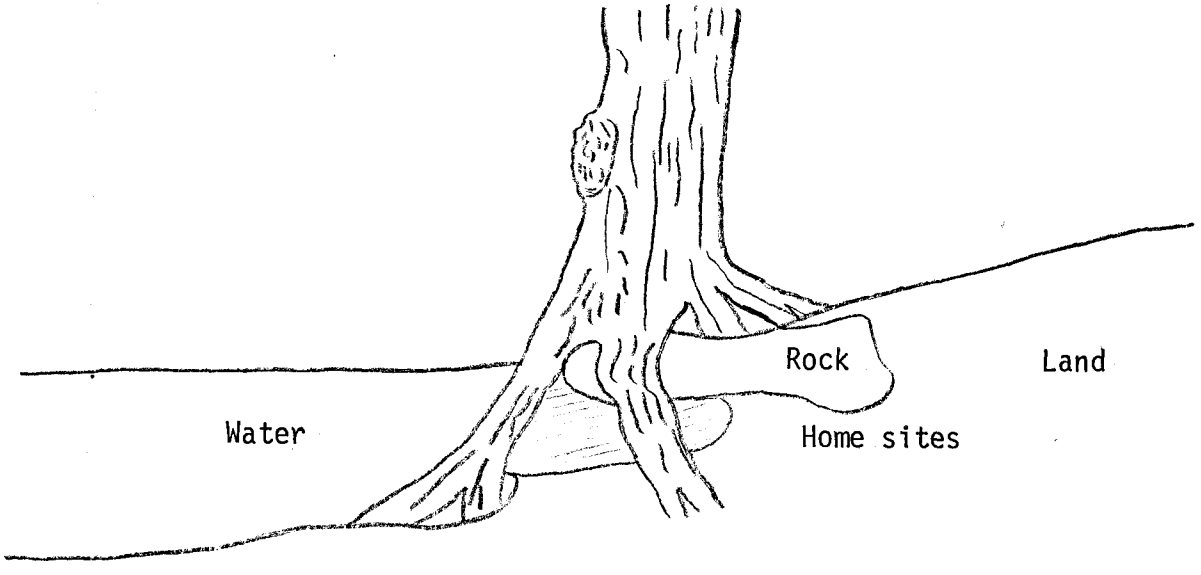


Figure 18. Vertical Cross Section of Undercut Bank.

which were adjacent to large rocks. These rocks were undercut at the bottom. Both turtles were facing the rock. These home site characteristics are remarkably similar to the "forms" described for the terrestrial box turtles (Stickel, 1950).

Home Ranges

Circular or radius based home range calculations were not appropriate because of the irregular pond shape and the suggestion that home ranges are largely determined by the physical characteristics of the habitat (Moll and Legler, 1971). A convex polygon home range was constructed for each turtle.

Convex polygons were constructed by connecting the points of location which included all positions at which the turtle was found. All of the resulting angles were < 180°. Jennrich and Turner (1969) suggested that the convex polygon was a useful technique for determining home range size, although biases due to sample size could be great. To account for sample size biases, Jennrich and Turner constructed tables which indicate the extent of these biases for various small sample sizes. These tables can be used to evaluate home range calculations from convex polygon data when fewer than 25 relocations are recorded. Jennrich and Turner (1969) also introduced a new home range area measurement which was unbiased by sample size. Neither did their measurement require any assumption of circularity of home range. Assumptions included bivariate and normally distributed activity throughout the home range area. Since it is unbiased by low numbers of relocations, this newer area calculation should agree closely with adjusted biased estimates from convex polygon calculations

Results

Home ranges for ten turtles are shown in Figures 19, 20a and 20b. Home range overlap is illustrated in Figure 21. The home range areas, as calculated by convex polygons as well as elipses (Jennrich and Turner, 1969) are shown for the ten turtles in Table 11, page 77. The average convex polygon home range area for all ten turtles was 216.6 m^2, or about 38% of the entire pond area. Home range sizes were quite variable between turtles (range = 3.2 m^2 to 568.9 m^2, or 0.56% to 99% of the pond area). Over all ten turtles, there was little correlation between turtle size and home range size (r = + .18). However, when only the six turtles with

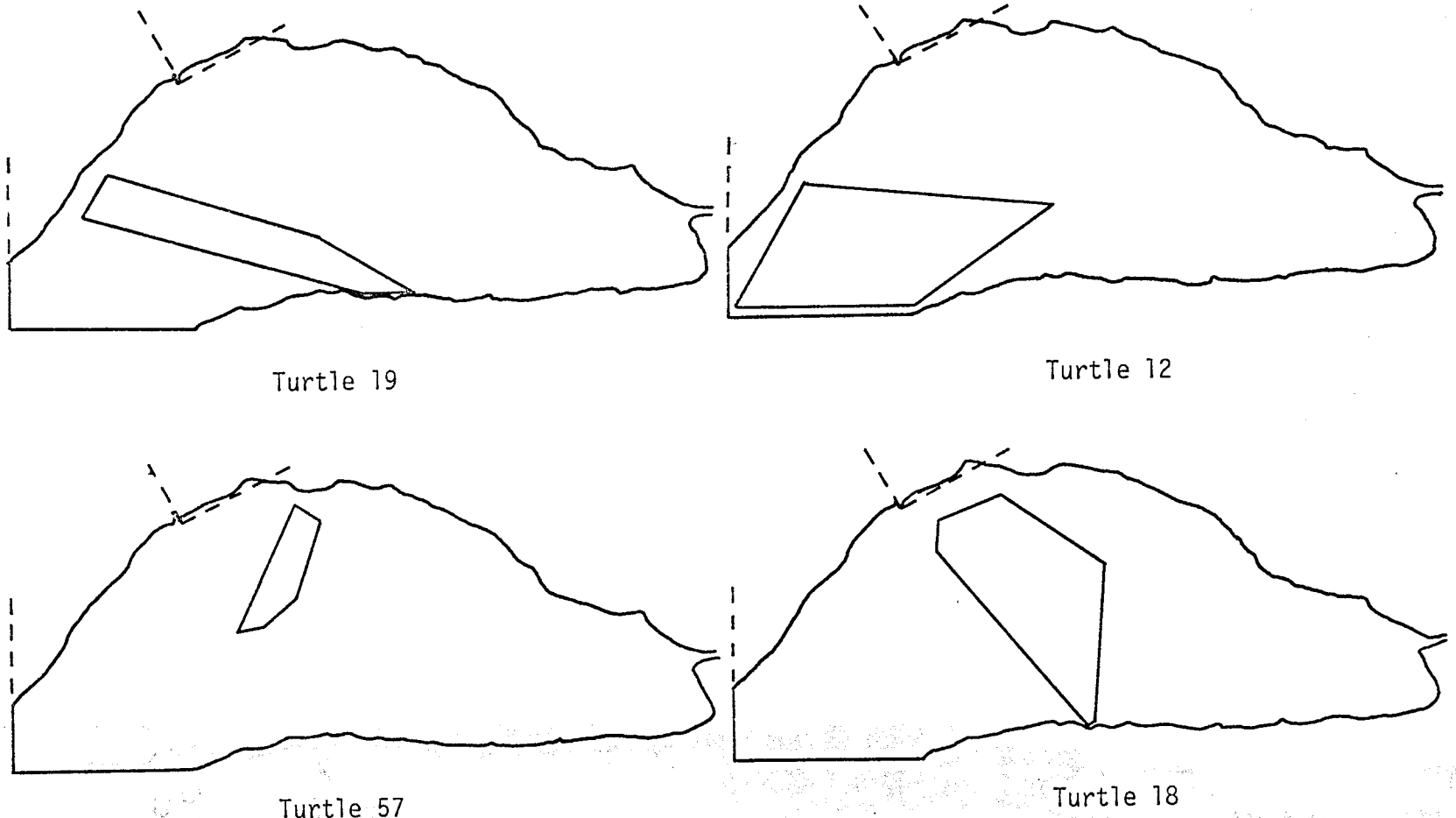
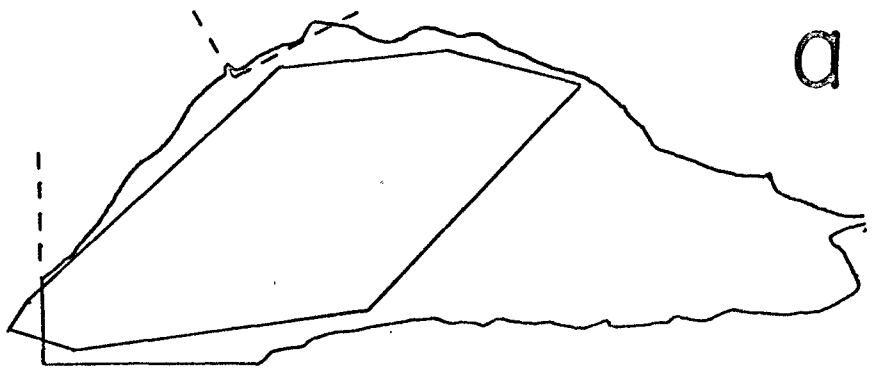
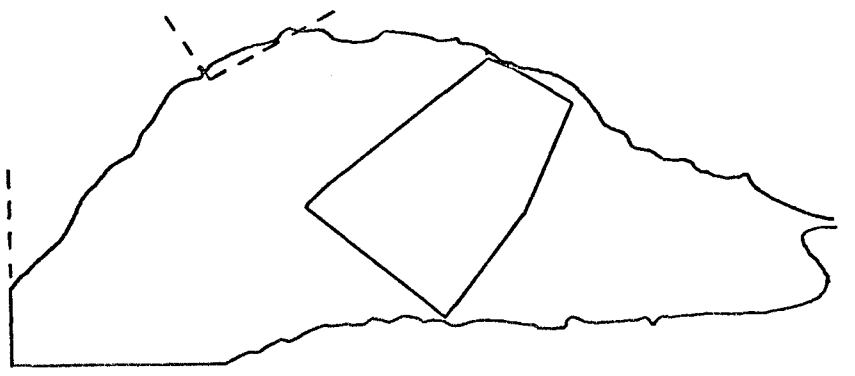


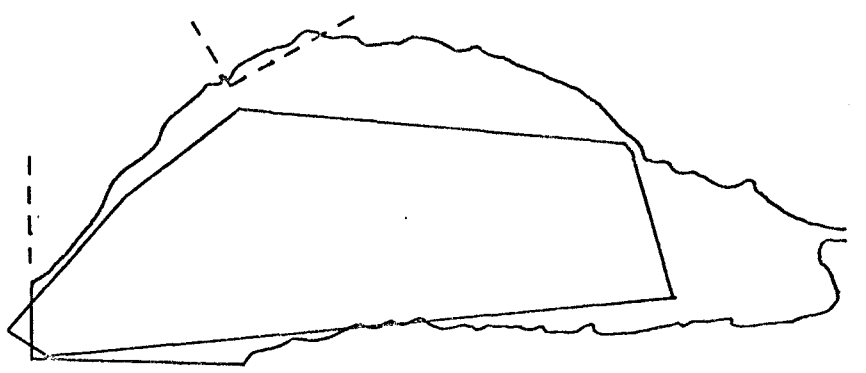
Figure 19. Convex Polygon Home Ranges for Four Turtles with Less than Seventy Relocations.



Turtle 51

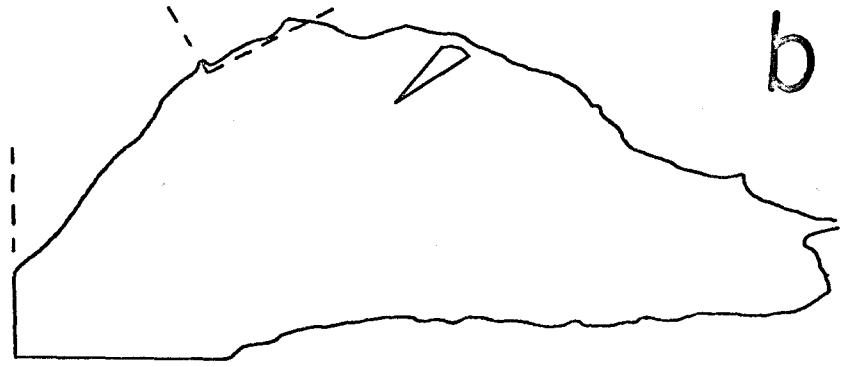


Turtle 59

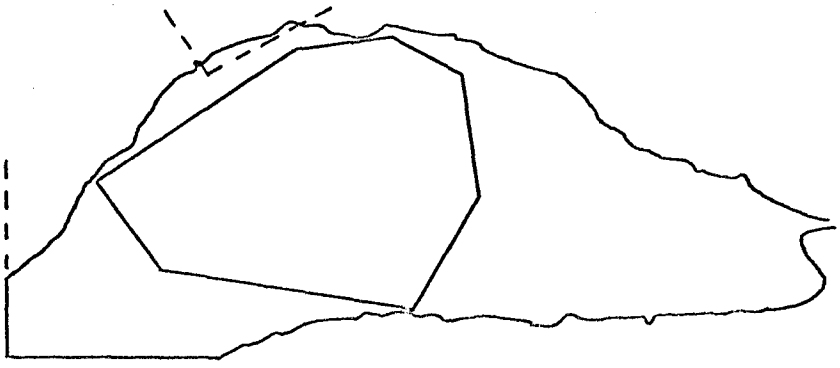


Turtle 71

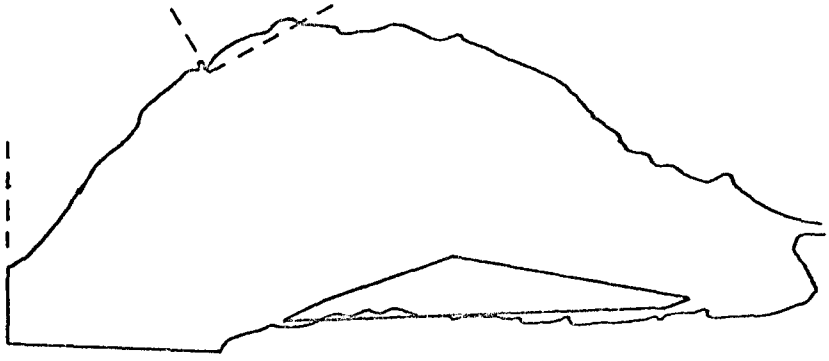
Figure 20. Convex Polygon Home Ranges for Six Turtles with More than Seventy Relocations: (a) Three Small Turtles; (b) Three Large Turtles.



Turtle 3



Turtle 13



Turtle 70

Figure 20 (continued)

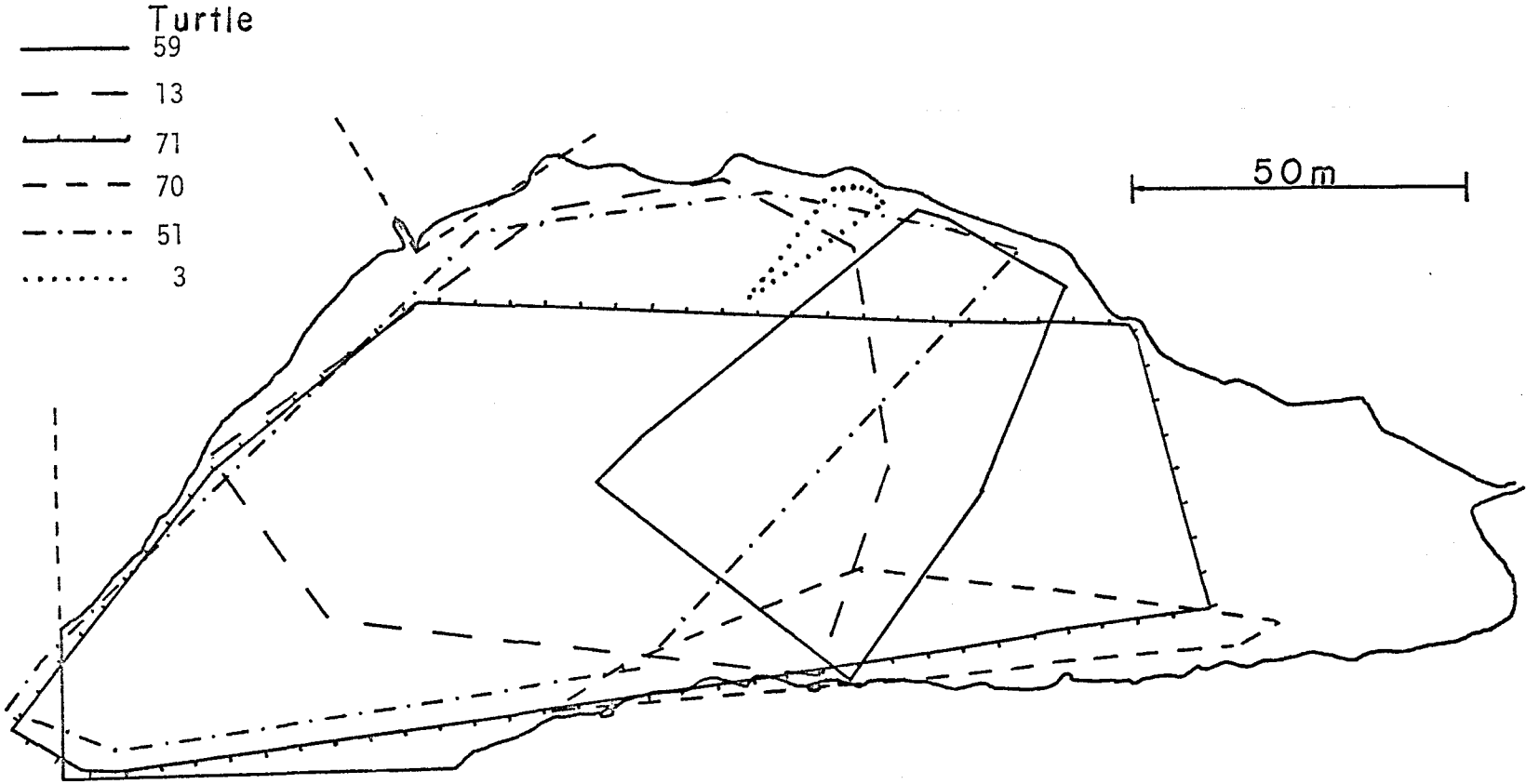


Figure 21. Home Range Overlap of Six Turtles with More than Seventy Relocations.

Table 11. Home Range Sizes of Turtles

Turtle Number	Number of Relocations	Xonvex Polygon Area	Correction Factor (Jennrich and Turner, 1969)	Corrected Estimate	Jennrich and Turner Elipse
3	>70	3.22 m^2	------	------	26.1 m^2
12	7	111.5 m^2	.196	568.9 m^2	1070.1 m^2
13	>70	238.0 m^2	------	------	1231.0 m^2
18	21	91.7 m^2	.468	195.9 m^2	617.4 m^2
19	11	59.5 m^2	.301	197.7 m^2	338.6 m^2
51	>70	299.3 m^2	------	------	1429.6 m^2
57	6	18.0 m^2	.171	105.3 m^2	124.2 m^2
59	>70	114.8 m^2	------	------	656.5 m^2
70	>70	45.6 m^2	------	------	313.0 m^2
71	> 70	397.4 m^2	------	------	1909.0 m^2

extensive relocation records were used, the correlation was negative (r = -.49), although still not significant. For six turtles, home range size was highly correlated with activity rate (r = + .84, p < .05).

Jennrich and Turner's (1969) technique greatly overestimated home range size. The average home range calculated by their method was 771.6 m^2, or 1.34 times the total pond area.

Home ranges overlapped extensively for all turtles. Five of the six turtles with more than 70 relocations had home ranges which overlapped the home ranges of at least four other turtles. It is noteworthy, however, that none of the home ranges extended into a 60 m^2 area on the east side of the pond. In this area, the water was quite shallow, vegetation was abundant, and many hatchling and juvenile snapping turtles could be found.

Discussion

The home ranges of most of the turtles included much of the pond area. Only a brief portion of total annual movement was sampled. Total

times each turtle was followed ranged from six weeks to eight days. Home range sizes were probably underestimated due to the brief recording time and the great amount of inactivity of the turtles (see Chapter II). These data substantiate the idea that home range size is highly habitat determined as suggested by Moll and Legler (1971), at least up to some as yet undetermined maximum.

These large home ranges and their concomitant extensive overlap imply that the turtles do not defend feeding territories. Several turtles (51 and 71 especially) indicated preferences for particular areas which were not home sites (turtles were active in these areas). These areas may have been foraging grounds similar to what Pell (1941) described as feeding territories. Both of these turtles were often found at the west end of the pond.

Much aquatic vegetation grew along the shallow western shore. Although it superficially appeared similar to the habitat on the east shore, no juvenile snapping turtles were ever seen on the western shore, and adults were regular visitors.

The adults may have directly or indirectly competed with the young, and thereby excluded them. Such an explanation, however, does not account for the absence of adults on the pond's east shore. Prevailing winds were from the west. It is possible that the wind affected the position of the young (drifting on moss), or influenced the habitat sufficiently to produce spatial isolation of young and adult turtles. The adults may have had a difficult time moving through the heavy moss characteristic of the east shore. Such spatial isolation would reduce competition between conspecifics and would protect young from being directly consumed by the adults.

The variety of techniques of estimating home ranges make comparisons between estimates very difficult (Jennrich and Turner, 1969). Jennrich and Turner's tables for comparing various calculated home range sizes are valuable. However, their new technique is not a panacea for area calculation problems. First, their model assumes that activity within the home range is distributed in a bivariate normal fashion from a high activity center, and decreasing activity away from the center (Turner, 1971). While such a distribution may hold for some animals, the turtles in the present study did not follow such a bivariate normal distribution. Metzgar (1972) warned that home range data from populations not conforming to the bivariate normal distribution should be cautiously used in comparisons, and then only when similar techniques, data, and sample sizes are used.

Jennrich and Turner's (1969) model does not adequately estimate large home ranges within restricted areas. Van Winkle, Martin, and Sebetich (1973) discussed this problem in relationship to ecotones, or zones of juxtaposition of two ecosystems. Probabilistic models, including that of Jennrich and Turner (1969) often fail to account for movement within heterogenous habitats. The pond boundaries can be viewed as an ecotone with a sharp juxtaposition and little intergradation of ecosystems. Home ranges are limited by these ecotonal zones. Since home ranges include much of the available habitat, estimates based on a model which assumes a large homogeneous habitat would be unduly large.

Calculation of home ranges of snapping turtles may still indicate dependencies of movement on environmental features. Home range maps may also indicate adaptive strategies for species survival, such as the apparent spatial isolation between young and adult turtles.

Although the home ranges were large, the turtles consistently returned to one or more home sites after extensive activity. Turtles appeared familiar with the various parts of the pond. Returning to home sites by the snapping turtles parallels accounts of homing ability (Moll and Legler, 1971; Williams, 1952) for other species. Returning to home sites was probably dependent on habitat familiarity rather than some general orientation processes (Gibbons and Smith, 1968).

Pond familiarity is adaptive when the turtles are threatened. Turtle 51 was in the mud in very shallow water on the west shore of the pond on 20 May, 1974. Since one turtle had recently been found dead, I was checking the condition of other accessible turtles. When I discovered the turtle, he moved out of the mud and moved along the bottom in a straight line towards his home site, over 150 m away. I followed this turtle in the shallow water for about 30 m, and several times, I turned him around with my paddle. His immediate reaction was again to turn towards his home site. When I next checked his position about 40 minutes later, he was at the home site, adjacent to a rock. I again disturbed him. However, he did not move from the home site following this disturbance. Other located turtles (Turtles 3 and 13) also did not move from home sites when physically disturbed. The home site, therefore, appears to be a portion of the home range offering protection.

Conspecific Dependent Movement

Movement of the turtles in response to conspecifics is important in evaluating social behavior of the species. I am convinced that even without aggressive encounter, turtles respond, under certain conditions,

to the close proximity of a conspecific. I once observed an adult turtle move under a rock very close to me. Within seconds, an immature snapper swam rapidly out of the same rock overhang. It appeared that the small turtle had been displaced by the larger one.

It is incongruous to look at the distribution of home sites and suggest that any large individual distance is maintained between conspecifics. Home site characteristics and the manner in which they are utilized however, may maintain the isolation of individuals despite close proximity to conspecifics. These features include: 1) the head first positioning in "forms," 2) the characteristics of a soft thick mud substrate, and 3) relative darkness of an undercut bank or an overhanging rock. Therefore, although physically very close, home sites may be perceptibly quite isolated.

Contrary to the low frequency of conspecific contacts suggested by Brattstrom (1974), the home range overlaps, dense clustering of home sites, and dense population in general, would permit high frequencies of such contacts. The behavior of turtles during such contacts would shed much light on the nature of social organization in snapping turtles.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Summary

In the preceding studies, I have gathered information on movement patterns and use of space in snapping turtles in the laboratory and field. Turtles in the laboratory preferred areas containing rock obstructions over open areas. They also demonstrated consistent diurnal activity patterns. Turtles in the field preferred habitats similar to those preferred by turtles in the laboratory. However, these turtles were more active at night. While the reasons for the differences between laboratory and field data are not clear, several possibilities include: 1) developmental differences, 2) habitat structural differences, or 3) the direct effects of captivity since hatching, and the possible training of activity cycles by feeding schedules. Such differences indicate caution in constructing laboratory simulations. However, habitat preferences were similar in the laboratory and in the field. This suggests the usefulness of laboratory studies if relevant aspects of the habitat are known to be similar to field situations (see Box, 1973). As in research on other animals (Mason, 1968; Hall, 1968), such a laboratory-field integration increases the scope of behavioral studies, and provides for the experimental manipulation of many variables affecting the animals.

In addition to the laboratory and field comparisons, field data on activity rates, activity cycles, and home ranges were obtained. Turtles had highly variable activity rates. Much of this variability was

related to turtle size. Larger turtles were less active than smaller ones.

Larger turtles remained inactive for longer periods than smaller turtles, and when active their movement generally showed lower peaks than the smaller turtles. Such differences suggest that large turtles could be easily underrepresented in population density and structure estimates. Ream and Ream (1966) indicated difficulties in estimating the population structure of *Chrysemys picta* due to habitat and capturability differences between turtles of different sizes. The present data extend such size class differences, and related problems of differential capture to adult turtles as well as the various sub-adult classifications.

The differences between activity rates of large and small adult turtles stand in contrast to Murphy and Sharber's (1973) conclusion of no individual differences in their three telemetered turtles. It is likely that the low number of turtles they followed influenced their conclusion. They also did not report the sizes or sexes of their turtles.

Little evidence for territoriality was found in the present study. Home ranges overlapped extensively. However, each turtle had at least one home site to which it repeatedly returned. These home sites were heavily concentrated in particular pond areas. Whether home sites were defended from intruders could not be determined. However, I reported some evidence for conspecific competition.

Approaches to the Study of Reptilian Social Behavior

The behavior of reptiles remains one of the major gaps in our knowledge of social behavior and organization (Box, 1973). Social

organizational patterns are highly variable between and within species. While such patterns are not subject to strict evolutionary processes (Crook, 1968), they are indicative of the evolution of certain adaptations in signal, and receiver systems of the animals (Barash, 1974). Social organizational patterns, therefore, may provide clues to specific animal adaptations, as well as to plasticity of the organism under various environmental conditions.

Reptiles have certain characteristics which make them difficult subjects for behavioral research. Brattstrom (1974) has referred to two such general characteristics: 1) they are not easily observed, 2) there is a "phylogenetic orientation" which limits the kind of behaviors to which investigators are sensitive. It is probably easier for Lorenz (1974) to defend his use of "marriage" and "divorce" in birds than to do the same for any reptile. In fact, Lorenz (1974) specifically indicated biased assumptions concerning reptiles in his statement that ". . . the last common ancestors of birds and mammals were lowest reptiles with minute brains and certainly incapable of any complicated social behavior . . . ." Lack of good information should never be interpreted as lack of a particular characteristic of the animal. Brattstrom (1974) pointed out that lack of complexity in many studies of reptilian social behavior has in part been due to unrealistic testing temperatures. Brattstrom (1974) reveals his own bias concerning reptiles in the statement "Social behavior is most complicated *or perhaps only best observed and studies* in the conspicuous diurnal lizards and in a few nocturnal lizards in laboratory studies" (italics mine).

Many researchers are biased by a tendency to confirm pre-existing principles in new species. If social organization patterns do not fit a "territorial" or a "hierarchical" model, researchers often conclude that the species is unsocial. It is quite clear that territories often intergrade with hierarchies under certain conditions (Brattstrom, 1974). The continuum may extend the other direction as well, so that under certain conditions (e.g., very low densities) territories may not be evident from any data. The investigator, therefore, must manipulate or find the conditions under which the organizational patterns shift, rather than draw conclusions concerning the presence or absence of social organization.

Conclusions

One of the important findings in the present research is the great variability and flexibility expressed in activity cycles, home ranges, and acceptable habitats. This variability helps explain contradictory accounts in the literature concerning nocturnal and diurnal activity (Pope, 1939; Wood, 1953; Lehman, 1966; Murphy and Sharber, 1973) and home range size (Hammer, 1969; Ernst, 1968; Pell, 1941).

Snapping turtles are apparently adapted to a wide range of aquatic habitats. Other turtles have been described as opportunists with regard to feeding (Moll and Legler, 1971). The snapping turtle is an opportunist with regard to general habitat utilization. The adaptations to widely divergent habitats might lead to differentiation and eventual speciation of the snapping turtle. However, such speciation would require long term isolation in a rather divergent habitat. The known migration of these turtles (Brumwell, 1951; Barbour, 1950; Klimstra, 1951; Newman, 1906;

Cahn, 1937; Cagle, 1944) and the dispersion of young and recently matured adults (Pell, 1941; Hammer, 1969) would work against such isolation.

An interesting finding was that turtles in the field tolerated dense aggregations in other than the winter hibernation sites. This aggregation along with the high population density in the study pond (Froese and Burghardt, In Press), refute the idea that snapping turtles rarely meet (Brattstrom, 1974). Rather, encounters could be quite numerous. However, temporal and spatial isolation could be enhanced by differences between turtles in habitat preferences, activity cycles, home sites, and home range sizes. Such isolation is also enhanced by habitat characteristics such as water turbidity and obstructions. The effects of such isolating factors in reducing competition require further clarification.

Since the snapping turtle is known for its aggressiveness towards men and conspecifics (Evans, 1952; Raney and Josephson, 1954; Hammer, 1969) some mechanisms for reducing competition are expected. Abundant food could be a variable reducing aggressiveness. However, competition for space (home sites) must occur at times since home sites are stable, and heavily concentrated. There is some evidence for different microhabitat selection in juvenile and adult turtles. Such spatial isolation undoubtedly reduces competition between turtles of various sizes. However, within a group of turtles of similar size, various signals or protective behaviors could reduce direct competition. Mertens (1946) and Legler (1955) described postures in the snapping turtle which might serve such functions. I have also observed lateral displays, consisting of tilting the carapace towards the conspecific, in the laboratory. Further evaluation

of these postures and other behavioral patterns will help fill the gaps which now exist in our knowledge of reptilian social behavior.

LIST OF REFERENCES

LIST OF REFERENCES

Anderson, P. 1965. The reptiles of Missouri. Univ. Missouri Press, Columbia.

Auffenberg, W. 1966. On the courtship of *Gopherus polyphemus*. Herpetologica 22:113-117.

Baldwin, F. M. 1926. Notes on oxygen consumption in turtles, *Chrysemys marginata belli* and *Chelydra serpentina* Linn. Proc. Iowa Acad. Sci. 33:315-323.

Barash, D. P. 1974. The evolution of marmot societies: A general theory. Science 185:415-420.

Barbour, R. W. 1950. The reptiles of Big Black Mountain, Harlan County, Kentucky. Copeia 1950:100-107.

Box, H. O. 1973. Organization in animal communities. Butterworths, London.

Boyer, D. R. 1965. Ecology of the basking habit in turtles. Ecology 46:99-118.

Brattstrom, B. H. 1974. The evolution of reptilian social behavior. Amer. Zool. 14:35-49.

Brown, R. 1969. Snapping turtles. Herpetology 3:9-12.

Brumwell, M. J. 1951. An ecological survey of the Fort Leavenworth Military Reservation. Amer. Midl. Natur. 45:187-231.

Bury, R. B. 1973. Aggression in free-living pond turtles (*Clemmys marmorata*). BioScience 23:659-662.

Cagle, F. R. 1944. Home range, homing behavior, and migration in turtles. Misc. Pub. Mus. Zool. Univ. Mich., No. 61, Nov. 21, 3-37.

Cahn, A. R. 1937. The turtles of Illinois. Illinois biol. Monogr. 16:4-217.

Carr, A. 1952. Handbook of turtles. Cornell Univ. Press, Ithaca, New York.

Clark, H. W., and J. B. Southall. 1920. Fresh-water turtles: A source of meat supply. Bureau of Fisheries Document No. 889, Govt. Printing Office, Washington.

Conant, R. 1958. A field guide to reptiles and amphibians. Houghton Mifflin Co., Boston.

Coulter, M. W. 1957. Predation by snapping turtles upon aquatic birds in Maine marshes. J. Wildl. Manage. 21:17-21.

Crook, J. H. 1968. The nature and function of territorial aggression, p. 141-178. *In*: M. F. A. Montagu [ed.] Man and aggression. Oxford Univ. Press, New York.

Crook, H. H. 1970. Social organization and the environment: Aspects of contemporary social ethology.. Anim. Behav. 18:197-209.

Davis, J. D., and C. G. Jackson, Jr. 1970. Copulatory behavior in the red-eared turtle, *Pseudemys scripta elegans* (Wied). Herpetologica 26:238-260.

Davis, J. D., and C. G. Jackson, Jr. 1973. Notes on the courtship of a captive male *Chrysemys scripta taylori*. Herpetologica 29:62-64.

Dolbeer, R. A. 1969. A study of population density, seasonal movements and weight changes, and winter behavior of the eastern box turtle, *Terrapene c. carolina* L., in eastern Tennessee. Master's thesis, Univ. Tennessee, Knoxville.

Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran. 1972. The relation between ecology and social structure in primates. Science 176:863-874.

Ernst, C. H. 1968. A turtle's territory. Int. Turtle and Tortoise Soc. J. Nov.-Dec.:9, 34.

Ernst, C. H., and H. F. Hamilton. 1970. Color preferences of some North American turtles. J. Herpetol. 3:176-180.

Etkin, W. 1964. Co-operation and competition in social behavior, p. 1-34. *In*: Etkin [ed.] Social behavior and organization among vertebrates. Univ. Chicago Press, Chicago.

Evans, L. T. 1940. Effects of light and hormones upon the activity of young turtles, *Chrysemys picta*. Biol. Bull. 79:370-371.

Evans, L. T. 1952. Endocrine relationships in turtles III. Some effects of male hormone in turtles. Herpetologica 8:11-14.

Froese, A. D., and G. M. Burghardt. 1974. Food competition in captive juvenile snapping turtles, *Chelydra serpentina*. Anim. Behav. 22:734-739.

Froese, A. D., and G. M. Burghardt. 1974. A dense natural population of the common snapping turtle (*Chelydra s. serpentina*). Herpetologica, In Press.

Gibbons, J. W., and M. H. Smith. 1968. Evidence of orientation by turtles. Herpetologica 24:331-333.

Gibbons, J. W., and D. W. Tinkle. 1969. Reproductive variation between turtle populations in a single geographic area. Ecology 50:340-341.

Grant, C. 1936. Breeding of *Pseudemys elegans* in California and notes on other captive reptiles. Copeia 1936:112-113.

Hall, K. R. L. 1968. Experiment and quantification in the study of baboon behavior in its natural habitat, p. 120-130. *In:* P. C. Jay [ed.] Primates. Holt, Rinehart and Winston, New York.

Hammer, D. A. 1969. Parameters of a marsh snapping turtle population Lacreek Refuge, South Dakota. J. Wildl. Manage, 33:995-1005.

Hammer, D. A. 1971. The durable snapping turtle. Nat. Hist. 80(6):58-65.

Hammer, D. A. 1972. Ecological relations of waterfowl and snapping turtle populations. Ph.D. Dissertation. Utah State Univ., Logan. 72p.

Jackson, C. G., Jr., and J. D. Davis. 1972a. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Wied). Herpetologica 28:58-64.

Jackson, C. G., Jr., and J. D. Davis. 1972b. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972:385-387.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. J. theoret. Biol. 22:227-237.

Kiviat, E. 1974. Measuring, sexing and marking common snapping turtles. Pers. commun.

Klimstra, W. D. 1951. Notes on late summer snapping turtle movements. Herpetologica 7:140.

Kruuk, H. 1972. The spotted hyena: A study of predation and social behavior. Univ. Chicago Press, Chicago.

Lagler, K. F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. Amer. Midl. Natur. 29:257-312.

Lardie, R. L. 1964. Pugnacious behavior in the softshell *Trionyx spinifer pallidus* and implications of territoriality. Herpetologica 20:281-284.

Legler, J. M. 1955. Observations on the sexual behavior of captive turtles. Lloydia 18:95-99.

Lehman, H. D. 1966. Daten zur Fortpflanzung von *Chelydra serpentina* in Gefangenschaft. Salamandra 2:1-5.

Leyhausen, P. 1965. The communal organization of solitary mammals. Sym. Zool. Soc. London 14:249-263.

Lorenz, K. Z. 1974. Analogy as a source of knowledge. Science 185:229-234.

Marchand, L. J. 1944. Notes on the courtship of a Florida terrapin. Copeia 1944:191-192.

Mason, W. A. 1968. Naturalistic and experimental investigations of the social behavior of monkeys and apes, p. 398-419. *In:* P. C. Jay [ed.] Primates. Holt, Rinehart and Winston, New York.

Mertens, R. 1946. Die Warn-und Droh-Reaktionen der Reptilien. Ahbandlungen der Senckenbergischen Naturforschenden Gesellschaft. Abh. 471:1-104.

Metzgar, L. H. 1972. The measurement of home range shape. J. Wildl. Manage. 36:643-645.

Moll, E. O., and J. M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles Co. Mus. Nat. Hist. No. 11, p. 1-102.

Murphy, G. G., and J. F. Sharber, Jr. 1973. Preliminary analysis of activity of the common snapping turtle, *Chelydra serpentina*, as determined by biotelemetry. J. Tenn. Acad. Sci. 48:56.

Newman, H. H. 1906. The habits of certain tortoises. J. comp. Neurol. Physiol. 16:126-152.

Noble, G. K., and A. M. Breslau. 1938. The senses involved in the migration of young fresh-water turtles after hatching. J. comp. Psychol. 25:175-193.

Norris-Elye, L. T. S. 1949. The common snapping turtle (*Chelydra serpentina*) in Manitoba. Can. Field-Naturalist 63:145-147.

Pell, S. M. 1940. Notes on the food habits of the common snapping turtle. Copeia 1940:131.

Pell, S. M. 1941. Notes on the habits of the common snapping turtle, *Chelydra serpentina* (Linn.) in Central New York. M.S. thesis. Cornell University, Ithaca, New York. p. 1-85.

Pope, C. H. 1939. Turtles of the United States and Canada. Alfred A. Knopf. New York.

Pough, F. H. 1970. A quick method for permanently marking snakes and turtles. Herpetologica 26:428-430.

Raney, E. C., and R. A. Josephson. 1954. Record of combat in the snapping turtle, *Chelydra serpentina*. Copeia 1954:228.

Ream, C., and R. Ream. 1966. The influence of sampling methods on the estimation of population structure in painted turtles. Amer. Midl. Natur. 75:325-338.

Self, J. T. 1938. Note on the food habits of *Chelydra serpentina*. Copeia 1938:200.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

Stickel, L. F. 1950. Populations and home range relationships of the box turtle. Ecol. Monogr. 20:353-378.

Taylor, E. H. 1933. Observations on the courtship of turtles. Univ. Kansas Sci. Bull. 21:269-272.

Turner, F. B. 1971. Estimating lizard home ranges. Herp. Review 3:77.

Van Winkle, Jr., W., O. C. Martin, and M. J. Sebetich. 1973. A home-range model for animals inhabiting an ecotone. Ecology 54:205-209.

Weaver, Jr., W. G. 1970. Courtship and combat behavior in *Gopherus berlandieri*. Bull. Florida State Mus. 15:1-43.

White, J. B., and G. G. Murphy. 1973. The reproductive cycle and sexual dimorphism of the common snapping turtle, *Chelydra serpentina serpentina*. Herpetologica 29:240-246.

Williams, J. E. 1952. Homing behavior of the painted turtle and musk turtle in a lake. Copeia 1952:184-186.

Wood, J. T. 1953. Protective behavior and photic orientation in hatchling snapping turtles, *Chelydra serpentina serpentina* (Linne), in an aquatic environment. J. Elisha Mitchell Sci. Soc. 69:54-59.

Yahner, R. H. 1974. Weight change, survival rate and home range change in the box turtle, *Terrapene carolina*. Copeia 1974:546-548.

APPENDIX

Table 12. Identification of Juvenile and Hatchling Turtles Used in Experiment

Turtle Number	Carapace length	Carapace width	Plastron length	Plastron width	Posterior Lobe	Pre-Cloacal	Weight
	mm						grams
Juvenile Turtles (hatched August, 1971							
March 1973							
1	66		52			19	113.4*
2	65		49			22	102.6*
3	59		48			18	101.4*
4	68		55			21	112.1*
5	61		49			19	88.8*
6	60		47			17	79.8*
7	60		48			21	98.1*
8	55		43			14	61.0*
9	59		44			15	73.7*
April 1974							
1	81	69.5	61	30	31.3	27	129.9
2	79	66	57.5	29	29	27	119
3	79	69	61	34	32.5	25.5	135.6
4	85.3	75	67	33.5	32.5	29	159.1
5	78	63.8	59.3	28	30	25.5	117
6	78.3	66	60.5	29.8	29.5	25.3	116.4
7	80	69.5	61.8	31.3	31	26.8	142.9
8	69	59	53	26.5	25.5	20.5	79.2
9	75.5	62	54.8	28.5	28	22.5	100.2
Hatchling Turtles (hatched September 1973)							
October 1973							
1	30	27	20	12	10.5	7.5	7
2	30	28	20.5	11.5	10.5	8	6.9
3	30.3	30	20.5	13	10.5	9	7.3
4	31	28.7	20.8	12.2	10.5	9.7	7.1
5	31.5	30	21.5	14	11	9	7.9

*Weighed July 1972.

Table 13. Identification of Field Turtles Used in Experiment

Turtle Number	Capture Date	Carapace length	Carapace width	Plastron length	Plastron width	Posterior Lobe	Pre-Cloacal	Weight
		mm						kg
				Fall 1973				
13	9/20	255	225	190	98	95	110	4.42
18	10/11	310	248	212	112	104	130	6.01
37	9/5	292	267	209	114	105	130	6.15
43	9/20	225	205	180	93	90	69	3.40
50	10/10	216	181	152	83	74	81	1.98
				Spring 1974				
3	5/8	273	232	189	110	88	125	4.76
12	4/16	303	258	222	125	103	135	6.35
13	3/30	275	235	188	98	90	115	3.97
18	4/6	318	255	211	113	114	135	6.15
19	4/16	233	194	162	100	80	82	2.72
51	5/8	206	173	147	80	74	82	2.04
57	4/16	223	199	167	98	85	50	2.59
59	4/26	208	177	149	78	68	75	1.98
70	5/9	229	203	174	88	84	92	3.12
71	5/9	200	166	145	78	74	55	2.04

VITA

Arnold David Froese was born in Manitoba, Canada on December 30, 1946. He moved to California with his family in 1958, and was graduated from high school in 1964. He received a Bachelor of Arts degree in Psychology from Pacific College, Fresno, California in 1968, and a Master of Arts degree in Psychology from California State University at Fresno in 1971.

He entered the Graduate School at the University of Tennessee in September, 1971, and received the Doctor of Philosophy degree with a major in Psychology in December, 1974. He is a member of the Animal Behavior Society, The American Psychological Association, the Herpetologist's League, the Society for the Study of Amphibians and Reptiles, and Sigma Xi.