Habits and Home Range of the Pacific Pond Turtle, *Clemmys marmorata*, in a Stream Community

Abstract

R. Bruce Bury

During the summers of 1968-1971 studies of pond turtles were done in a natural area along 3.5 km (2.2 mi.) of Hayfork Creek, Trinity Co., Calif. A total of 578 turtles were marked, measured, and released, and 70% of these were later relocated one or more times. The estimated density was 214 turtles per hectare (85/acre). Turtles aggregated in the large, deep pools with cover. Measurements of short and long term movements revealed that: home ranges of males were twice the size as those of females; juveniles were sedentary; and individuals often used the same area year after year.

Deep body temperatures (measured by thermosensitive radio transmitters) rose sharply after emergence, remained high (28-34°C) during atmospheric basking, and fell quickly after submergence. Regulation of body temperatures at preferred levels apparently were achieved by employment of a number of basking strategies and responses. Aggressive behavior occurred during times of atmospheric basking, and may be important in promoting spacing of turtles.

The widespread occurrence and abundance of this turtle in many parts of western North America appears to be a result of the generalized and opportunistic features of this species.

David B Wake

David B. Wake for Robert C. Stebbins

Table of Contents

Introduction

The Pacific pond turtle, Clemmys marmorata (Baird and Girard), is the only widespread freshwater turtle native to the Pacific Coast of North America. It was formerly common in streams, rivers, ponds and lakes from the Columbia River to northern Baja California. Indians and settlers used this species for food, and in the early parts of the twentieth century they were an economically important food in California markets (Storer, 1930). In recent years, however, parts of its habitat have been eliminated or disturbed by man, and the numbers of pond turtles in many areas appear to be declining.

This turtle is one of the larger resident animals of Pacific Coast waters, yet we know little of its ecology or its role in freshwater ecosystems. Storer (1930) reported on the natural history of the species in the Sacramento Valley of California, and Seeliger (1945) analyzed aspects of its color patterns, size, sexual dimorphism, and geographic variation. References on the fossil record, distribution, and general ecology of the animal are provided elsewhere (Bury, 1970a; Appendix).

The present study was designed to provide information on the ecology of the species in a natural ecosystem. Investigations were done on specific aspects of its life in a stream community. Objectives were: (1) to examine the age and sex composition, density, and spatial distribution of a natural population of turtles; (2) to assess short and long term movements of individuals; (3) to determine home range; (4) to investigate basking and thermoregulatory behavior; (5) to observe any social interactions among individuals; and (6) to compare these data with known information on the biology of freshwater turtles.

Several characteristics of the pond turtle made field study possible and were reasons for selecting it as a subject. The animals are still abundant in certain remote areas, where they are long-lived and hardy; the shell can be conveniently measured and marked for permanent recognition of individuals; they are relatively large reptiles and, with the use of blinds, can be observed undisturbed during their daily activities; radio transmitters can be easily inserted or attached to them; and they are closely associated with bodies of water where the same individuals can be found repeatedly.

Ecological studies on freshwater turtles are rare and concern species inhabiting ponds, lakes, or slow lakes. Examples are studies of _Pseudemys_ _scripta_ (Cagle, 1950, and Moll and Legler, 1971), _P._ _concinna_ (Jackson, 1970), _Deirochelys_ _reticularia_ (Gibbons, 1969), and _Chrysemys_ _picta_ (Ernst, 1971, Gibbons, 1968, and Sexton, 1959). There are incidental notes on other species. The present investigation is the first major study of any turtle in the genus _Clemmys_ and of any species in a stream community. Hopefully, this study will increase our understanding of freshwater turtles in nature so it can be possible to make wise decisions about the conservation and protection of these reptiles.

Acknowledgements

This study was carried out under the guidance of Dr. Robert C. Stebbins. I owe him special thanks for his careful review of the manuscript, sustained interest in the project, and untiring assistance both in writing and in the field work.

Drs. Robert C. Stebbins, David B. Wake, and Don C. Erman kindly read the manuscript. They provided valuable comments on approachs to problems and clarification of concepts advanced.

I thank Dr. Samual M. McGinnis for use of biotelemetry equipment and advice on operational techniques. Mr. Roger G. Bury executed the design and construction of tracking transmitters. Ms. Jaclyn H. Wolfheim advised me on the analysis of behavioral data and made many helpful suggestions. Robert Stebbins, Nate Cohen, and many friends and relatives visited my study area, freely giving of their knowledge, philosophy, companionship, and support. All of us found the wildness, peace, and adventure along the stream to be among the most rewarding times of our lives. Long may it remain wild.

Mr. Larry J. Larsen, District Ranger, and Mr. Larry Cron, Ranger, U.S. Forest Service, Hayfork, California, helped to obtain summer campsites, which aided my field studies.

Telemetry studies in the summer of 1970 were supported by a Grant-in-Aid from the Society of Sigma Xi. Parts of the field work in 1969, 1970, and 1971 were supported by the Museum of Vertebrate Zoology and the Department of Zoology, University of California at Berkeley. This aid was of great assistance to my work.

The Area of Study

Figure 1 shows an aerial view of the study area, a 3.5 kilometer (2.2 mile) stretch of Hayfork Creek, Trinity Co., California. Its location in northwestern California is shown in Figure 2.

This stream was chosen for several reasons. Prior collecting in 1960-61 indicated that this section of Hayfork Creek had a large number of Pacific pond turtles and was suitable for capture of this wary species. Most of the natural habitats occupied by the turtle are creeks, streams, and rivers, particularly since in the western states there are relatively few ponds and lakes at low elevations. Hayfork Creek is typical of many inland waters of California where the species occurs. Of notable importance was the wild nature of the region, because I desired to study this species in an undisturbed environment. Hayfork Creek was relatively free of human impact.

The study area consists of two sections. The upstream part contains 10 pools denoted hereafter as "S" pools (south of the main study area). The main study area is the downstream part and included 27 pools. These pools are described later.

The region is characterized by marked seasonal differences in weather. Winters are cold with light snowfall and freezing temperatures. However, the study area is at about 610 meters (2100 ft.) elevation, and conditions are not as severe in winter as at higher altitudes. Occasionally, days may be mild in winter. Springtime weather varies, but in general is mild with air temperatures reaching a mean maximum of 20° to 25° C. Summers are warm to hot with mean maximum temperatures of about 30°C in June, 34°C in July, 33°C in August, and 31°C in September. Mean minimum temperatures are about 6°, 8°, 7°, and 5°, respectively. October temperatures are lower: mean maximum, 22°, and mean minimum, 2°C. Air temperatures seldom rise above 15°C from November until April.

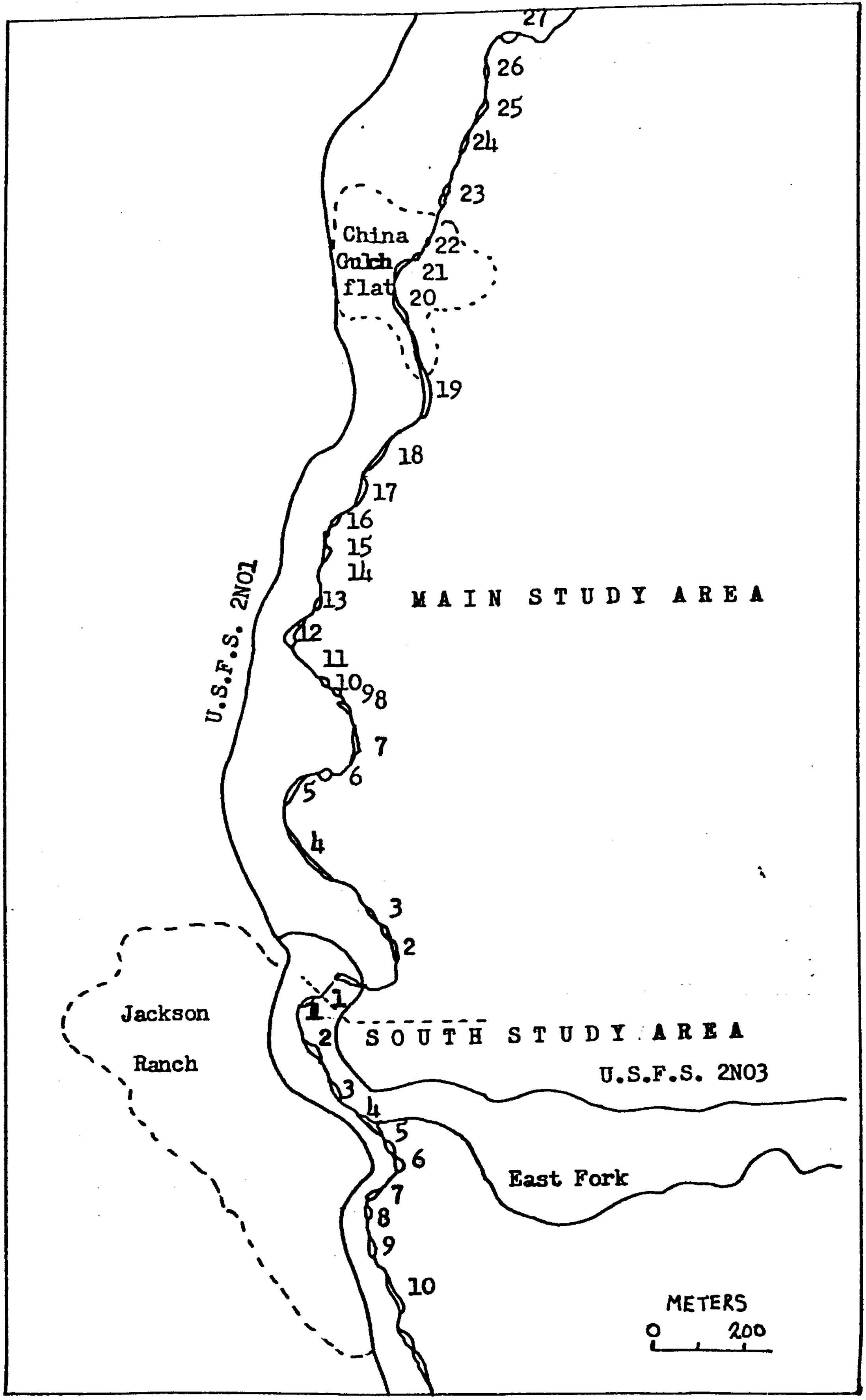
Precipitation is mostly rain that falls from late fall until early spring, but thunderstorms with little rain may occasionally occur in the summer months. Annual precipitation is about 1000mm (40 inches). However, nearby mountains may receive between 1525-2025mm (60 and 80 inches) of precipitation a year, mostly as winter snowfall. The runoff from these mountains supplies Hayfork Creek with water throughout the year.

Vegetation near the stream consists of woods (oak, Ponderosa pine, a few Douglas fir), chaparral, and open, grassy areas. The diverse nature of the vegetation is apparent in Figure 1.

The surrounding topography is composed of mountains 760-1065m (2,500 to 3,500 ft) high. Limestone outcrops form cliffs near parts of the main study area. Gold mine tailings were adjacent to many sections of the creek; these operations were carried out about 1860-70. About 24 km (15 airline miles) south of the study area are the Yolla Bolly Mountains, which rise up to 2600m (8,500 ft).

Details of the major features in the region can be obtained in Bary (1970b).

Figure 1. Pacific pond turtle study area at Hayfork Creek, Trinity County, California. There are 37 pools: 10 in the South Study Area and 27 in the Main Study Area. Aerial photograph taken at an elevation of 1980m (6,500 ft) on August 12, 1969.


China Gulch flat
MAIN STUDY AREA
SOUTH STUDY AREA
U.S.F.S. 2N01
U.S.F.S. 2N03
Jackson Ranch
East Fork
METERS
0
200
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
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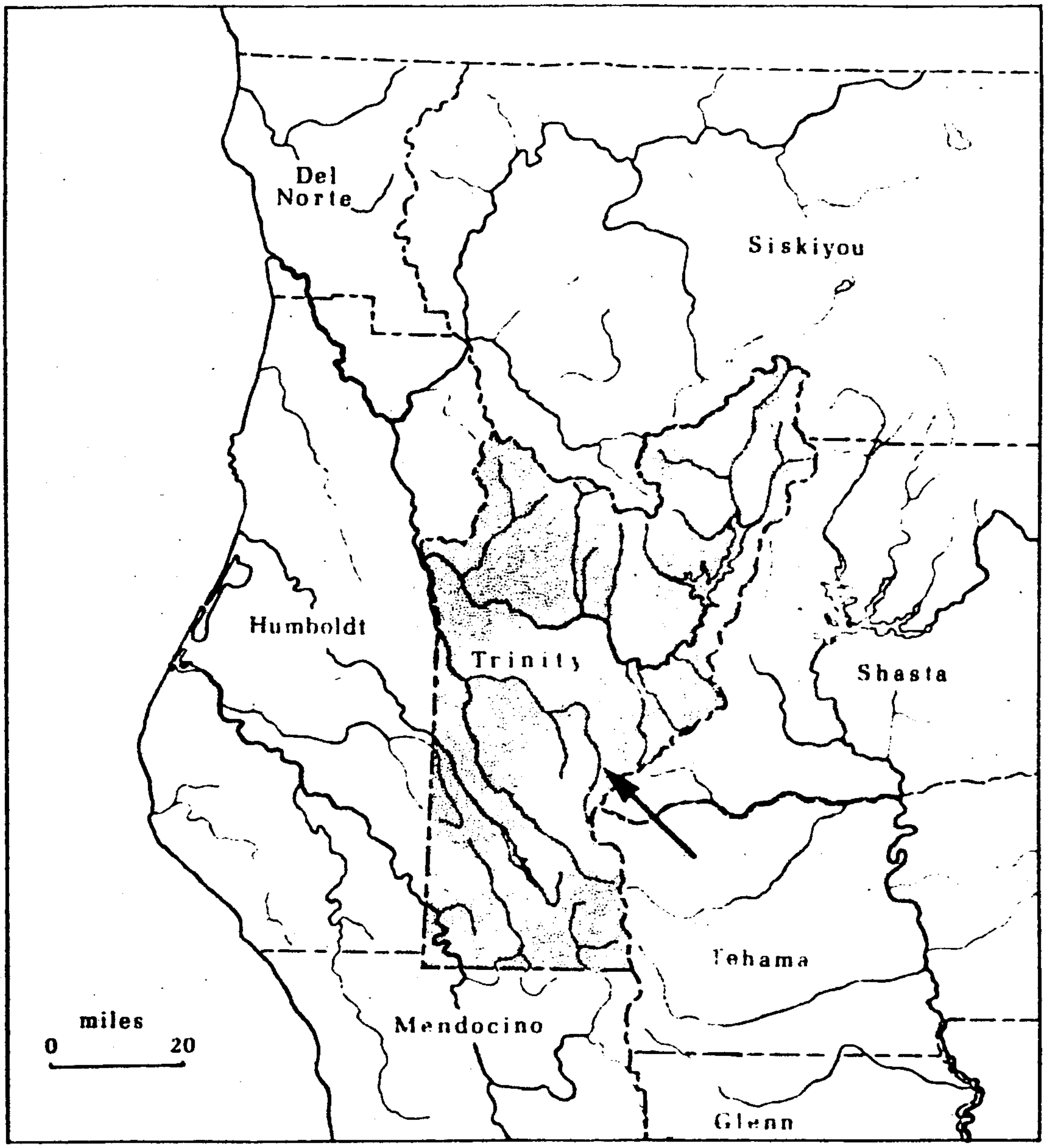
26
27

Figure 2. Location of Pacific pond turtle study area in Trinity County, California. Hayfork Creek is denoted by arrow. It flows into the South Fork of the Trinity River, a major tributary of the Klamath River.


Del Norte
Siskiyou
Humboldt
Trinity
Shasta
Tehama
Mendocino
Glenn
miles
0
20

Home Range

The area occupied by an animal and utilized for feeding, reproduction, and other purposes has been generally regarded as the home range (Tinkle, 1967). Recently, Brown and Orians (1970) defined it as the area in which an animal normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings. In their study of the slider, Pseudemys scripta, Moll and Legler (1971) defined the home range as the total area used in the normal daily activities of an individual turtle, excluding areas traversed during seasonal migrations (i.e., nesting). These definitions are used for home range in this study.

Turtle tracks in sand leading to and away from Hayfork Creek were seen in summer, and apparently some animals occasionally left the stream for egg laying or other terrestrial activity. Unfortunately, these periods could not be followed. Extensive search was made adjacent to the stream, but only one adult female was found on land. It seemed that turtles mostly remained in or near Hayfork Creek, a perennial stream, during the summer months, and my examination of home range in this species is restricted to activities of the turtles during times of their aquatic existence.

A stream was chosen for study of the home range in Clemmys marmorata because of the ease with which the turtles could be observed in such an environment. The width and depth of Hayfork Creek are relatively minor distances in the movements of turtles, since individuals can traverse these dimensions in a short time (less than one minute). Such dimensions were omitted from most determinations of distances travelled, but the total area occupied by animals was used to calculate home ranges. The majority of measurements presented here are movements of turtles along the length of the stream in relation to time. This two dimensional system offers a simple but accurate means to examine the dispersion of turtles in space and time. Other methods for assessing home range of freshwater turtles are given by Moll and Legler (1971) and Ernst (1971), but most of these require a large number of recaptures per turtle or calculations based on assumptions that do not apply to a stream environment.

Home ranges of freshwater turtles have apparently been neglected because of difficulties in acquiring adequate recapture data (Ernst, 1970). Further, habitat conditions and habits of the animals have greatly influenced the ways workers relocated turtles. For example, Moll and Legler (1971) marked a total of 431 P. scripta, and of these 197 individuals were relocated 1,642 times by use of electronic equipment, visual sightings of turtles painted with numbers, and some recaptures. Adults lived in open water and few were recaptured after release. It was necessary for these workers to use sonic tags to follow the movements of adults, and 14 animals were relocated a total of 310 times with such equipment. They also relocated a large number of juveniles because these turtles mostly remained in shallow water where they could be sighted visually and identified by numbers painted on the carapaces of the animals.

Recently, Bider and Hoek (1971) cautioned against sampling turtle populations by hand collecting because they thought it usually was biased and favored the capture of juveniles. However, my review of determinations of distances travelled, but the total area occupied by animals was used to calculate home ranges. The majority of measurements presented here are movements of turtles along the length of the stream in relation to time. This two dimensional system offers a simple but accurate means to examine the dispersion of turtles in space and time. Other methods for assessing home range of freshwater turtles are given by Moll and Legler (1971) and Ernst (1971), but most of these require a large number of recaptures per turtle or calculations based on assumptions that do not apply to a stream environment.

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Materials and Methods

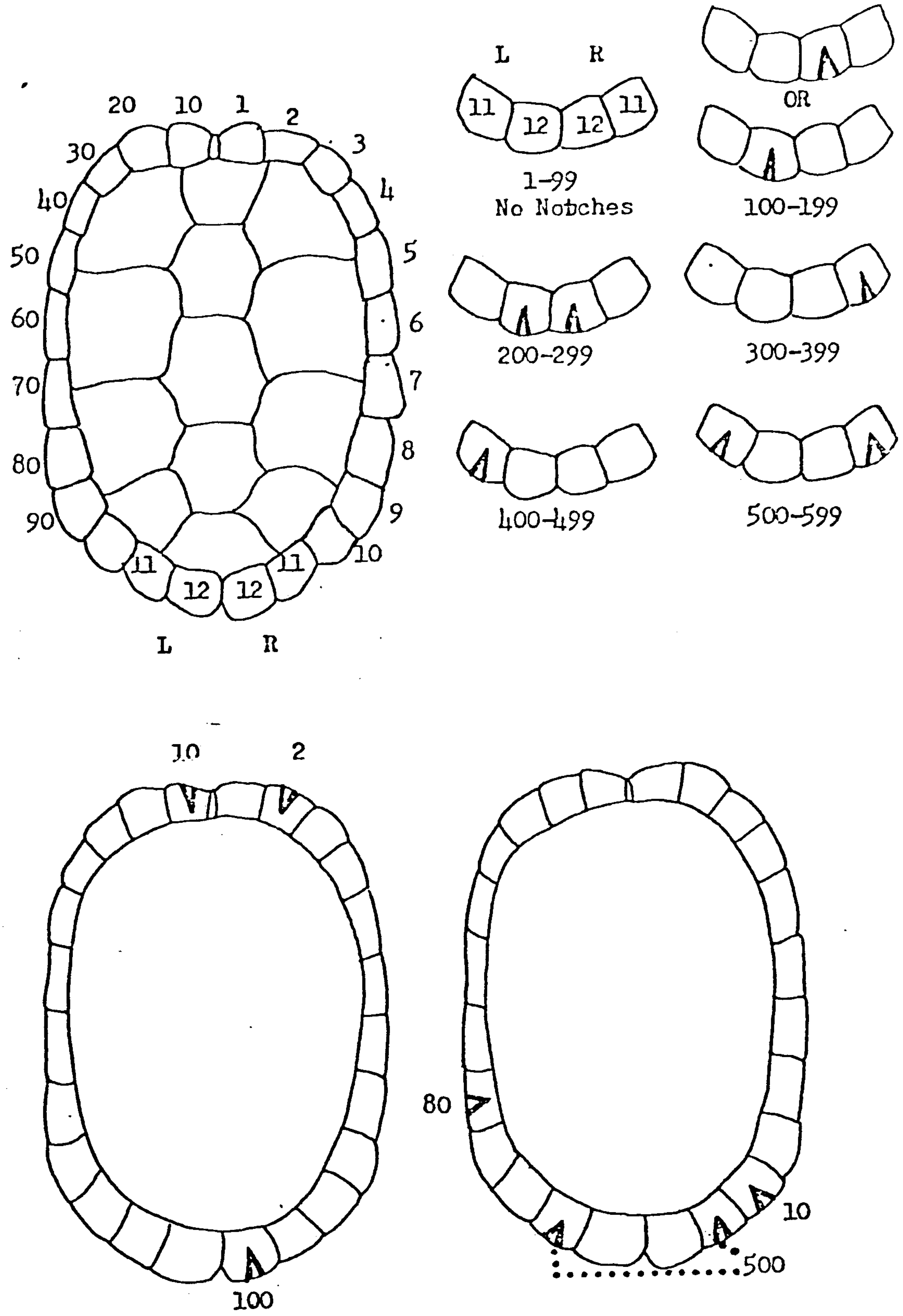
Turtles were collected by hand during the summers of 1968-71. The equipment was simple and inexpensive, consisting of a face mask, snorkle, collecting bags, and a plastic 5 gallon garbage can, which contained a measuring board, calipers, file, file brush (wire), and miscellaneous supplies. The garbage can also served as a container to hold turtles after capture and before measurements were made. A pack sack was worn out of the water and contained my notebook and other gear. Tennis shoes were required to walk in the rocky stream.

Collecting was always done facing upstream so disturbed waters would not interfere with underwater vision. Collecting trips lasted from 1 to 10 hours, but were usually about 5-6 hours in duration. Most turtles were found by reaching underneath objects such as undercut banks, boulders, logs, and branches. Often they were wedged under such objects or in crevices. With practice it was possible to feel quickly under objects and to distinguish the shell of a turtle from a rock. At many pools there were "pot-holes", which were crevices or holes 1 to 3 m deep that opened under water and ended in an air space where turtles could surface to breath. I found up to 28 turtles at one time in such pot-holes. These sites were regularly searched and they supplied many turtles for this study. However, I thoroughly searched every pool to be sure there was no bias for turtles living in these pot-holes. Only a few deep crevices and undercut banks could not be investigated by approaching them underwater.

Every turtle collected was measured to the nearest mm with a measuring board or vernier calipers. These measurements included straight-line carapace length and width, and shell height. Turtles were marked using a new coding system (Figure 3). Notches were made with a fine hack-saw blade on juveniles, and with a rough hack-saw or half-round bastard file on larger turtles. The marks were all permanent and could be distinguished up to four summers later. A notch 6-8 mm deep at the scute margin was sufficient. The first 50 turtles marked were deeply notched (12-20 mm) and it was discovered later that these deep cuts closed with scar tissue and the scutes in a few animals degenerated. However, these individuals could still be clearly recognized as marked turtles.

Radio tracking transmitters employing solid state circuitry and powered with Mallory TR-175 batteries were used to follow the movements of several turtles. One of these units is depicted in Figure 4. Each radio transmitter and battery was sealed in Silicone Rubber Cement and then wrapped in waterproof black tape. The sealed unit weighed about 25 grams. The unit was securely tied to the carapace of the turtle with the antenna (15 cm diameter) circling the shell and the unit on the posterior slope of the carapace. Small holes were drilled into the first left, tenth left, and tenth right marginal scutes. Pieces of wire inserted through these holes were fastened to the antenna and around the radio unit. A radio could be attached to a turtle in about 5 minutes. Signals were transmitted through water and at a depth of 1 m could be detected in air at 150 m away. At a depth of 0.5 m, signals could be heard up to 500 m away. A loop antenna was used for directionality and signals were picked up on a Lafayette HA-303 Transceiver (2 watt).

Figure 3. Method used in marking Pacific pond turtles at Hayfork Creek. There are 12 marginal scutes on either side of the carapace. Upper Left: Viewed from above, the marginals on the left side were used to denote numbers 10 through 90 and on the right side 1 through 10. Upper Right: The four posterior marginals were used to mark numbers over 99. Code 1-99 had no notches, code 100-199 had one notch either in the 12th left (12L) or 12th right (12R) marginal, code 200-299 had both 12L and 12R notched, code 300-399 had one notch in 11R, code 400-499 with 11L notched, and 500-599 had both 11L and 11R notched. Bottom: Examples of the coding system. The code number is obtained by adding the total for all marks.



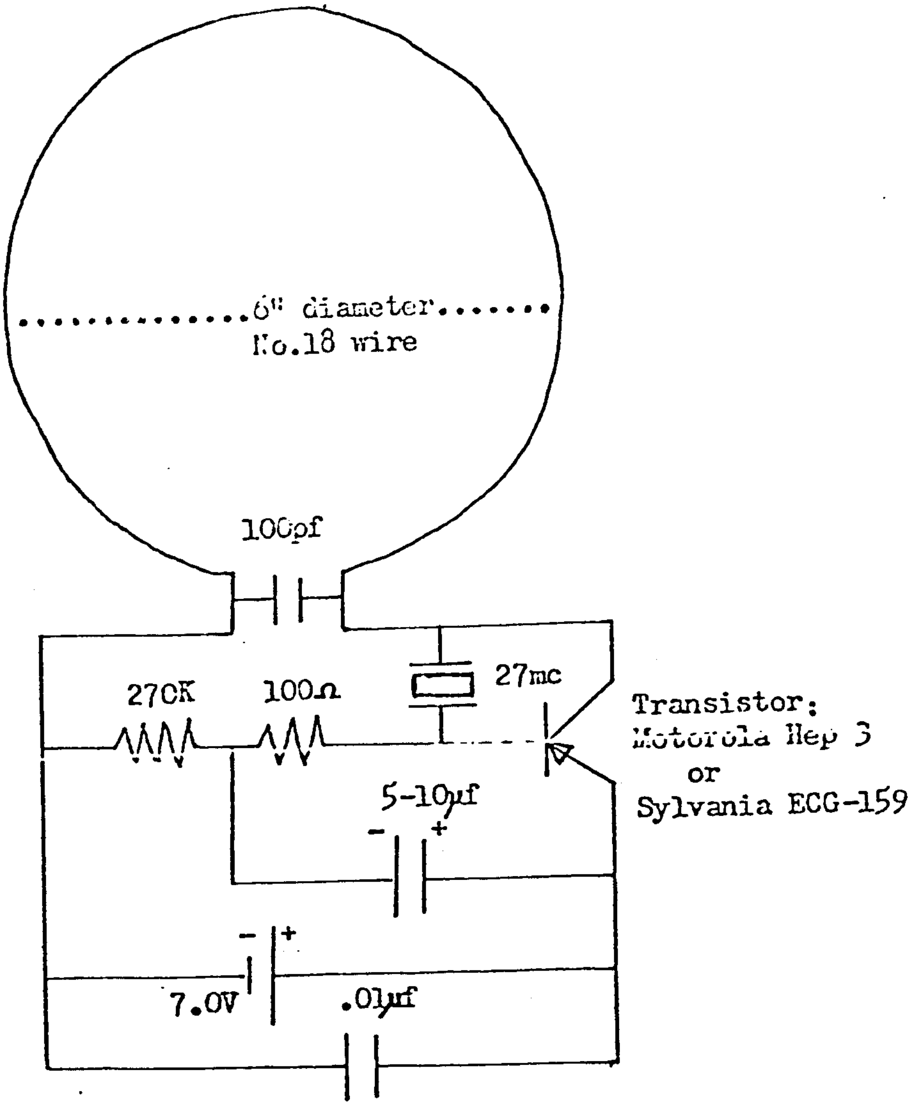
Code = 100 + 10 + 2

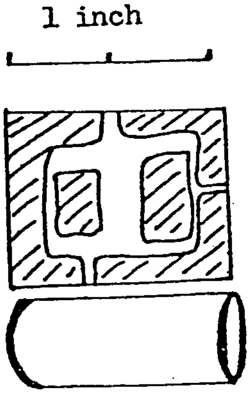
= 112

Code = 500 + 80 + 10

= 590

Figure 4. Citizen band radio transmitter (27 megacycles) used to follow the movements of turtles in Hayfork Creek.





Circuit board with copper connections

Mallory TR-175 battery (7.0V)

All home range studies were done along 3.5 km (2.2 mi.) of Hayfork Creek. Aerial photographs of this section of the creek were taken in August, 1969, and later enlarged to 66 X 81 cm (scale 6.3 cm or 2½ inches = 100 meters). On these photographs it was possible to locate boulders 1 m in diameter, and all cliffs, large trees, and other prominent landmarks noted in and around the stream. Starting from the southernmost point of the study area (upper part of pool 10S), the creek was divided into 25 m sections by running a line down the middle of the watercourse and distances plotted on a master map. Distances measured between relocations of turtles were recorded to the nearest 25 m interval.

Sampling Method

Estimates of population structure and home range may be biased by the sampling method (Ream and Ream, 1966; Ernst, 1971). Trapping of turtles has been used in large bodies of water, but some animals apparently become trap shy after being captured. Tinkle (1958) pointed out that turtles become more wary after initial capture, possibly leaving the area under study. Collecting bias often reflects environmental conditions, and the habits of the species being examined. Moll and Legler (1971) found that juvenile P. scripta in Panama occur in aggregations and are easy to collect but adults are scattered and more difficult to catch. Dip netting and hand collecting seemed to result in larger proportions of juveniles than mature turtles in prior studies (Cagle, 1950; Gibbons, 1968; Moll and Legler, 1971).

Almost all captures at Hayfork Creek were of turtles hiding under objects and most of the animals were already in these positions before collecting started. This sampling method resulted in many larger sized turtles because they were more likely to be felt or seen underwater and they could not move into small crevices. But extensive search of many pools and shallows revealed that juveniles were nowhere common from June to early September. Further, in late summer, algal blooms were frequent in shallow water and these areas were purposefully avoided by me due to the presence of belostomatid water bugs which inflict painful bites. Juveniles may use these algal blooms for cover, but search of many mats of algae by tearing the blooms apart with a stick did not result in more juveniles than in areas without algae. Some adults and juveniles occurred in the algae mats. On the basis of prior studies on freshwater turtles it was thought that a disproportionately large number of juveniles would be found by hand collecting, but it seemed that adults were more often taken at Hayfork Creek. The age composition of the population is discussed in a following section.

There were some disadvantages to hand collecting, but in a stream it was a more efficient sampling method than dip netting or trapping turtles. Costs of hand collecting included lacerations and bruises on rocks, insect nuisances (water bugs, hornets, etc.), and exhaution from repeated diving. However, with avoidance of algal blooms in shallow water and periodic rests it was possible to search about 0.5 km of stream per day. The entire study area (3.5 km long) was searched in 5-7 days.

Bider and Hoek (1971) reported that use of a floating blind yielded 5-6 captures of turtles per hour, which they thought was unusually efficient. I captured 1,513 individuals in Hayfork Creek by searching the pools 409 times (0-28 turtles per pool, $\bar{X} = 3.7$ per pool searched). Collecting was done on 94 days and 1-38 turtles were captured per day ($\bar{X} = 16.1$ per day), including some days when only one or a few pools were checked. Table 1 indicates a yield of about 4 turtles per hour, but this includes time devoted to rest periods and to measurements on turtles. The number of turtles per man-hour of collecting was closer to 10-15; in some sections of the study area I found over 25 turtles in less than one hour.

Population Parameters

The concept of home range cannot be divorced from the structure and dynamics of natural populations and, in fact, is meaningless without such information. I, therefore, present here data on the density, age composition, and sex ratio of the Hayfork Creek population of turtles. The relationship of these parameters to home range is discussed later.

Assessment of Density

A total of 578 turtles were marked, measured, and released in the study area during the summers of 1968, 1969, and 1970. Of 200 individuals marked during the summer of 1968, 120 (60%) were recaptured one or more times in 1969 and 168 (85.7%) were recaptured one or more times in 1969-1971. There were 188 turtles marked in the summer of 1969 and 123 (65.4%) were relocated in subsequent years. In the summer of 1970, 194 turtles were marked and 115 (59.3%) found later.

Table 1. Comparison of representative samples of Pacific pond turtles obtained during collecting periods at Hayfork Creek.

Date	Hours	Pools	No. Captured	Number/hour
Aug. 5, 1968	3½	1-6	24	6.8
July 16, 1969	6	12-18	33	5.5
July 17, 1969	4	5-11	22	5.5
July 18, 1969	7½	1S-5	38	5.1
July 29, 1969	7½	12-19	34	4.5
July 30, 1969	7	5-12	26	3.7
July 31, 1969	8	1-5	26	3.3
Aug. 17, 1969	7½	1S-10S	32	4.3
Aug. 18, 1969	4	6S-10S	16	4.0
Aug. 19, 1969	6½	5-19	13	2.0
Aug. 20, 1969	4½	4-3S	11	2.4
May 30, 1970	4	13-19	24	6.0
July 26, 1970	3	12	22	7.3
July 7, 1971	3½	2S-10S	16	4.5
July 10, 1971	4½	19, 23-27	25	5.5
Aug. 12, 1971	7	12, 16-19	23	3.3
Aug. 13, 1971	4	21-27	29	7.2
Aug. 14, 1971	5½	1-11	24	4.3
Aug. 15, 1971	5	1S-10S	8	1.6
Average =	5.4	7.4	23.5	4.4

Early in the summer of 1971 a total of 3 turtles were marked, but afterwards marking was discontinued and efforts were concentrated on recapturing coded individuals. Overall, there were 581 turtles marked and of these 406 (69.9%) were recaptured one or more times. These 406 individuals were captured a total of 870 times and observed on 34 occasions (turtles painted with numbers) for a total relocation of 904 times (1-10 times relocated per turtle, $\bar{X} = 2.2$). There was a relocation of almost 70% of the marked turtles, but these usually were not found more than a few times. Table 2 compares the frequency of relocation of marked turtles in several studies; and the present study has the highest relocation percentage.

Some marked animals undoubtedly were lost during the study (1968-1971) due to predation, old age, winter losses, and to emigration out of the study area. As mentioned previously, 85% of those turtles marked in the first summer (1968) were later relocated, and subsequent summer samples were not as high due to fewer chances to capture these animals. In general, it appeared that most of the turtles in the area were marked and, apparently, collecting did not result in turtles leaving the study area in large numbers. These are important components of home range determinations, which will be discussed later.

Estimates of the numbers of turtles in the Hayfork population were done with the Lincoln Index. The errors in this calculation are discussed by Gibbons (1968), who pointed out that each estimate of population size must be considered as a general assessment, not as a calculated number of individuals.

Table 2. Comparison of relocation frequency reported by investigators in studies of different species of freshwater turtles.

Species	Number marked	Number relocated (%)	Times relocated	Reference
Clemmys marmorata	581	406 (69.9)	904 (2.2)*	
Chrysemys picta	1010	258 (25.6)	408 (1.6)	Gibbons, 1968
" "	491	58 (11.8)	-	Cagle, 1944
Pseudemys scripta	1885	589 (31.2)	-	" "
" "	431	197 (45.4)	1642 (8.3)	Moll and Legle 1971
Pseudemys concinna	237	142 (60.0)	-	Jackson, 1970

* - number of times relocated per turtle

Assessment of density in the Pacific pond turtle was based on two samples taken in 1971. During the period July 2-7, 93 of 123 captured turtles of all sizes were marked individuals. This gives an assessed density of 764 turtles per 3.5 km (2.2 mi.) of stream or 218 turtles per km (347 turtles per mi.). During August 10-15, 82 of 104 captured turtles were marked. This results in an assessed density of 210 turtles/km (333/mi.). These samples average 214 turtles per km (340 turtles per mi.). The study area contained about 35,000 sq. m. (3,500 m long X average width of 10 m), and had an assessment of about 214 turtles per hectare (85 turtles per acre).

An assessment of turtle density in relation to habitat used by animals is obtained by eliminating shallow parts of the stream from calculations. The shallows, consisting of long riffles or wide open areas, were seldom occupied by turtles and most of those in these situations appeared to be moving toward deeper waters. Ground surveys and examination of aerial photographs revealed that such waters (<0.5 m in depth) constituted about two thirds of the stream by area. The assessed density is actually closer to 642 turtles per hectare (255 per acre). There is an estimate of 0.60 turtles per meter of stream length for areas deeper than 0.5 m.

The assessed population size of Hayfork Creek *Clemmys marmorata* for the entire study area is similar to that determined for river dwelling *P. scripta*, but less than that found for *C. picta* living in ponds (Table 3). Considering only *C. marmorata* in suitable habitat (255/acre) there is similarity to the estimates for *C. picta*. However, these studies differ in many aspects and comparisons at this time need to be cautious.

Table 3. Assessment of population density in freshwater turtles based on Lincoln Index (number/acre and number/linear meter).

Species	Habitat		Density	Reference
Clemmys marmorata	Stream		85/acre	
			0.20/meter	
Pseudemys scripta	River	Juv	77/acre	Moll and Legler, 1971
		Ad	0.17/meter	
" "	River		0.30/meter	Tinkle, 1958
" "	Fw Bay		36/acre*	Gibbons, 1970
Deirochelys reticularia	" "		16/acre*	" "
Chrysemys picta	Pond (low)		166/acre	Sexton, 1959
	" (high)		40/acre	" "
" "	"		233/acre	Gibbons, 1968
" "	"		239/acre	Ernst, 1971

* = estimated from data

Age and Sex Composition

The population structure of C. picta and P. scripta is provided by Ernst (1971) and Moll and Legler (1971), respectively. In the two studies juveniles (sexually immature turtles) constituted 19% of the C. picta and 37% of P. scripta populations. Moll and Legler (1971), however, thought an estimate of 20% juveniles would probably be more accurate because it was difficult to evenly sample their population of P. scripta; juveniles were concentrated and adults were scattered. These studies also report variations in the proportions of juveniles in other populations of these two species; estimates range from 9 to 70%, mostly 20-30%. Of the 704 C. marmorata taken during summer months in Hayfork Creek, 35.2% were juveniles. No hatchlings were found. I considered animals under 120 mm carapace length to be immature since up to about this size the secondary sexual characteristics are undeveloped or indefinite. Hayfork turtles resembled most freshwater turtle populations in that adults predominated. Few predators can subdue or harm an adult turtle compared to the vulnerability of juveniles, and, presumably, the adults are long lived. Further, there may be high mortality of eggs and hatchlings. These factors may result in the high proportions of adults in most turtle populations.

Based on captured turtles in the study area, the sex ratio was 246 males to 210 females, or 1.17 to 1.00. Ernst (1971) found a 1:1 ratio in C. picta, whereas Moll and Legler (1971) reported a 1.9 to 1 ratio in P. scripta. Among 12 prior reports on freshwater turtles, 8 had more females than males. There are no clear reasons to explain uneven proportions of sexes in local populations and different species of turtles at this time.

Spatial Distribution

Brown and Orians (1970) stated that the dispersion of animals in space and time results, in a proximate sense, from the direct response of individuals to features of the envirorment and to the presence or absence of other individuals of the species. To my knowledge, the local distribution and spacing of a freshwater turtle in a stream community has never been examined. The present study explores whether the pond turtle in Hayfork Creek responds to environmental features such as length, depth, and cover of pools in the stream, and whether these factors are correalted with the distribution of the turtles in the stream.

Characteristics of pools in the study area were quantified where possible and comparisons made for the length and maximum depth of each pool. Cover was classed into five categories: I. No apparent cover, i.e., absence of objects where turtles could completely hide. II. Small rocks or scattered vegetation present, but no areas in which turtles could hide themselves. III. Underwater rocks, ledges, and vegetation accesible as hiding places but turtles forced to surface for air. IV. Extensive underwater cover, such as spaces under large rocks and sunken logs or branches, but turtles required to surface for air. V. Underwater cover that was mostly inaccesible to predators and where turtles could reach air without exposing themselves, such as overhanging ledges, crevices in large rocks, or spaces under large objects along the edges of the stream. The last category comprised most of the pot-holes which were occupied by large numbers of turtles. These five categories of cover occurred in more than one pool each and in general indicate the preference of turtles for certain types of cover. The characteristics of pools in the study area are presented in Table 4, while the distribution of all turtles found in the pools are given in Table 5. Figure 5 illustrates the dispersion of turtles in the study area, and two categories are used for comparison. The total number of turtles marked at each pool is shown and the average number of turtles taken per search. The latter is used because some pools were searched more often than others. Also, collecting yielded turtles that were subsequently marked and released, turtles previously marked (recaptures), and turtles caught and released unmarked. There is some similarity between the total number of turtles marked at each pool and the average number of turtles taken per search of each pool (Figure 5). In both categories, high numbers occurred in pools 10S, 1, 2, 3, 5, 6, 12, 19, 22, 23, and 27; few animals were present in pools 5S, 4S, 8, 9, 10, 11, 20, and 25. Extremes in the range of densities were sometimes found in adjacent or nearby pools (pools 8-11 low, but pool 12 high; pool 20 low, 19 high; and 25 low, 27 high). The data indicates that in a stream community the pond turtle has a clumped or aggregated distribution, occurring in high numbers where there are special environmental features. A comparison of pool characteristics and distribution of turtles is given in Table 6.

Table 4. Comparison of length, depth, and cover of pools.

Pool	Length (ft)	Maximum Depth (ft)	Type of Cover
S10	350	3	V
S 9	120	3	II
S 8	60	2	II
S 7	80	4	IV
S 6	80	5½	III
S 5	110	2½	II
S 4	100	3	I
S 3	150	2½	III
S 2	120	2	III
S 1	100	2½	V
1	180	5	IV
2	270	7½	V
3	320	3	V
4	420	2½	II
5	220	3½	V
6	110	9	III
7	260	3	IV
8	90	4	II
9	50	2	II
10	20	2	I
11	30	2	II
12	200	11	V
13	130	10	IV
14	140	2½	V
15	20	4	III
16	90	6	III
17	180	3½	III
18	300	4	V
19	400	3½	V
20	50	2	II
21	310	4½	IV
22	150	2½	IV
23	140	5	V
24	40	2	III
25	80	3½	II
26	60	2	V
27	130	7	V

Table 5. Number of turtles marked, recaptured, and collected in the study area.

Pool	Number Marked	Number Recaptured	Number Not Marked	Total	Times Pool Searched	Average Number Turtles Per Search
S10	40	15	2	57	8	7.1
S 9	4	4	2	10	8	1.3
S 8	4			4	6	0.7
S 7	6	6	5	17	10	1.7
S 6	14	22	7	43	13	3.3
S 5	2	5		7	7	1.0
S 4	1			1	7	0.1
S 3	10	13		23	10	2.3
S 2	8	11	4	23	11	2.1
S 1	24	11	1	36	12	3.0
1	36	39	1	76	17	4.5
2	44	62	4	110	19	5.8
3	30	55	1	86	17	5.1
4	13	13		26	9	2.9
5	25	44	1	70	13	5.4
6	34	69	1	104	16	6.5
7	18	20	1	39	13	3.0
8	4	6		10	12	0.8
9	2	6		8	9	0.9

continued

Table 5, continued.

Pool	Number Marked	Number Recaptured	Number Not Marked	Total	Times Pool Searched	Average Number Turtles Per Search
10	1	2		3	10	0.3
11		2		2	10	0.2
12	46	106	3	155	22	7.0
13	18	52	4	74	17	4.4
14	14	12		26	11	2.4
15	1	1		2	1	2.0
16	10	20		30	12	2.5
17	11	17		27	11	2.5
18	21	42	2	65	14	4.6
19	25	63	7	95	12	7.9
20	2			2	4	0.5
21	4	9	1	14	6	2.3
22	21	13	4	38	9	4.2
23	21	39	3	63	11	6.6
24	8	21		29	12	2.4
25	2	4		6	7	0.9
26	16	21	5	42	12	3.5
27	41	40	8	89	11	8.1

Figure 5. Distribution of turtles by pool in the study area. A. Total number of animals marked at each pool. B. Average number of animals taken per search of each pool.

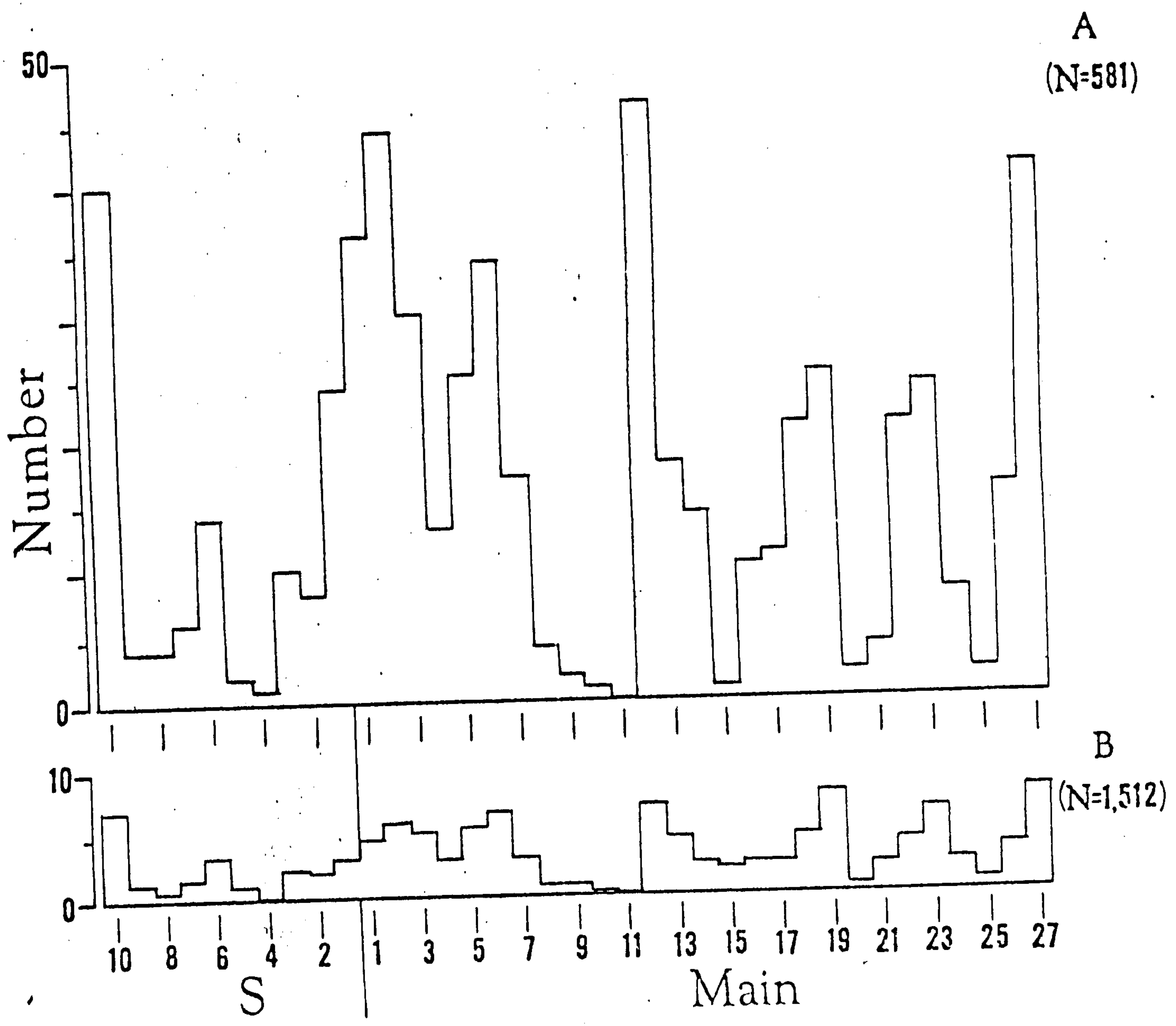

A
(N=581)
B
(N=1,512)
Number
50
0
10
0
10
8
6
4
2
1
3
5
7
9
11
13
15
17
19
21
23
25
27
S
Main

Table 6. Distribution of turtles in the study area classed by the categories of pool length, maximum depth, and cover.

Category	Number of Pools	Number Marked Turtles		Average Number All Turtles Per Pool	Average Number Per Hectare
		Total	$\overline{X}$ (range)/Pool		
Length (m)					
120–149	2	38	19.0(13–25)	5.4	3.8
90–119	4	95	27.2(4–40)	4.8	4.5
60–89	4	133	33.2(18–46)	5.3	6.9
30–59	14	245	17.5(1–41)	3.5	7.6
0–29	13	70	5.4(0–16)	1.5	9.8
Depth (m)					
2.7–3.2	3	98	32.6(18–46)	5.9	
2.1–2.6	2	85	42.5(41–44)	6.8	
1.5–2.0	4	84	21.0(10–36)	4.2	
0.9–1.4	14	192	13.7(1–40)	3.2	
0.3–0.8	14	122	8.8(0–24)	1.9	
Type of Cover					
V	12	350	29.1(14–46)	5.5	
IV	6	103	17.2(4–36)	3.3	
III	8	96	12.0(1–34)	2.9	
II	9	30	3.3(0–13)	1.0	
I	2	2	1.0	0.2	

With pool characteristics and distribution of turtles summed (Table 6), it is possible to test them for any correlation. Spearmann rank correlation coefficients (r_s) and the significance of the obtained r_s values were appropriate. These were tested for large samples using the Student's t test and at a level $p<0.01$ (Siegel, 1956).

The length of the pool and the number of coded turtles were correlated ($r_s = 0.653$, $t = 5.09$) as was the average number of turtles per search ($r_s = 0.680$, $t = 5.33$). That is, long pools had more turtles than short ones. This result may be expected since long pools have greater size. However, assuming an average width of 10 m for the stream, there was an inverse relationship between the surface area (length X width) and the number of turtles (Table 6). This relationship does not hold up in nature since the long pools were usually wider than 10 m. In general, long pools had greater surface area than short pools per meter of length, and more turtles inhabited long pools than short ones.

Depth of pools was also correlated to the number of marked turtles ($r_s = 0.519$, $t = 3.59$) as was the average number of turtles per search ($r_s = 0.554$, $t = 3.94$). In other words, deep pools had more turtles than shallow pools.

Categories of cover from I to V were correlated to the numbers of coded turtles ($r_s = 0.824$, $t = 8.59$) and average number per search ($r_s = 0.856$, $t = 9.87$). There is a high t value between cover and turtle dispersion, moreso than for length and depth of pools.

Cover and length of pools were all significantly correlated to the number of turtles at $p<0.001$, but depth was not correlated at this level of significance. It appears that the depth of pools is the least important factor in the distribution of turtles in the stream. Length of the pool apparently is important to the number of turtles in a pool. Cover appears to be the most vital factor in the distribution of turtles in the stream.

The dispersion of the turtles in the stream apparently is correlated to specific environmental factors and is not random. I thereby reject the null hypothesis that C. marmorata is a nomadic animal. Instead, they appear to restrict their activities to certain areas in the stream.

Radio Tracking of Turtles

A pilot study was undertaken to test the feasibility of using radiotelemetry to provide information on the activities of pond turtles over more continuous periods of time than is possible using traditional methods of mark-recapture. The goal was to follow several individuals by telemetry and to plot their movements in the stream over as many days as possible.

On August 30, 1970, to test projection distance and waterproofing, a transmitter was sealed in rubber cement and tape, then placed in 0.5 m of water. This unit transmitted continually for a period between 64 and 67 hours in duration.

On the following day radio units were attached to three adult male turtles captured from 1800 to 1900 hours (Pacific time) in pool 19. They were immediately used in the experiments and returned to the place of capture about 1 hour later. Turtles used in the study were code number 430 (165 mm in carapace length; Channel 8 transmitter), code 516 (158 mm long; Channel 18), and code 565 (161 mm long; Channel 6). A check at pool 19 and vicinity was done at 2100 hours; code 430 transmitter could not be located and presumably was damaged by some malfunction or waterleakage. The other two units were broadcasting signals up to 0.5 km away from pool 19.

On September 1, code 516 was faintly detected at 1330 hours in pool 21, which is 250 meters downstream from the release site. Code 565 was not located at pool 19 or downstream, but was estimated to be transmitting from the lower end of pool 17 at 1400 hours. This turtle had apparently moved 250 m upstream from the point of release. At about 1830 hours I lost contact with code 516, but code 565 was still in the vicinity of pool 17.

On the next day, code 516 had also failed to transmit signals. At 1830 hours code 565 had moved to pool 13, which is 300 meters upstream from the last presumed location point (pool 17). To double check this new location, I searched pool 13 by swimming along the bottom and edges. Code 565 was observed partly hidden under roots on the east side of the pool. It was not disturbed by my presence.

On September 3, a strong signal was detected as pool 13 was approached. However, I observed the turtle sunning itself on rocks in pool 12, which is 100 meters upstream from pool 13. It was first observed at 0930 hours and its behavior suggested it had become accustomed to the presence of the transmitter and had recovered from handling. It sunned until 1009 hours, dipped itself into the water, emerged and remained out from 1010 to 1027 hours, dipped again, sunned from 1028 to 1040 hours, swam to another site, sunned from 1043 to 1058 hours, dipped, sunned from 1100 to 1137 hours, dipped, and sunned from 1142 to

1206 hours. It then left the vicinity of the basking sites and slowly swam upstream along the west side of the pool. It was continually observed moving for about 50 meters upstream and then it appeared to hide itself in a willow thicket in the upper part of the pool. At 1845 hours the radio signal was strong, and the turtle was determined to be located in the middle part of pool 12. Apparently it had moved downstream from the willow thicket during my absence.

On September 4, code 565 was again observed in pool 12. It engaged in atmospheric basking from 0950 until 1130 hours. Skies were partly cloudy and direct sun seldom struck the animal. Air temperatures varied from 15° to 22°C. Radio signals were distinct during the times of basking and when the turtle entered the water at 1130. Once submerged the turtle swam under large rocks on the west side of the pool and disappeared from view. It did not return within half an hour, and observations were terminated. I returned at 1730 hours but could not detect a signal at pool 12 nor from any area 500m on either side of the pool. This radio Code 565 was followed for a period of 98 hours (2000 hours on August 31 until 1200 hours on September 4).

During the times of radio transmitting, Code 565 had moved upstream a total of 700 meters, an average distance of 175 meters per day. In a 24 hour period, starting at 1830 hours on September 1, it had moved 300 meters. The pond turtle apparently is capable of long, sustained moves over relatively short periods of time. This single record indicated that two days after being handled and attached with a radio, the animal displayed a normal atmospheric basking sequence. However, it had moved 250 meters the first day after release, and 300 meters the second day, 100 meters on the third day, and 50 on the last day. This suggests it was upset by the handling procedure necessary to attach the radio unit.

Further testing is necessary to determine the reliability and use of data on movements in pond turtles taken by telemetry. The technique appears to be a worthwhile one for freshwater turtles. However, the expense and difficulty of relocation often limit the value of radio tracking free-living animals.

Short Term Movements

The bulk of the field work involved mark-recapture records and the results of short term movements are reported here. These concern the distances moved by turtles between the original release and sites of successive recaptures from late May to early September of the same year. Most turtles were recaptured from July to early September.

The distances moved (0 to 1550 meters) in the stream and the time between recaptures (0 to 94 days) are shown in Figure 6. There is not apparent correlation, regardless of sex or size, between the distance moved and the interval of time between recaptures. Some animals moved relatively long distances only a few days after release whereas others were at the same site months later. Males, however, appeared to move farther distances than females of juveniles.

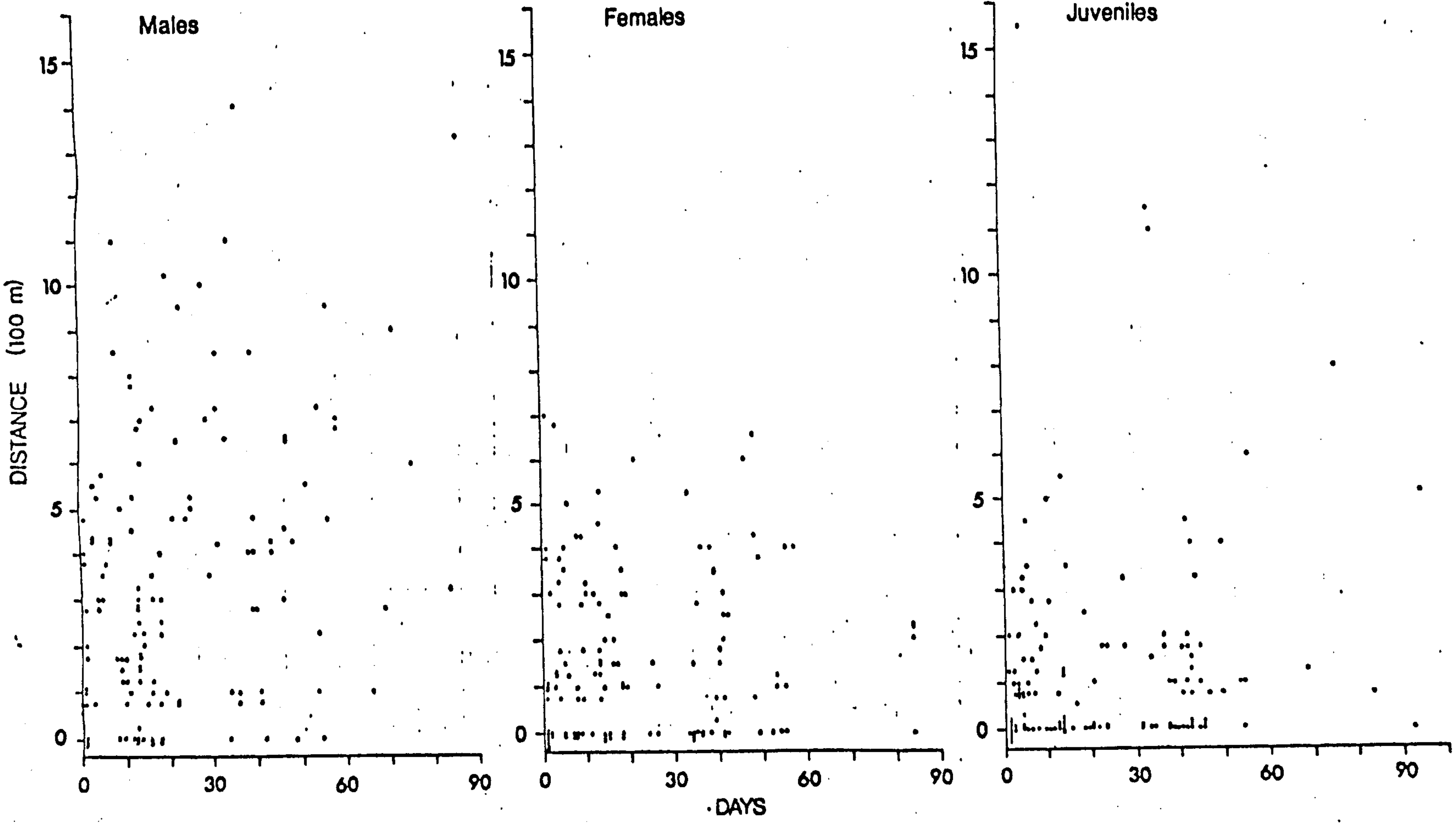
Frequency distributions of the distances moved by males, females, and juveniles are shown in Figure 7, and a comparison of the short term movements is provided in Table 7. These data indicate that males moved greater distances during summer months than either females of juveniles. The average distance moved by them was 2.1 times farther than juveniles. About twice as many males as females and three times as many males as juveniles travelled over 200 meters during one summer. Four times as many males as either females or juveniles traveled over 500 m during the summer months.

Long Term Movements

I obtained records on individuals that were present in the study area year after year. Distances recorded were from the site of last relocation to that of the first relocation in a summer 1 to 3 years later. The same individual thus could be relocated up to three times (1968 to 1969, 1969 to 1970, and 1970 to 1971). There were 475 turtles recorded more than one summer: 401 with an one year interval; 71 with a two year interval, i.e. 1968 to 1970 or 1969 to 1971; and 3 with a three year interval, i.e., 1968 to 1971 (Figures 8 and 9). The total distances between points of capture, regardless of direction moved, are shown in Figure 10. Table 8 gives the net and total distances moved, and the percentage total of turtles that went over 200 and 500 meters.

The average distance that males moved in one year was 2.5 times farther than that for females and 2.6 times that for juveniles. About twice as many males as either females or

Figure 6. Scatter diagram showing relation between distances turtles moved and days between recaptures.


Males
Females
Juveniles
DISTANCE (100 m)
15
10
5
0
0
30
60
90
DAYS

E

Figure 7. Comparison of the number of turtles and the distances moved during summer months. Intervals are 100 meters each.

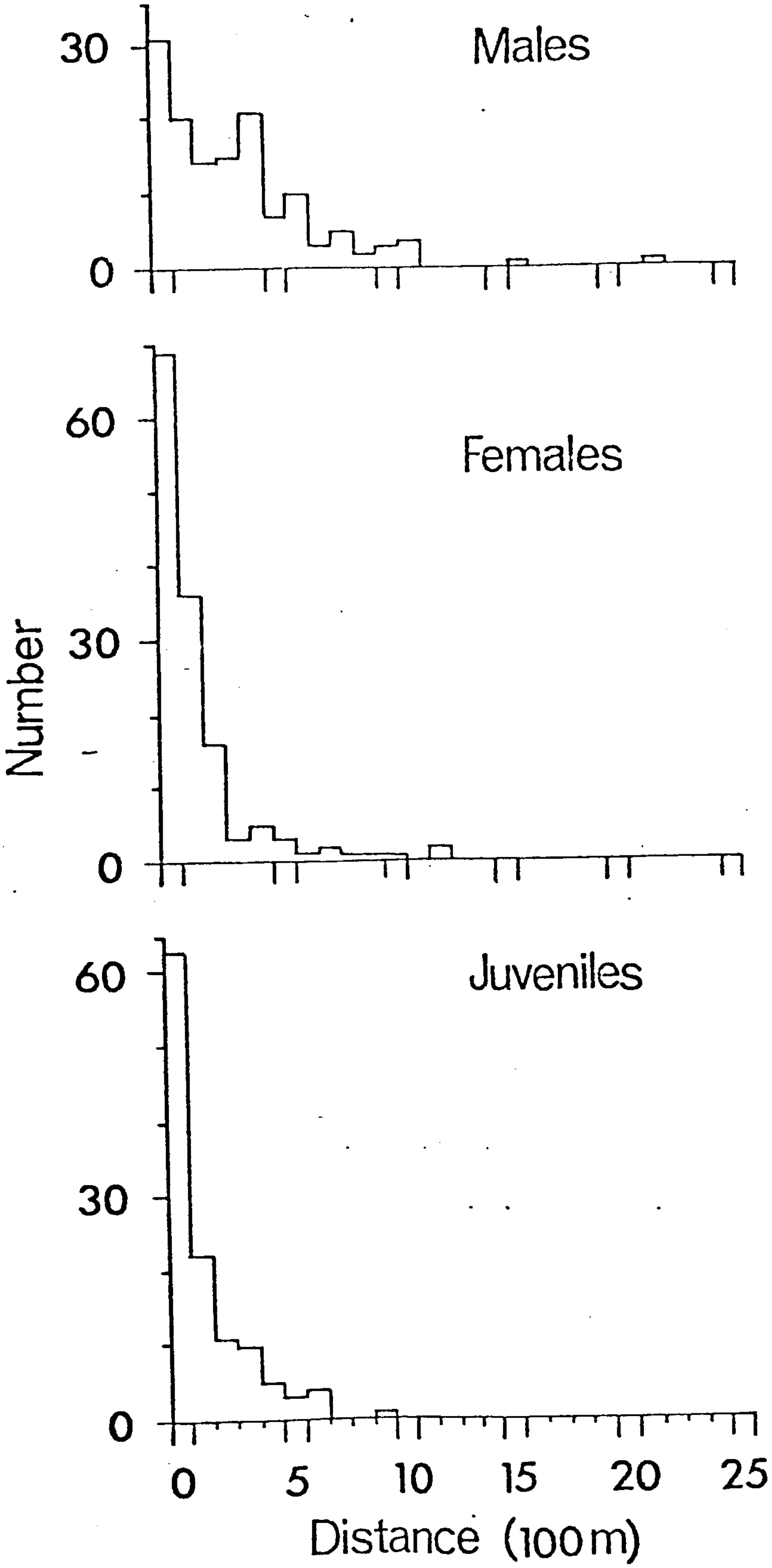

Males
30
0
Females
60
30
0
Number
Juveniles
60
30
0
0
5
10
15
20
25
Distance (100m)

Table 7. Comparisons of the distances and directions of movements in Hayfork *C. marmorata* within summer months.

	Males	Females	Juveniles
Number	135	131	129
Moved upstream - %	53.5	27.5	32.6
Moved downstream - %	34.0	38.9	27.1
Moved less than 100 m - %	12.5	33.6	40.3
Net total movements - m	+8800	-3025	+2115
average - m/individual	+65	-23	+16
Total distance - m	47800	22075	18315
average - m/individual	354	169	142
N that moved 200+ m - %	61.5	36.6	22.5
N that moved 500+ m - %	26.6	6.1	6.2

juveniles traveled over 200 meters, and, similarly, about three times as many males went beyond 500 meters.

Results obtained from turtles found after a two year interval differed somewhat from the previous sample. Males again moved the farthest, but their distances traveled were less. They went 2.0 times that for females and only 1.1 times that for juveniles. About 40% of all the turtles captured had moved over 200 meters. The males went over 500 meters four times as frequently as females and twice as frequently as juveniles.

The three records of males obtained three years after release had all traveled long distances (average of 816m/turtle), and 2 of 3 animals went over 500 meters.

The net total distances were determined by subtracting the total of all downstream moves from all upstream travels. Many turtles changed direction of travel and it was desired to find out which way they were heading from one year to the next. The net total and net average distance (meters/turtle) showed that overall there was a downstream tendency in movements from one year to the next, and after a two year interval (Table 8). This subject is discussed later.

Assessment of Home Range

Ernst (1971) and Moll and Legler(1971), used five different methods of estimating home range. It seems that home range is determined by the habits of the study animal, size and shape of the habitat, and preference as to method of assessment by the investigator, among other variables.

Figure 8. Distances traveled by juveniles between the point of release and relocated in subsequent years. N = 118. A. Distribution of turtles found two summers later. B. Distribution of turtles relocated the summer following release, i.e., released in 1968 and found in 1969.

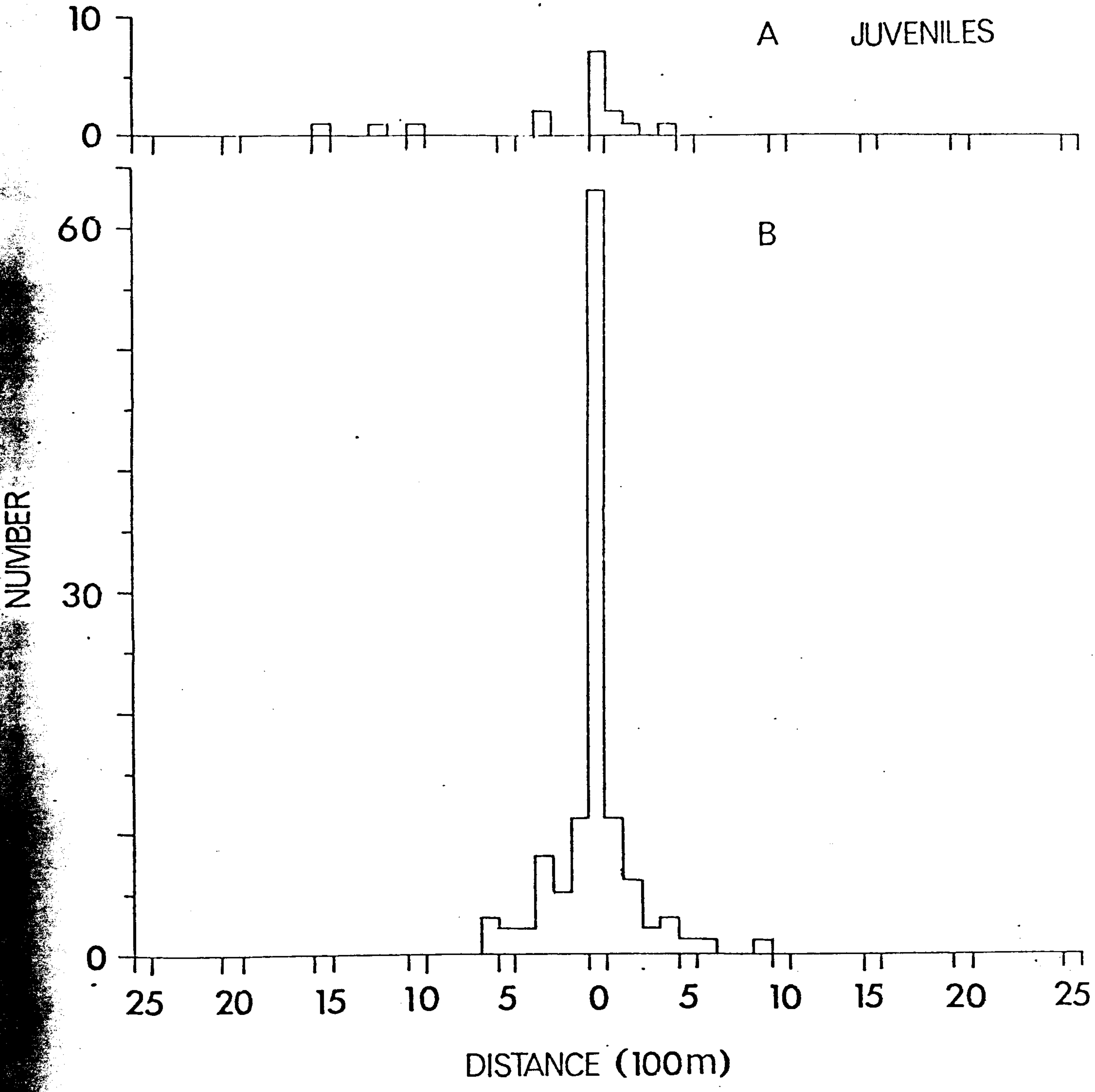

10
0
A
JUVENILES
60
30
0
B
NUMBER
25
20
15
10
5
0
5
10
15
20
25
DISTANCE (100m)

Figure 9. Distance traveled between point of release and relocation. Top: Adult males. N = 137. A. Distribution of turtles found two summers later (open rectangles) and three summers later (hatched). B. Distribution of turtles relocated in the following summer. Bottom: Adult females. N = 146. A. Two summers later. B. One summer later.

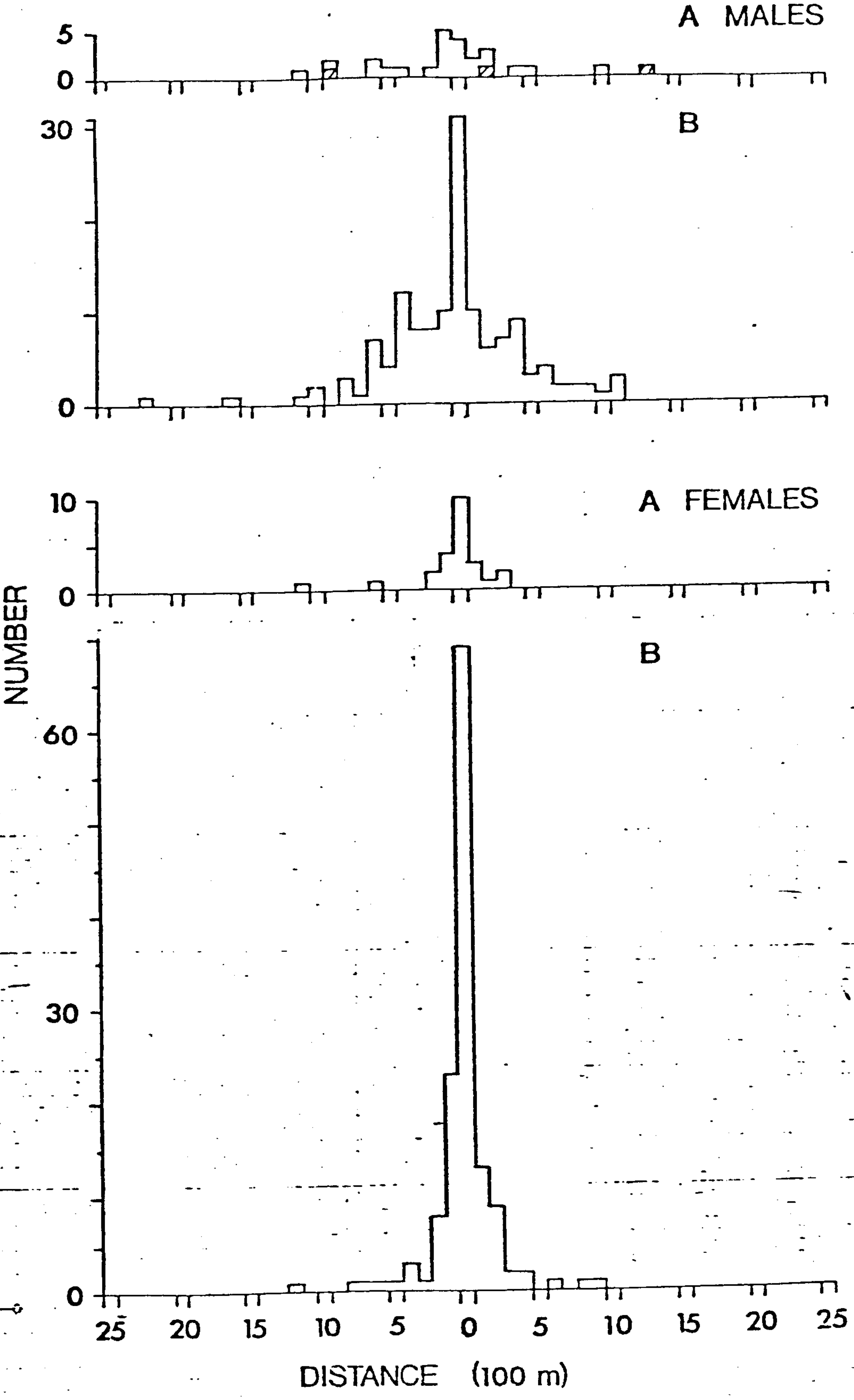

A MALES
5
0
B
30
0
A FEMALES
10
0
B
60
30
0
NUMBER
25
20
15
10
5
0
5
10
15
20
25
DISTANCE (100 m)

Figure 10. Comparison of the number of turtles and distances traveled in a one year interval.

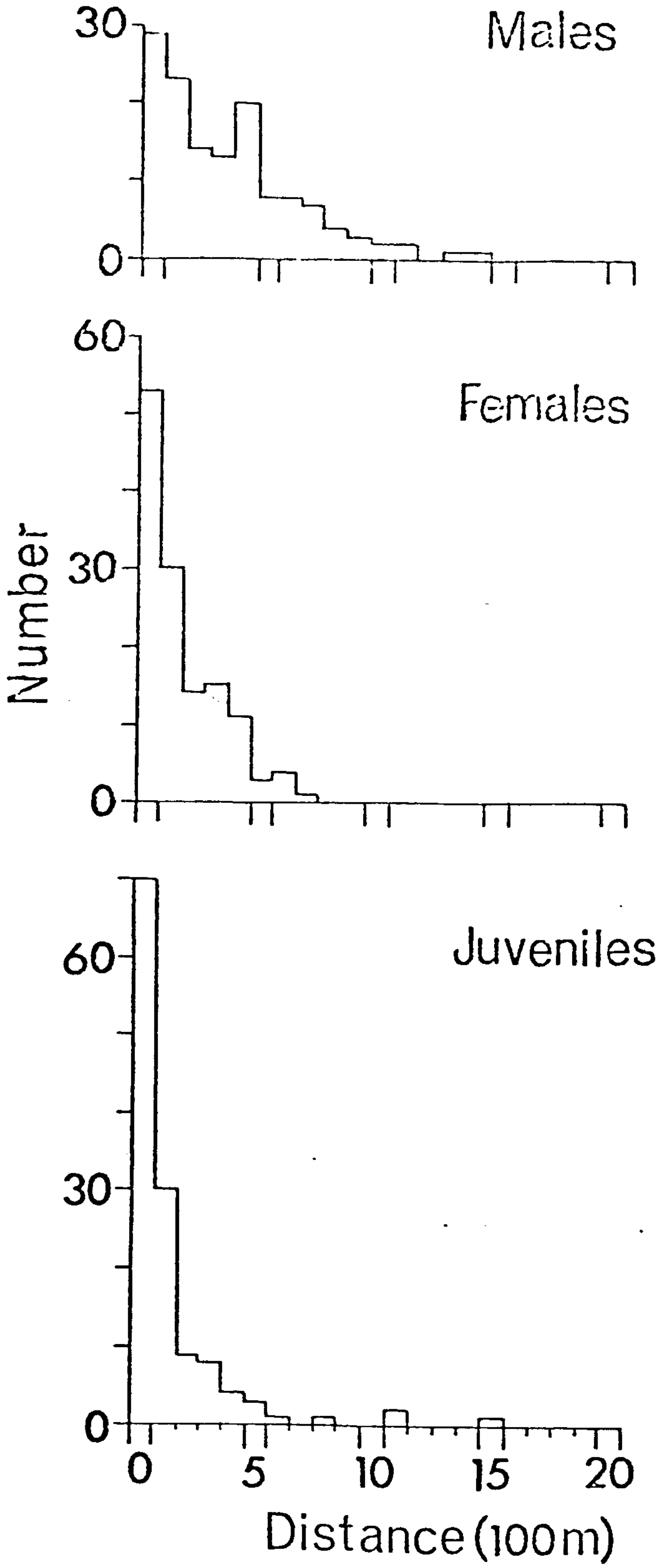

Males
Females
Juveniles
Number
30
0
60
30
0
60
30
0
0
5
10
15
20
Distance (100m)

Table 8. Comparison of the distances and directions of movements in Hayfork _C. marmorata_ over long term periods (year to year).

	Males	Females	Juveniles
One Year Interval:			
Number	137	146	118
Net total - m	-4200	-175	-2835
average - m/individual	-30.7	-1.2	-24.0
Total distance moved - m	50300	21755	16815
average - m/individual	367.2	149.1	142.5
N that moved 200+ m - %	62.8	23.9	28.8
N that moved 500+ m - %	26.3	7.5	6.8
Two Year Interval:			
Number	28	27	16
Net total - m	-5250	-1400	-3500
average - m/individual	-191.1	-51.9	-218.7
Total distance moved - m	10407	5000	5350
average - m/individual	371.7	185.2	334.3
N that moved 200+ m - %	39.3	37.0	43.7
N that moved 500+ m - %	32.1	7.4	17.5
Three Year Interval:			
Number	3		
Net total - m	+650		
average - m/individual	+216.7		
Total distance moved - m	2450		
average - m/individual	816.7		
N that moved 200+ m - %	100.0		
N that moved 500+ m - %	66.6		

My home range estimates for Clemmys marmorata were based on several criteria but are dependent chiefly on the measurements of turtle movements up and down the stream. The stream is about 10 meters wide along its length, and area can be readily calculated by multiplying the length moved times 10 m.

For analysis the Hayfork turtles were grouped as males, females, and juveniles (under 120 mm carapace length) at time of first capture. Animals determined to be juveniles were not changed later even if they grew over 120 mm in size. The frequency of relocations per turtle was low (2.2 average), therefore, I used two estimates of home range size. One was for animals relocated three times, and the other for those found four or more times. The former value was subject to error due to its small sample size, but was considered worthwhile when compared to those estimates obtained for animals relocated more frequently.

It was evident during my field studies that there were great differences in the movements of certain individuals, and large samples would be necessary to determine accurately home range sizes in Pacific pond turtles. However, due to the nature of the study area and species it was not possible to relocate individuals frequently. The maximum frequency of relocation for any turtle was 10. Home range sizes are based on 507 relocations of turtles, and these consist of 26 sightings of turtles with numbers painted on their carapaces and 481 recaptures. Some examples of the extremes in distances traveled by turtles follow.

Several individuals apparently remained at or near the site where first collected. A medium-sized turtle (code 85) was found July 18, 1968, in pool 12 and subsequently recaptured a total of 8 times in the same pool: 1968 (1), 1969 (2), 1970 (2), and 1971 (3). An adult female (code 316) was taken August 8, 1969, at pool 6 and later found at the same site on 5 other occasions: 1970 (3) and 1971 (2). Shifts sometimes varied greatly in length. For example, an adult female (code 95) was first collected July 19, 1968, in pool 13 and later that summer moved 100 m upstream to pool 12. In 1969 I found her three times in pool 12, but in 1970 she was first taken in pool 13 and then again in pool 12. In 1971, she was found on three separate occasions at pool 12 but toward the end of the summer she was collected at pool 6, a distance of 400 m upstream from pool 12.

The longest record of distances traveled in the study area was that of an adult male (code 108) first taken July 19, 1968, in pool 12. In 1968, he moved to pool 7 (+300 m) 18 days after being released, and in an additional 28 days had moved upstream to pool 1S (+100 m). In 1969, he was first taken in pool 18 (-2275), and then at pool 19 (-150). Early in 1970 he was again at pool 19, but 55 days later showed up at pool 13 (+550). In 1971, he was first recaptured at pool 6 (+500) and then found 31 days later at pool 18 (-850). He moved a total of 5625 m during 4 summers of study.

Distances traveled by turtles are summarized in Table 9. Three criteria were used.

First, the distance between extremes indicates the maximum points of their ranges expressed on a linear scale. This estimate of home range was used for hatchling and adult Pseudemys scripta by Moll and Legler (1971). In Clemmys marmorata examined it is clear that adults have a larger linear home range than either the females or juveniles. For turtles captured 4 or more times, the average home range of males was 2.93 times greater than for females and 2.68 times greater than that of juveniles (Table 9). For turtles relocated only 3 times, distances for males were 2.2 times greater than those for either females or juveniles.

Second, the average distance between relocations was determined regardless of direction moved up or downstream. These values were 36.6-57.7% (average 47.1%) less than those for distances between extremes. For turtles taken 4 or more times, the distance between relocations was 3.87 times greater in males than females and 3.01 times greater than that for juveniles. For turtles relocated 3 times, males were 2.44 times greater than females and 2.52 greater than juveniles.

Lastly, the net distances were determined, i.e., distances moved upstream (+) and downstream(-) were pooled for each individual. It is obvious that this category is the smallest of the three, indicating that many turtles were moving in a restricted area. Again, though, males had the largest values. For those turtles relocated 3 times, males yielded values 2.05 times greater than those for females and 2.57 times greater than those for juveniles, and for male turtles relocated 4 or more times, the values were 3.61 and 3.11 times greater, respectively.

Table 9. Assessed mean home ranges of Hayfork Creek _C. marmorata_.

Group	N	Relocations per turtle (range)	Distance between extremes (range)	Distance betwean relocations (range)	Net movements (range)
Males	26	3	599 (75-1325)	346 (175-3200)	121 (0-1225)
	19	4.9 (4-8)	976 (225-2425)	400 (200-5625)	112 (0-1475)
Females	26	3	270 (0-650)	146 (0-1225)	59 (0-650)
	23	5.1 (4-10)	248 (0-750)	104 (0-2100)	31 (0-525)
Juveniles	19	3	269 (0-1025)	137 (0-1850)	47 (0-550)
	18	4.7 (4-8)	363 (0-1150)	133 (0-3175)	36 (0-575)

Assessment of home range size depends on the frequency of relocation. Comparisons of animals relocated 3 times to those found 4 or more times was different by 32.8% (2.9 to 47.5%). There was an underestimate of 21.6% for distances between extremes, and an overestimate of 10.5% for distances between relocations. Net distances were all overestimated (average 26.1%). Thus, it is possible to estimate in rough outline the home range size of a stream dwelling turtle with relatively few recaptures, but large samples are preferred to reduce possible sources of error. Also, the similarity of results in this study may largely be due to relatively large sample sizes. The home range assessments are based on a total of 131 individuals relocated 509 times.

Other studies had fewer individuals but more relocations per turtle (Table 10) and were done under different environmental and habitat conditions. There is little resemblance between the length of travel or maximum estimated home range in _Clemmys marmorata_, _C. guttata_, and _Pseudemys scripta_. In _C. marmorata_, I used the distances traveled in the stream between the farthest points of recovery and multiplied this by 10 m to obtain the area occupied (the stream is about 10 m wide). Moll and Legler (1971) similarly calculated the home range of adult _P. scripta_ but they worked along a wide river and multiplication of length times width gave much larger values than for _C. marmorata_ in a stream. Home ranges of _C. guttata_ were determined by Ernst (1970) in a pond and marsh area, and he used the minimum area method, among others.

Comparison of the estimated home range sizes in Clemmys marmorata to other species of freshwater turtles is difficult because of the great differences in habitats, sizes and habits of turtles, and methods of determining home ranges. The maximum home range for P. scripta are markedly greater than C. marmorata (Table 10), but parts of these areas were not used by the sliders. Moll and Legler (1971) also defined the observed home range of P. scripta: juveniles, 0.104 hectares (range 0.031-0.188), or, stated differently, an average of 0.26 acres (0.08-0.46), and adults, 1.997 hectares (0.669-5.017) or 4.94 acres (1.65-12.40). These are still greater than for C. marmorata, but such corrections may alter comparisons of data. Ernst (1971) also reported the average distances moved between recaptures. He found that 5 juveniles (recaptured 8 times) averaged 156.5 m (150-350 m range), 42 males (193 recaptures) 86.1 m (3-420), and 44 females (173), 91.1 m (2-440 m). These are surprisingly different from distances recorded for C. marmorata: 37 juveniles (142 relocations) averaged 135.0 m (0-3175 m), 45 adult males (172 times) 372.9 m (0-5625), and 49 adult females (195 times) 125.1 m (0-2100). The few juvenile C. guttata studied had moved the farthest distances, whereas adult male C. marmorata averaged the greatest distances between relocations. Adult C. guttata appear to be more sedentary than adult C. marmorata. However, the studies concern a pond situation and stream community, respectively.

Summary of Findings on Movements and Home Range

A total of 581 turtles were individually marked and released, and about 70% of these were recaptured or, in a few cases, observed without recapture. This high relocation rate suggests that few animals left the study area during the duration of my work and that collecting by the described method is to date the most efficient means to relocate marked pond turtles. Due to the secretive nature of the animals, the large study area (3.5 km), and only one collector, there were relatively few relocations per turtle (average = 2.2). However, after 4 summers of collecting there were large samples for estimation of population density, spatial distribution, sex ratios, short and long term movements, and, collectively, sufficient recaptures for assessment of home range.

The density of turtles was assessed at 214 per hectare (85/acre) of stream and 642 hectare (255/acre) for those parts of the stream over 0.5 m deep. This is presumed to be a relatively high density of turtles. If so, this may result in increased movements by individual turtles as they seek out needed resources, such as atmospheric basking sites, food, and cover. Answers to these queries rest on further studies of this species in different habitats or densities, and investigations on other stream-dwelling turtles.

The sex ratio of the Hayfork population was 1.17 males to 1 female, which may be a real difference or an apparent one caused by greater activity by the males. That is, there may be a greater probability of finding male turtles if they travel farther since new animals would then be entering the study area at both ends at a greater rate than females. Also, collecting was heavily done in early July, the presumed egg laying time for C. marmorata and females at this time, and possibly at other intervals, may be on land.

It is clear that Hayfork C. marmorata have a spatial distribution greatly influenced by environmental conditions. Large numbers were present at certain pools whereas at others no turtles were found. There was a highly significant correlation between high numbers of turtles and pools of large size (length), and with deep waters and abundance of cover. Turtles were repeatedly found associated with particular pools in the study area, such as pools 2, 12, and 27, but were rarely taken in the shallower areas between pools. Present evidence suggests that pond turtles spend most of their time at a few pools, and when they move to a different one it is probably done in a relatively short time. Shifts between pools can be accomplished relatively fast, thereby reducing times they are more open to attack. Radiotelemetry data on one adult turtle and hundreds of relocations of marked turtles indicate that mature and juvenile animals are capable of moving 200 to 400 meters within a 24 hour period. There is probably a high selective advantage for such a strategy since in the large, deep pools there are more opportunities to avoid predation from terrestrial animals (coyote, bear, mink, man) than is possible in shallow water where the main defense in camouflage. Familiarity with particular hiding places may also be at a high premium to avoid aquatic predators such as river otter.

The turtles spent many hours sunning, foraging, and moving about in the deep, large pools, but few turtles were observed or found in shallows during the day. They may move under cover of darkness, but this needs to be examined further. I observed turtles actively moving in riffles at 0530 hours, and as late as 2000 hours. Occasionally a turtle was observed moving during daylight hours.

The clumped or aggregated distribution pattern of stream dwelling C. marmorata is an obvious feature of their spatial distribution and must be considered in analyzing their home range behavior. Centers of activity apparently are the large, deep pools with ample cover, which presumably contain most of the resources for existence. Movements to another pool undoubtly entails some risk since the animals are exposed temporarily to predators. Further, any forays into new areas may place the turtle in an already crowded pool or into parts of the stream with which it is less familiar.

The short and long term movements of marked turtles revealed that males consistently moved farther than females or juveniles. The average distance moved during a single summer for males was 354 m and from one summer to the following summer 367 m; females moved 169 m and 149 m, and juveniles 142 m and 142 m, respectively. About twice as many males traveled over 200 m and four times as many went over 500 m than did either females or juveniles.

Females may be more sedentary than males because of several reasons. Restricted movements may reduce the risk of predation in unfamiliar territory and improve the chances of continually locating suitable feeding, basking, and nesting areas. Since males may inseminate more than one female, they may travel distances in search of receptive females. Moreover, the long distance moves by the males promote gene flow that may be important to maintenance of genetic variability and results in exploration of new areas.

The migration and dispersal strategies in freshwater turtles appear to be variable in different species. Juvenile _P. scripta_ may wander farther from the point of release than adults (Cagle, 1950), and dispersal of the species in Panama occurs chiefly at juvenile stages (Moll and Legler, 1971). On the other hand, Sexton (1959) found that adult _Chrysemys picta_ had a greater tendency to emigrate than juveniles. In another study, Ernst (1970) found no significant difference between the home range of adult males (1.30 acres) and adult females (1.31 acres) of the spotted turtle, _Clemmys guttata_, when determined by the minimum area method, but in another comparison the mean distance between recaptures was 156 m for a few juveniles, 86 m for males, and 91 m for females. Hayfork Creek _C. marmorata_ were also different: males were mobile and moved long distances whereas the females were mostly sedentary. Juvenile _C. marmorata_ did not disperse great distances. There are no clear reasons explaining the differences in the dispersal patterns of these turtles.

Present evidence suggests that the home range sizes of Clemmys marmorata are not comparable to other species of freshwater turtles. Male pond turtles had large home ranges while both females and juveniles had smaller, similar sized ones. These data for a stream dwelling turtle indicate that in general the same individuals return year after year to the same home range, rather than establishing a new home range each summer. Assessment of home range based on 3 relocations per turtle showed larger fluctuations in sizes than home range determined on 4 or more relocations per turtle, but the former value may be a useful measure when used with other information.

The net movements of pond turtles varied, too. Within summer months there were no movements beyond 100 m in 12% of the males, 34% of the females, and 40% of the juveniles. Males and juveniles had more individuals move upstream than downstream, but the reverse occurred in the females (Table 7). The net distances moved in both one year and two year intervals were all in a downstream direction (15.3 and 153.9 m/individual, respectively). Differences in these times of travel may be due to spring floods that possibly move turtles downstream; most recaptures at yearly intervals are records from the latter parts of one summer until the first part in subsequent summers. Flowing waters may tend to displace animals downstream, but as the summer progresses the stream becomes more sluggish and it may be less of an effort to move upstream. There may be a positive rheo-taxis to flowing waters. Field data suggests that there is an overall net gain of upstream movements during summer months, which may counteract the downstream displacements during times of high water (spring months).

There was no evidence of territoriality reported in P. scripta (Moll and Legler, 1971) or C. picta (Ernst, 1971), although home ranges overlapped broadly in time and space. There was wide overlap in the home ranges of Clemmys marmorata; territoriality per se was not observed, but aggressive actions were frequent during times of atmospheric basking and is described later. Territoriality has not been observed in any species of freshwater turtle, but this may be due to the lack of studies rather than being a biological phenomenon.

Studies of distances moved and home range sizes in the past past often were not directed toward biological questions. As suggested by Turner (1971), why measure the home range and what questions are involved? He urged that home range estimates contribute to the solution of some specific problem, or to the understanding of particular ecological processes. Earlier, Tinkle (1967) stated that studies of home range are important in indicating the size of area necessary to sustain an individual and the degree of overlap of home ranges indicates something about the social structure of the population. As already discussed for Clemmys marmorata, the spatial and temporal relationships are important components of life history strategies and modes of life. There are few comparative studies of home ranges and their role in the ecology of freshwater turtles, but present evidence suggests that there are advantages for remaining in a given area, such as being familiar with areas inaccessible to predators and sites suitable for basking.

Thermal Ecology

Attaining body temperature levels suitable for activity is an important requirement of reptilian life, and there are many strategies employed by reptiles to attain and maintain elevated body temperatures. Elevated temperatures, often of narrow range and at a level characteristic for a species or group, are necessary for the vital life processes of foraging, digestion, reproduction and escape from predators (Cowles and Bogert, 1944).

In the aquatic environment, there are greater limitations in thermal range available than on land, especially for animals living in large bodies of water. Thermal selection is possible in water, but some aquatic and semi-aquatic animals achieve high body temperatures, well above that of the water, by emerging and exposing themselves to sources of heat on land.

Basking in the sun has long been known as a common attribute of aquatic and semi-aquatic turtles. Traditionally, the term "basking" in freshwater turtles was used for those periods when animals engaged in deliberate and sustained exposure to sunlight out of water. Less well recognized is their habit of basking while immersed. Recently, Moll and Legler (1971) proposed two types of basking behavior: "atmospheric basking" referred to times when turtles were lying quiescent on some object out of water for variable but usually long periods, and "aquatic basking" described the behavior of turtles that basked at the surface of the water. They used the term "sunning" more or less synonymously with atmospheric basking.

Distinctions should be made between sunning and basking. By definition, basking means to bathe, especially in warm water, or to warm by continued heat (Neilson et al., 1959). Herein, basking is regarded as sustained, deliberate exposure to heating by external sources and includes heating by direct or indirect absoption of solar insolation and by selection of warm water. In the present paper, I recognize that basking may occur out of water and in water, i.e. atmospheric and aquatic basking, respectively. Further, the term "sunning" specifically denotes direct exposure to the sun and is only part of the basking repertoire of freshwater turtles.

Boyer (1965) has examined several physical and biological factors that effect sunning in Pseudemys scripta, and Moll and Legler (1971) described various environmental parameters influencing both atmospheric and aquatic basking in the species. However, there has been little study of basking behavior in individual turtles. Further, there is meager information on the frequency and duration of basking or of the behavior of individuals on sunning sites. Indeed, there is at present uncertainity as to the significance of basking in the life activities of aquatic and semi-aquatic turtles. and if these turtles regulate their body temperatures.

In view of these problems, I have undertaken to: (1) study thermoregulation in turtles under natural conditions, (2) determine the daily and seasonal frequencies of sunning, (3) quantify and compare the durations and periods of sunning of individual turtles, and (4) ascertain individual behavior during atmospheric and aquatic basking.

Materials and Methods

Studies of basking on free-living individuals were made mostly during the summers of 1970 and 1971, from late spring to early fall and at different pools in Hayfork Creek. I observed turtles at pools 12, 24, 27, and near Shiell Gulch, which is three miles upstream from the study area.

The observation area at Shiell Gulch was 18-22 m east of my campsite in the summer of 1971. Turtles did not seem frightened by my presence in this camp and emerged to bask in the sun throughout the day. Low shrubs aided in my concealment. A pool about 50 m long and 3-4 m wide was formed here by a cement dam (1 m high). Depth in the middle of the pool varied from 0.5-1.5 m, but most of the water was less than 0.8 m deep. Turtles sunned on rocks in the middle of the pool. In July, 1971, sunlight was on the pool at about 0800 hours and continued until 1300 hours. Partial shade occurred from 1300 to 1700 hours, and afterwards the pool was entirely in shade.

Pool 24 was about 15 m long, 5 m wide, and 1 m deep. Sunning sites were the buttress of a tree and two boards. Direct sunlight was on this pool from 1000 to 1200 hours and partial sunlight occurred between 0900-1000 and 1200-1500 hours.

Pool 12 was 6-8 m wide and 65 m long. It reached a depth of 3.5 m and much of the pool was over 2 m deep. Turtles sunned on rocks on the west side on the pool (Figure 11). From July to early September, there was sunlight on the sunning sites at about 0800 hours, and is continued to 1300 hours when shade from trees and nearby cliffs began to fall on the pool. The sunning sites were in full shade by 1530 hours.

Figure 11. Pool 12, Hayfork Creek, viewed from blind and facing to the north. Note turtles sunning on rocks in center. Photograph taken July, 1970.

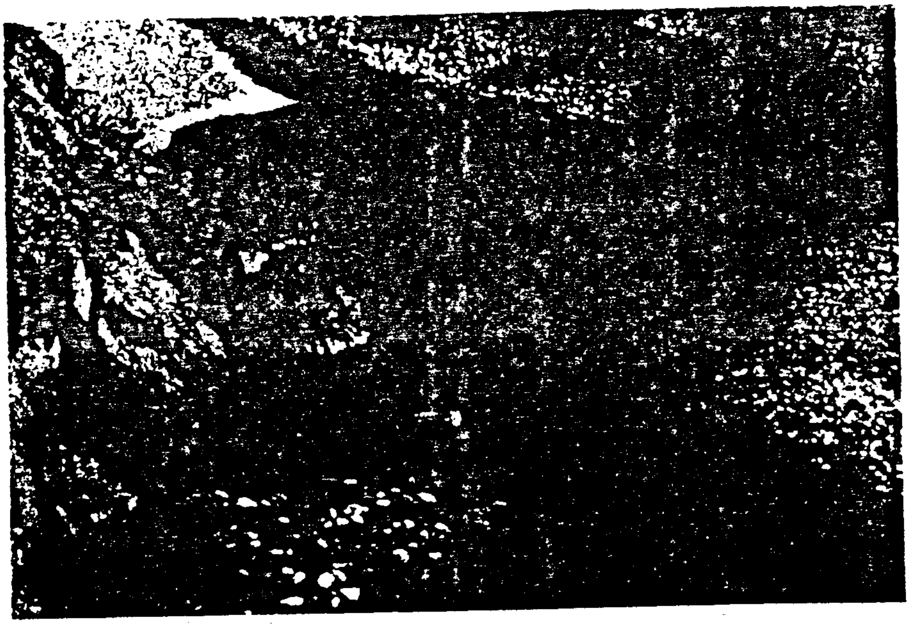
Pool 27 was about 7 m wide, 30 m long, and 2.5 m at maximum depth. Turtles sunned on rocks in the north part of the pool (Figure 12). From July to early September, sunlight was on the pool at about 0730 hours, and partial shade did not occur until about 1430 hours. Full shade was on the pool at about 1800 hours.

I observed turtles with binoculars. The size, sex and position of individuals aided in their identification. Also, 70 individuals were collected in pools 24, 25, 26, and 27 in June and July, 1970. These were painted with white enamel paint (numbers 3-4 cm high on each side of the carapace) and released at the place of original capture. Several of these were later observed to bask in pool 27.

Individual animals could often be observed for several hours. If a turtle dove into deep water, moved behind any object, or shifted its position so there was doubt about its identification, the record was discontinued.

Turtles terminated atmospheric basking voluntarily and when frightened or threatened. Animals that slowly returned to the water were regarded as voluntarily terminating basking. These individuals usually turned toward the water and then moved to the edge of the basking site. They often dunked their heads into the water before departing. Clemmys marmorata is wary, and on several occasions all the basking turtles out of water suddenly dove off their basking sites. They were frightened by several natural events, including landslides into the pools from nearby cliffs, attacks by predators (mink), approach of deer near the water, disturbance in the water by animals (Merganser, Great Blue heron), and, rarely, persons fishing in the stream.

Figure 12. Pool 27, Hayfork Creek. Top: View from blind looking downstream and to the east. Sunning sites were rocks at left in the photograph (below the cliff). Bottom: View of pool facing north. Blind was on top of bluff in left of photograph. Photographs taken July, 1970.

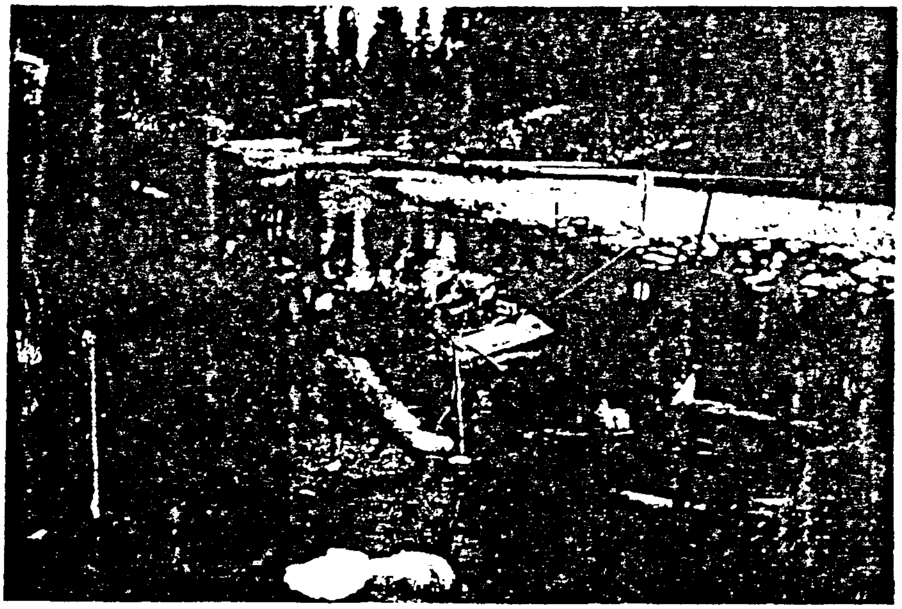


These instances of rapid departure from basking sites plus voluntary terminations represent the natural basking habits of the species and in my analysis they are defined as "natural basking". In the complex natural ecosystem at Hayfork Creek, turtles were often frightened or threatened from their basking sites but, in most cases, they returned to the sites 1 to 10 minutes later if the real or potential danger disappeared.

Pool 24 was selected for a site of radio-telemetry studies because it previously was known to be occupied by turtles, possessed a log suitable for construction of an antenna system, and was small enough (15 m long, 5 m wide, and 1 m deep) to be enclosed with a fence to keep the turtles in one pool. The buttress of a dead alder (Alnus rubra) formed a natural sunning site in the middle of the pool (Figure 13). Previous collecting revealed that turtles in Pool 24 sought cover under the tree buttress and beneath the roots of a live alder on the west shore of the pool. The sunning area was increased by placing two boards on the buttress. A 2 cm thick board 25 cm wide and 1.5 m long was nailed to the east side of the buttress; another 2 cm thick plank 15 cm by 2 m extended from there southward to the upper end of the pool (Figure 13). A fence (chicken wire) enclosed the pool, except on the west shore where a 1 to 1.5 m high bank formed a natural barrier.

A loop antenna was tacked along the edges of the boards and the lower east-facing side of the tree buttress. A co-axial cable connected the antenna to a receiver in my observation post 20 m east of the enclosure. This AM radio system is described in detail elsewhere (McGinnis, 1967a). Turtles were continosly observed with binoculars during times when temperature data were recorded.

Figure 13. Pool 24 looking north (downstream). Note antenna wires on boards where turtles sunned. Photograph taken July 20, 1970, at 1000 hours.



Environmental Temperatures

On July 9-12 and July 16-19, 1970, environmental temperatures were recorded at Pool 24 as follows: Shore Air Temperatures (T_{sh}) - taken in shade of the observation post; Surface Water Temperatures (T_s)- recorded at a depth of 10 m upstream from the enclosure. Surface water temperatures were taken with a temperature sensitive transmitter placed in the creek and near a separate antenna loop system. These environmental temperatures were recorded at about 30 minute intervals.

Between July 9 and 19 there were similar changes in the daily air and water temperatures. These data are given in Table 11. Prior to 0900 hours in the morning, sunlight did not illuminate the enclosure. At these times the water was cool ($T_s = 17^o$ to 18.2^o), but, in fact, it was warmer than the air ($T_{sh} = 11.6^o$ at 0730 hours on July 10). Once sunlight struck the pool, air temperatures rapidly increased. Shore air temperatures rose from about 18^o at 0900 hours to a maximum of $31^o - 35^o$ ($\overline{X} = 32.7^o$) between 1400 and 1630 hours. After this daily peak, shore air temperatures cooled faster than the water as the pool received less sunlight in the late afternoon and evening hours.

Table 11. Comparison of daily changes in air temperatures (in shade) and water temperatures (10cm deep) at pool 24 in 1970.

Time	July 9		July 10		July 11		July 12	
	Air	Water	Air	Water	Air	Water	Air	Water
0730			11.6	17.0				
0800								
0830			17.0	17.2				
0900			19.2	17.4	18.0	17.6		
0930			20.5	17.4	19.6	17.7	19.2	17.7
1000			21.6	17.6	21.2	17.8	21.8	17.8
1030	24.2	19.2		17.8	23.6	18.7	22.4	18.0
1100			24.4	18.5	24.0		23.8	19.4
1130	24.8	20.2	24.5	19.0	25.0	20.0	25.0	20.0
1200	26.0	21.0	25.6	21.0	27.2	21.0	26.4	20.6
1230	28.8	22.1	26.2	21.4	28.5	21.2	26.6	21.8
1300	28.8	23.2	27.5	22.6	28.2	23.0	29.4	22.8
1330	29.2	24.0	28.2	24.0	28.4	23.4	30.2	24.1
1400					30.2	24.2		
1430					30.3	25.0		
1500					29.5	26.0		
1530	30.4	26.2			31.8			
1600								
1630	31.0	27.0						
2000								
2030	23.2	24.8						

Table 11. Comparison of daily changes in air temperatures (in shade) and water temperatures (10cm deep) at pool 24 in 1970.

Time	July 16		July 17		July 18		July 19	
	Air	Water	Air	Water	Air	Water	Air	Water
0730								
0800								
0830								
0900	18.0	18.2						
0930	18.6	18.6	19.8	18.5			20.6	18.7
1000	19.5	19.0	22.6	19.2	21.6		23.4	
1030	22.5	19.3	23.8	19.3	23.8			19.6
1100	24.0	19.8	26.4	20.2	26.5		25.8	
1130	25.2	20.3	27.2	20.4	27.2		26.4	20.8
1200	25.6	21.0	28.4	21.2	29.0		29.0	
1230							29.0	22.3
1300					33.2		30.0	
1330							31.0	24.3
1400					34.8			
1430					33.4			26.6
1500					35.2	27.0	31.5	27.0
1530								
1600								
1630								
2000					23.5	25.0		
2030								

Additional environmental temperatures were taken at 2 hour intervals from 0800 to 2100 hours on July 21, 1970 (Figure 14). They included the temperature of the air 1 m over the sunning site in shade (T_p), the surface of the sunning site on a board exposed to available sunlight (T_r), and water at a depth of 10 cm (T_s) and 1 m (T_d) in the pool. No turtle behavior was recorded on this day. I used a Schultheis quick recording thermometer for temperatures, except deep water temperatures that were taken using a radio transmitter on the end of an antenna.

On August 14 to 16, 1970, Shore Air Temperatures (T_{sh}) and Surface Water Temperatures (T_s) were taken as previously described, but on these days a Springfield Outdoor Thermometer (T_{st}) (attached to the tree buttress 0.5 m above the sunning site) recorded temperatures in sunlight and shade, depending on the time of day (Figure 15).

Figures 14 and 15 show a marked rise in environmental temperatures when there was direct insolation for about 2 hours daily (1000 to 1145 hours) and some increase in temperatures when there was partial sunlight on the pool (0900-1000 and 1145-1500 hours). These data clearly indicate that the temperature of a transmitter or thermometer exposed to direct sunlight rapidly increases and attains levels much higher than that in shaded areas on land or in the water. Further, the air temperature was greater than that of the water at about 0930 hours, but after about 2000 hours the water was warmer than the air.

Figure 14. Environmental temperatures taken at pool 24 on July 21, 1970. T_r = air temperature on basking site recorded with radio transmitter; T_p = air temperature 1 m over pool (in shade); T_s = water temperature at surface (10 cm deep); T_d = water temperature at depth of 1 m. Scale at bottom indicates percent of pool in shade.

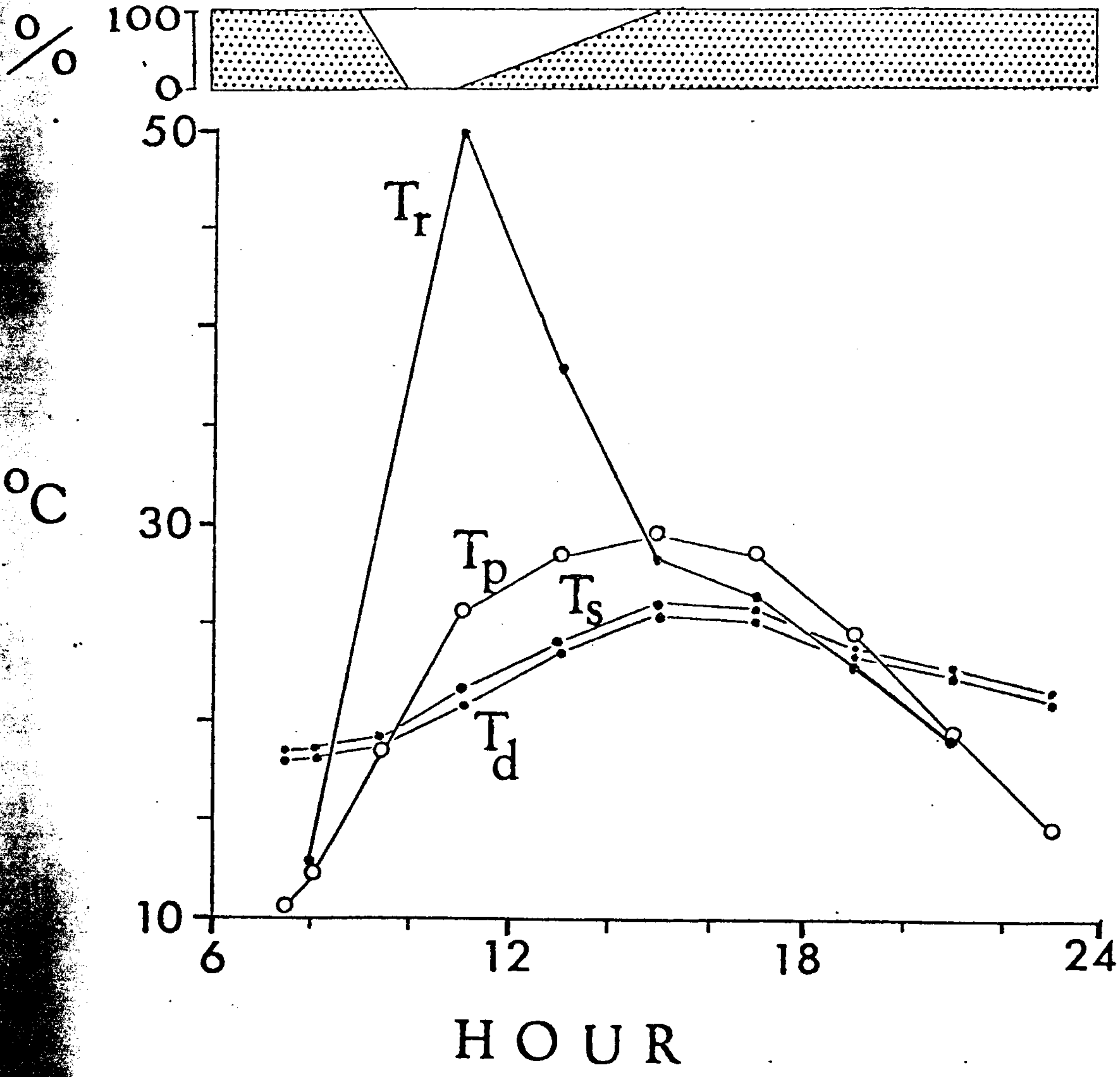
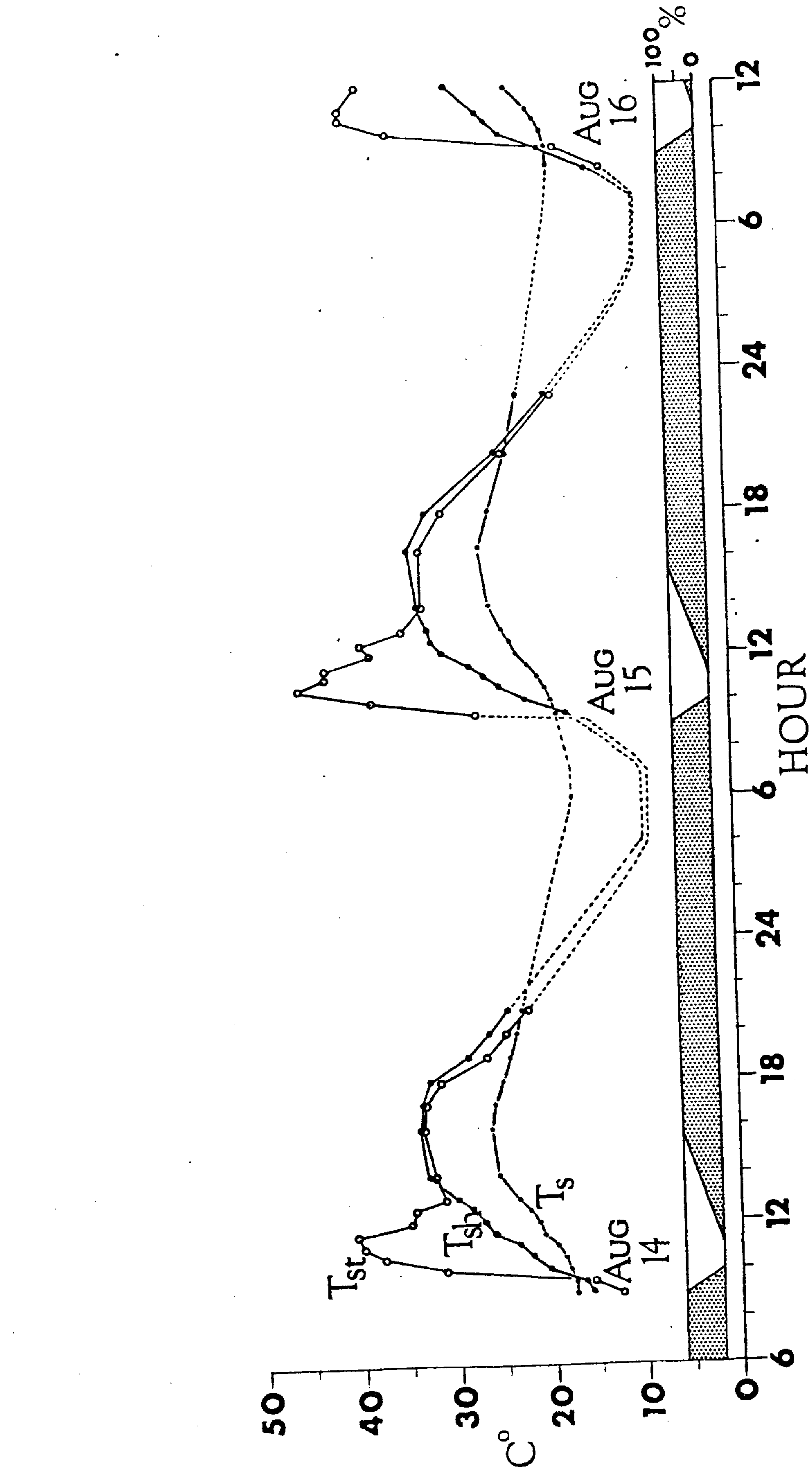

%
100
0
50
30
10
°C
T_r
T_p
T_s
T_d
6
12
18
24
HOUR

Figure 15. Environmental temperatures taken at pool 24 on August 14, 15 and 16, 1970. T_{st} = air temperature 0.5 m over pool and on tree buttress recorded with a Springfield Outdoor Thermometer; T_{sh} = air temperature in shade (Shore Temperature); T_s = water temperature at surface (10 cm deep). Scale at bottom indicates percent of pool in shade.


50
40
30
20
10
0
C°
Tst
Tsh
Ts
AUG 14
AUG 15
AUG 16
6
12
18
24
6
12
18
24
6
12
HOUR
100%
0

The study area is at an elevation of about 630 m (2300 ft.) and warm days (i.e. over 30°C) are frequent in the summer. However, the night air temperatures drop to 8-12° because of cool air moving down from nearby montane areas.

Temperatures available to _C. marmorata_ in the summer vary widely during the day. There are water temperatures about 20° at midnight and as the morning progresses there is a slight drop until the water is about 17° at 0900 hours. Partial and then direct sun rapidly heat the sunning sites and surrounding air between 0900 and 1500 hours; during these times the air is markedly warmer than the water. After 1200 hours the water remains above 22° (maximum of about 26° in the late afternoon) until about 2300 hours. Thus, the turtles have thermal gradients available where temperature selection can be made for the greater part of the day. Between 0900 and 2300 hours there were environmental temperatures of over 20° continually available either on land or in the water.

Radiotelemetric Study of Free-living Pond Turtles

There have been no radiotelemetric studies of freshwater turtles in North America. The only telemetry study of deep body temperatures in a freshwater turtle was done by Moll and Legler (1971) on one female _P. scripta_ in an outdoor enclosure. I used this technique to study temperature changes in _C. marmorata_ because it provided deep body temperatures of unrestrained turtles in natural situations, where the animals could select their preferred temperatures. A continuous record is possible, thereby permitting examination of both heating and cooling rates. Field observations on the turtles made it possible to correlate changes in behavior with body temperatures. These studies provided information on the importance of sunning in the ecology and physiology of _C. marmorata_, and also suggested why atmospheric basking behavior is a major component of the daily lives of certain turtles.

Small temperature - sensitive transmitters (see McGinnis, 1967b) sealed in beeswax and lodged in the gut recorded changes in deep body temperatures of turtles.

To insert a transmitter, the turtle's mouth was gently pried open with a ruler, and then a wooden rod was placed against the angle of the jaws. The transmitter at the end of a plastic aquarium tube was inserted deep into the throat and slowly manipulated down to or near the stomach; at this point the plunger (pencil) inside the tube was pressed, releasing the transmitter, and the tube and plunger were removed. No turtle regurgitated or damaged a radio unit inserted in this manner. Two units were placed into turtles; one was later recovered but the other passed out of the turtle and was lost in the creek.

Records of body temperatures were taken 6 days after insertion and the transmitters continued to emit signals up to 16 days after implantation. The two units I used in the field were passed out of the turtles 10 and 16 days after insertion.

After pool 24 was fenced, I found five adult turtles inside the enclosure. They were painted with small white numbers (3 cm high) on each side of the carapace for individual recognition. Testor's gloss white enamel was used since prior work showed that this brand was durable when applied to the shell of a turtle. The turtles were returned to the enclosure after being measured and painted. During the first few days after capture, they did not regularly emerge and were probably disturbed by handling. After 3 to 5 days they began to use the boards and buttress of the tree for sunning purposes. Dead frogs and tadpoles, and live caddisfly larvae (Trichoptera) were placed in the pool two or three times a week as a source of natural food.

An adult female (White 47) and an adult male (W10) were used for telemetry studies since they both regularly emerged to bask on the boards a few days after handling. Radio units were inserted on July 5 and 12, 1970, respectively. Body temperatures were recorded six days later. After this period, the turtles with transmitters behaved like other turtles in the enclosure. It was necessary to wait six days because during the first few days after insertion of the transmitters they failed to sun and appeared to be exceptionally wary.

On July 11, 1970, the adult female exhibited a single basking period out of water (Figure 16). Between 1030 and 1050 she remained near the surface with her neck fully extended out of the water, but did not emerge. A slight rise in body temperature (0.6°) during this period may be due to: (1) heat absorbed by the shell through the water; (2) heat picked up through the neck out of water; (3) warmer water on the surface; and/or (4) slight differences between the transmitter inside the turtle and the transmitter recording water temperatures (accuracy of the units was usually within 0.2°). She emerged at 1050 (BT = 19.6°) and sunned for about 15 minutes. At 1110 hours (BT = 29.0°) she moved into partial shade that was available on the board, and during the next 54 minutes maintained her body temperature within a narrow range (BT = 29.2 to 30.0°) by moving in and out of shaded and illuminated areas on the board. She shifted position on the board at least once every five minutes. Approaching deer frightened her into the water at 1204 hours, and her body temperature rapidly dropped (BT = 22.7° at 1214 hours). The temperature of the water and the turtle were equal at 1245 hours (22°). Between 1245 and 1500 hours she remained submerged but came up for air frequently (at least once every 15 minutes) or rested with her head out of water for up to 5 minutes at time. Water temperatures rose from 21° at 1200 hours to 26° at 1500 hours; between 1245 and 1500 her BT increased from 22° to 25.5°.

On July 12, 1970, there was an extended basking period out of water from 0954 (BT = 18.6°) until 1226 hours (BT = 32.3°). She sunned for about the first 25 minutes after emerging. Between 1035 and 1226 hours she moved in and out of shade (Figure 17), and regulated her body temperature between 31.5 and 33.3°. The highest body temperature obtained during the basking period was at 1055 (33.3°) and as she approached 33° there were movements into shade. She often shifted her position while sunning and seldom faced the same direction for over 5 minutes. There were fewer movements when in partial or full shade, but she continued to rotate the body to different positions at least once every 10 minutes. On first emerging out of the water the legs and neck were fully extended, but as the BT approached 30° they were withdrawn into the shell. These changes in posture and position are discussed later.

On July 19, 1970, the adult male emerged at 1011 hours (BT = 19.7°) and reached his highest temperature of 34.0° at 1058 hours (Figure 18). He was in full sun most of this time, and the appendages were fully extended out of the shell. When his BT approached 34° he withdrew his appendages and moved into the shade. The turtle was frightened off the sunning site at 1111 hours by movements of deer near the creek, and his body temperature dropped rapidly once in the water. After 18 minutes he emerged again, exposed himself to full sun for about 5 minutes, and then moved into partial shade. This area became entirely shaded after 1235 hours and he was quiescent during most of this time. The water temperature rose from 19.2° when he first emerged at 1011 hours to 25.4° at the time of his second submergence (1359 hours).

Figure 16. Changes in deep body temperatures of a free-living adult female Clemmys marmorata (W47) in relation to changes in environmental temperatures recorded on July 11, 1970. Solid line = body temperature, botton broken line = water temperature (10 cm deep), and top dashed line = air temperature (in shade). Stippling indicates percent of turtle's body that was shaded during emergence. Arrows indicate movements out and into the water; distance between vertical lines is amount of time out of water.

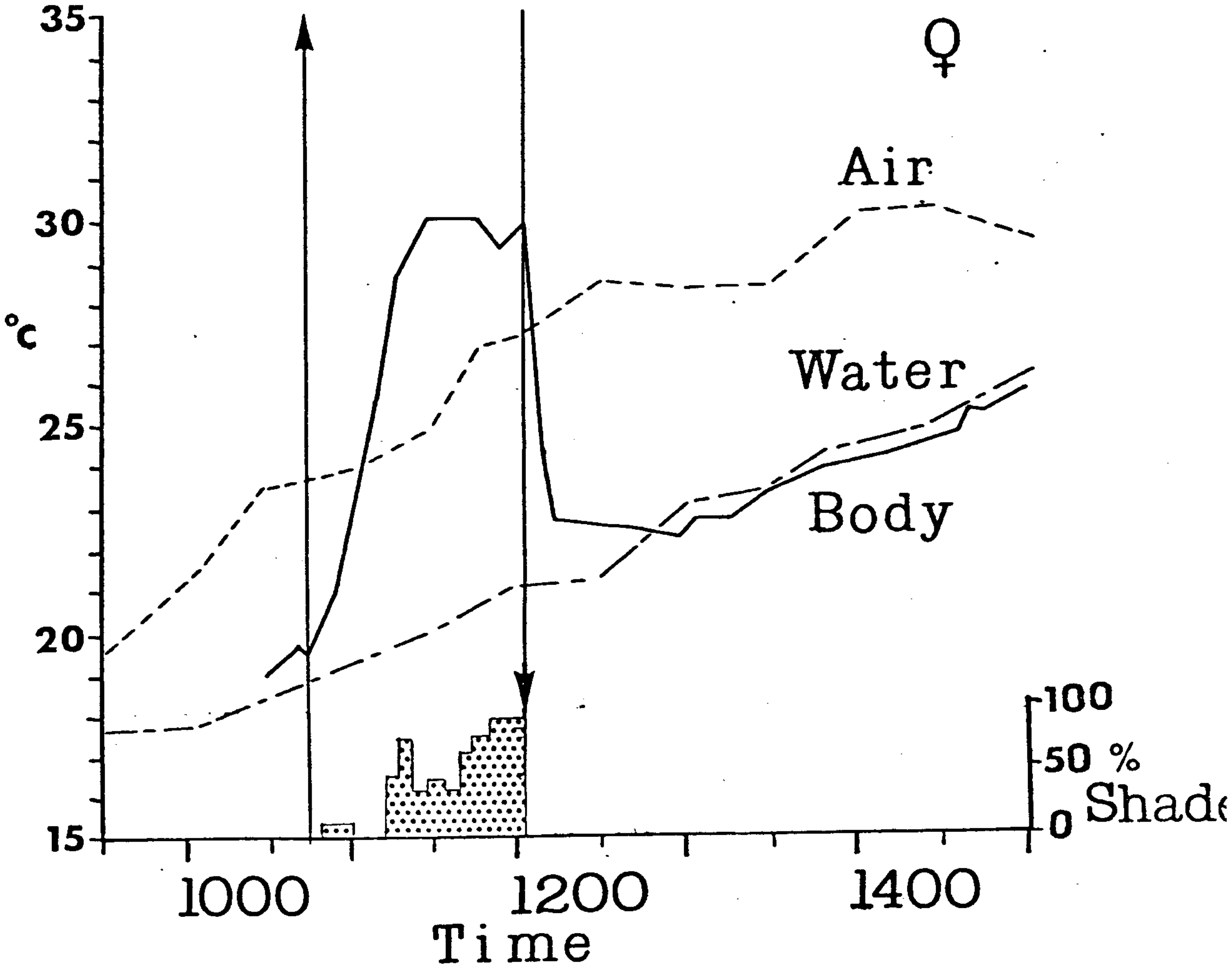

35
30
25
20
15
°c
♀
Air
Water
Body
100
50 %
0
Shade
1000
1200
1400
Time

Figure 17. The same animal shown in Fig. 16 studied on July 12, 1970.

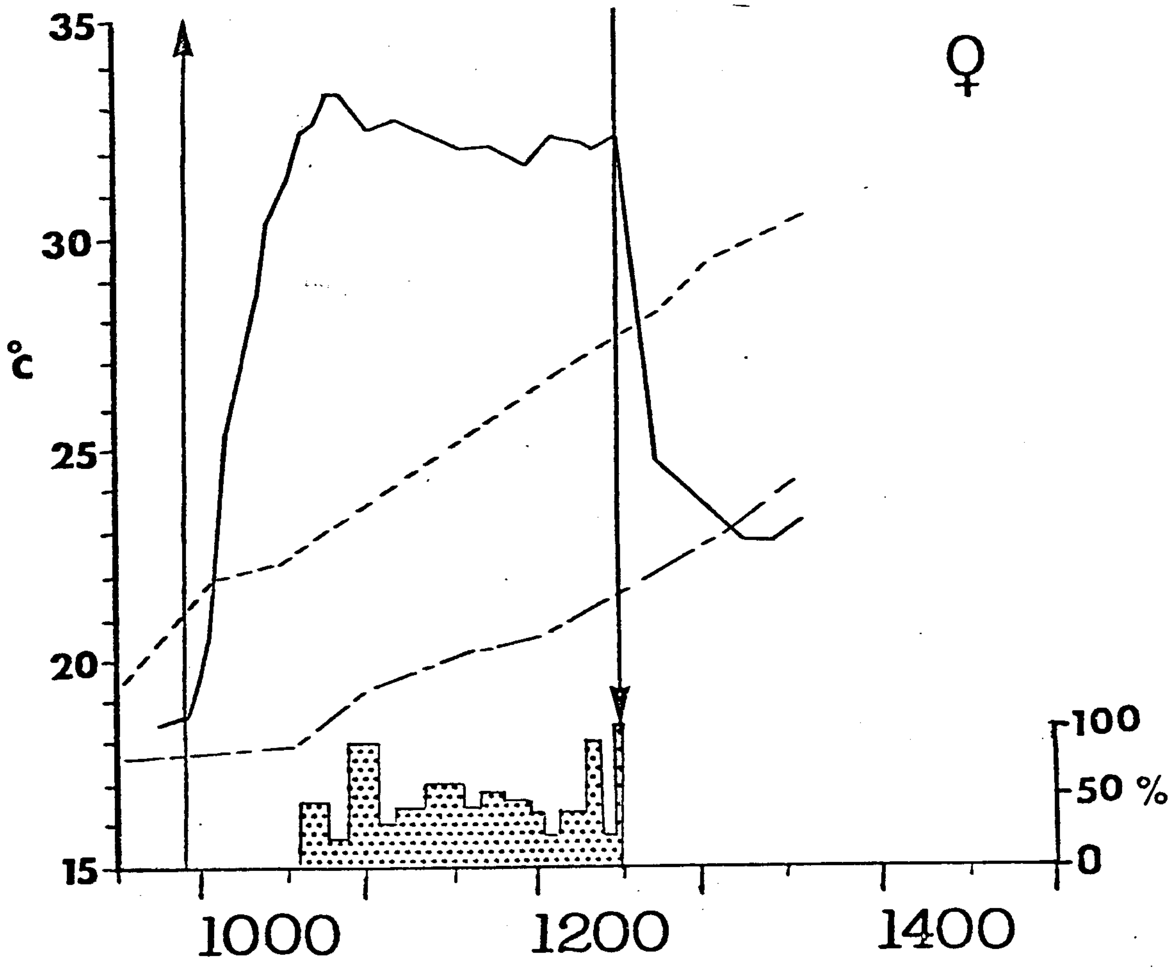
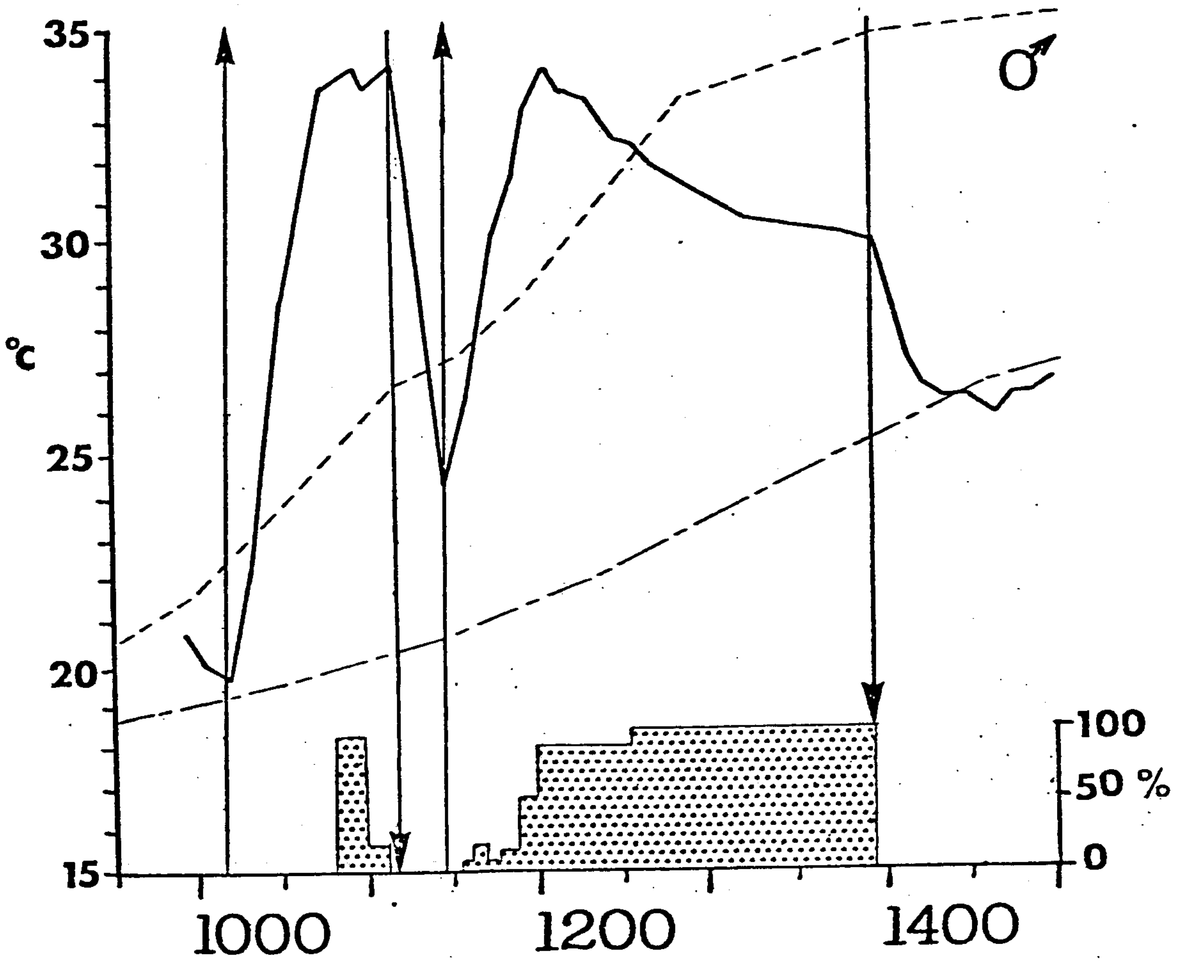

35
30
25
20
15
°C
♀
100
50 %
0
1000
1200
1400

Figure 18. Changes in deep body temperatures of a free-living adult male Clemmys marmorata (W10) in relation to changes in environmental temperatures recorded on July 18, 1970. See Fig. 16 for explanation of symbols.


35
30
°C
25
20
15
100
50 %
0
1000
1200
1400
♂

Daily Patterns of Atmospheric Basking

The general times of sunning have been noted by several workers for a number of aquatic and semi-aquatic turtles of the family Testudinidae. Cagle (1950) found that the slider, Pseudemys scripta, had its height of basking (= sunning) during mid-morning and mid-afternoon but some individuals basked out of water during the night. He also reported that feeding could occur at any time but was usually restricted to early morning and late afternoon. Boyer (1965) observed that normal basking (= sunning) in species of Pseudemys usually began within a few minutes after sunrise if weather was favorable, and very few individuals remained on sites half an hour before sunset. His field observations revealed that the turtles exhibited a marked preference for unshaded basking sites. As the position of the sun changed, unshaded sites sometimes became shaded, but this rarely caused cessation of basking or shifting on the site. Further, he stated that immediate physical conditions had much greater influence than season on the presence of animals on sites. Pritchard and Greenhood (1968) observed the total number of P. nelsoni, P. concinna, and P. floridana sunning on a single log at a Florida locality. The turtles began to sun at 0720 hours, reached a maximum number of 45 individuals at about 1300 hours, and then there was a decline until the last turtle left the log at 1640 hours. On this one day of observations the highest black bulb temperature (49°C) was at about 1130 hours and the highest air temperature in shade (28.5°C) was at about 1100 hours; the greatest number of basking turtles on the log occurred after the highest temperatures of the day were obtained.

In Panama the slider, P. scripta, foraged for most of the day, and basked out of water at all times during the day but chiefly between 0900 hours and 1500 hours (Moll and Legler, 1971). The highest frequency of basking (=sunning) by hour was found to be 1200 to 1259 hours. The level at 0900, 1000, and 1100 hours was higher than at 1300, 1400, and 1500 hours. Although not discussed, the data of Moll and Legler indicate that most sunning occurred in the morning hours with peak times about noon. They suggested that basking out of water was probably done at opportune times, in short bursts, when basking conditions were suboptimal (overcast or rainy days), and that atmospheric basking may not be necessary in long periods of sunny weather. They also found that the intensity of atmospheric basking waned gradually in the dry season (January through April) and picked up again at the beginning of the rainy season (May and June).

The foregoing studies on several species of Pseudemys all point to a general pattern of sunning in which the turtles emerge soon after sunrise (0700 to 0800 hours), gradually increase the intensity of sunning up to about 1200 to 1300 hours, and then decline in numbers in the afternoon until no turtles are present on sunning sites as darkness approaches. There appears to be less sunning behavior during months with higher temperatures.

Among North American chelonians, the daily activity cycle of the painted turtle, Chrysemys picta, is one of the best known. Sexton (1959) described in detail the annual activity cycle of this species, and found that a number of factors effect their habits and distribution. Since many of the turtles he observed were partly submerged on top of floating vegetation, it was not clear how much time was spent sunning each day. Ernst (1971) reported that the activity of C. picta was limited to daylight hours. When the sun rose, they left their nighttime resting places and basked in the sun several hours before foraging during the late morning hours. Afterwards, the turtles again basked in the sun and remained inactive through midday and early afternoon hours. Foraging again occurred in late afternoon and in the early evening before dusk. A few turtles foraged during the midday periods of inactivity. Further, Ernst (1971) stated that the daily periods of basking, foraging, and resting varied in length, depending upon environmental conditions. In periods of cool weather, painted turtles may bask in the sun for most of the day, feeding very sparingly, if at all, and during rains only a few turtles were seen out of the water.

The daily activity cycle of Hayfork Creek Clemmys marmorata differs from that of Pseudemys scripta and Chrysemys picta. My field observations indicate that Hayfork C. marmorata forage early in the morning (0530 to 0800 hours in the summer) and emerge to sun early in the day (0800-0900 hours depending on local conditions). Most sunning occurs in mid-morning. Afterwards many turtles continue to bask out of water until early afternoon at which time it appeared that most animals became inactive and apparently sought shelter. In the summer turtles were seen foraging throughout the day (0530 to 1930 hours), but it appeared that foraging was chiefly done early in the day. None were observed at night, but it was difficult to spot objects, let alone turtles, in water with flashlights.

At pool 12 in Hayfork Creek a large number of turtles were observed to display a similar pattern of sunning during the summer months (Figures 19-21). Turtles were seen foraging and moving in the pool as early as 0630 hours, but they rarely left the water until direct sunlight reached the basking sites on exposed rocks. With sun on the basking sites they soon emerged. The number of individuals basking out of water increased during the early morning hours (0800 to 1000 hours). Most atmospheric basking occurred between 0830 and 1200 hours. The greatest number of turtles out of the water at any time were 28 animals on July 24 (1020 hours), 29 on July 26 (0920 hours), 20 on Sept. 3 (0955 hours), and 6 on Sept. 9 (1015 hours), 1970. Following this daily morning peak the number decreased steadily until about noon when there appeared to be a marked drop in numbers of basking animals (Figures 19 and 20). After 1300 hours from 0 to 6 turtles were basking, mostly less than 2 animals. Occasionally in the afternoon turtles would emerge on rocks that were entirely shaded. For example, on July 23, 1970, two turtles emerged at about 1415 hours and remained in shade until 1600 hours. Overall, atmospheric basking occurred during times when the pool was in full sun. Similar patterns of basking out of water occurred in 1971, but for unknown reasons fewer turtles emerged (Figure 21).

The greatest numbers of turtles engaged in atmospheric basking at one time were 6 on July 21 (0900 hours), 8 on August 11 (0945), and 4 on August 12 (between 0940 and 1040), 1971. Times at which the first turtles emerged on July 21, August 11 and 12 occurred at 0815, 0830, and 0825 hours, respectively.

Figure 19. Number of emerged turtles at pool 12 in Hayfork Creek. Observations were made at five minute intervals. Solid line is the number of individuals observed on July 26, 1970; dashed line those seen on July 24, 1970. Bar graph above indicates with stippling the percent of the pool in shade.

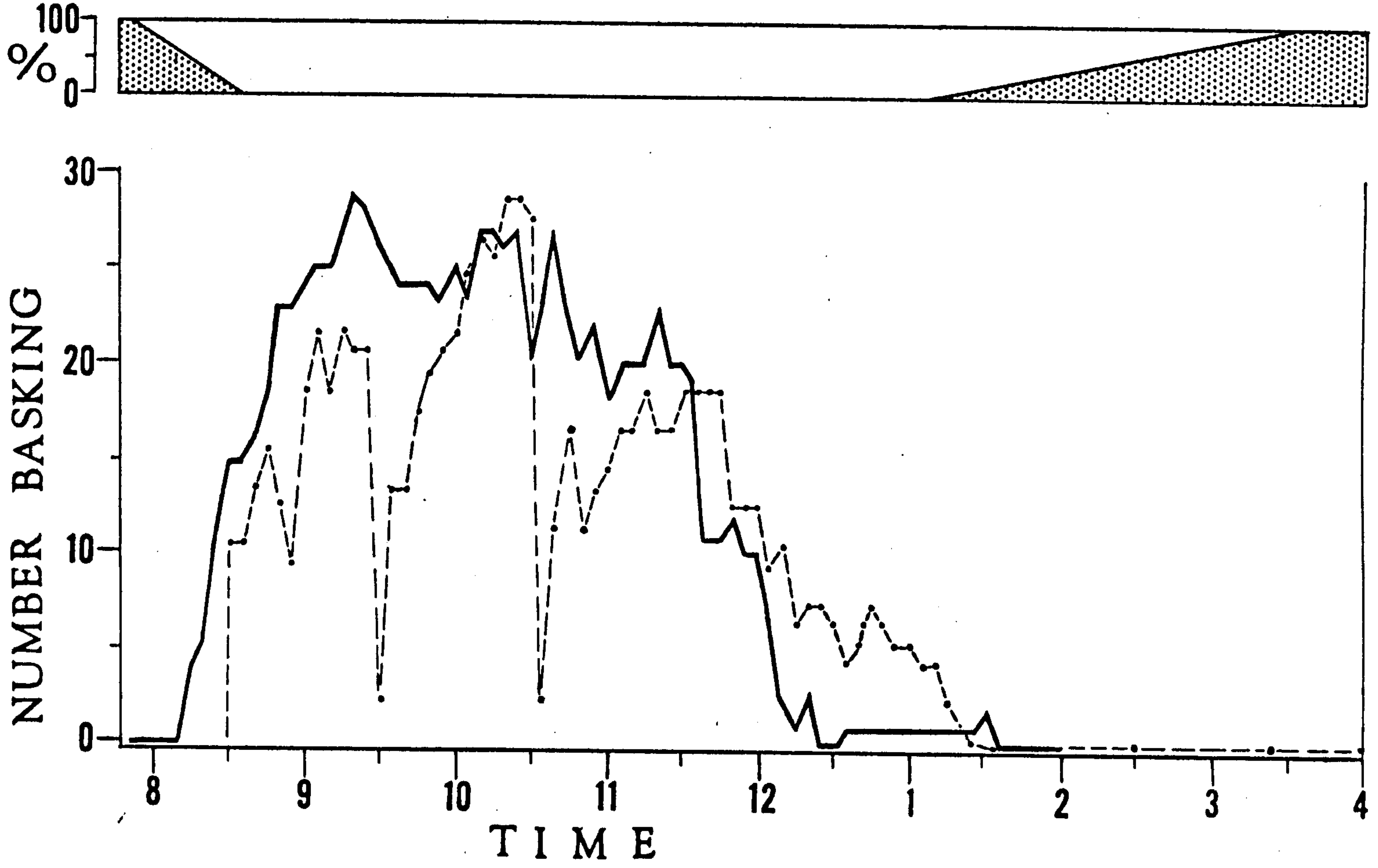

100
%
0
30
20
10
0
NUMBER BASKING
8
9
10
11
12
1
2
3
4
TIME

Figure 20. Number of turtles emerged on basking sites at pool 12. Solid line indicates turtles observed Sept. 3 and dashed line represents turtles seen Sept. 9, 1970.

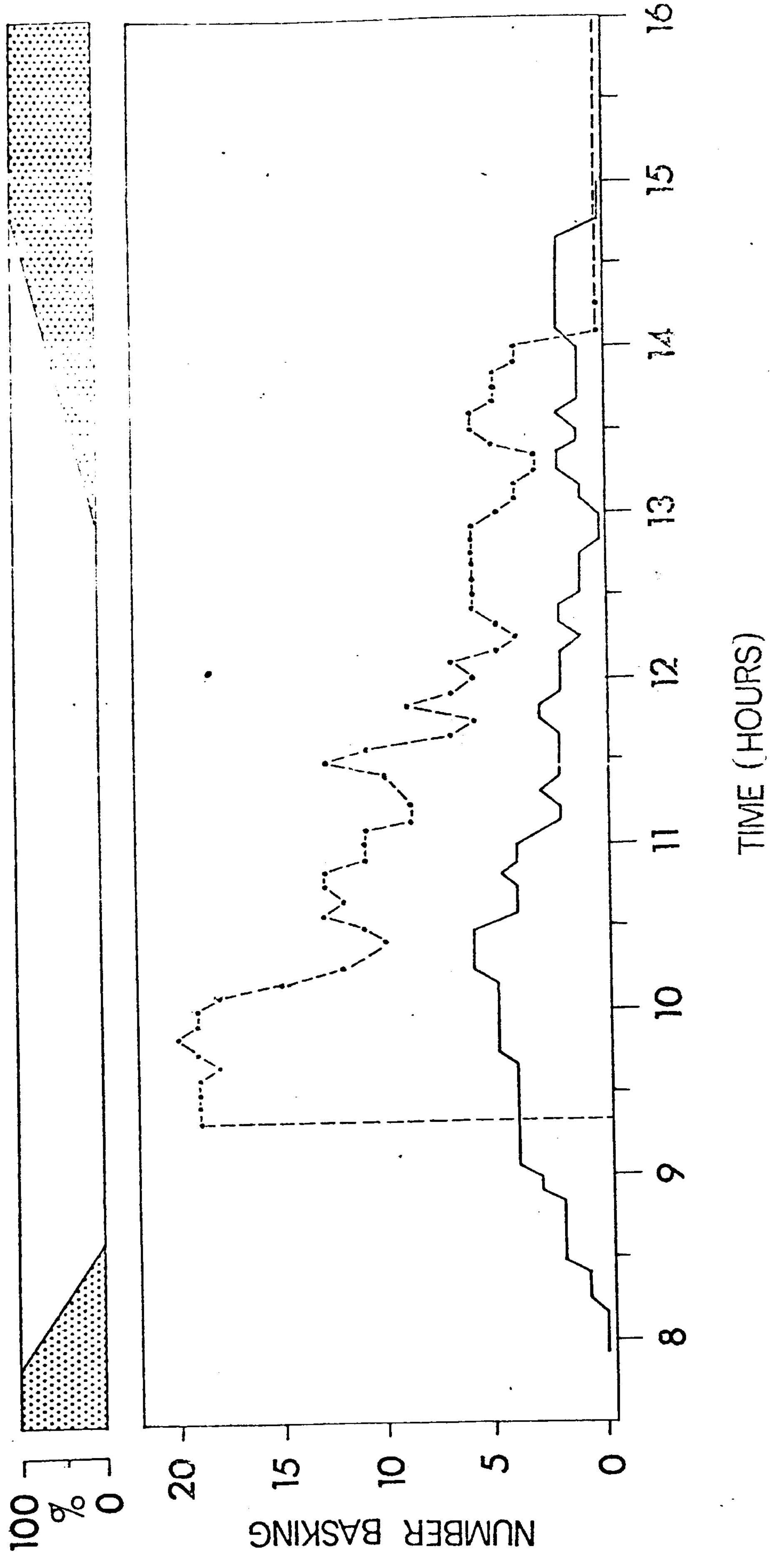
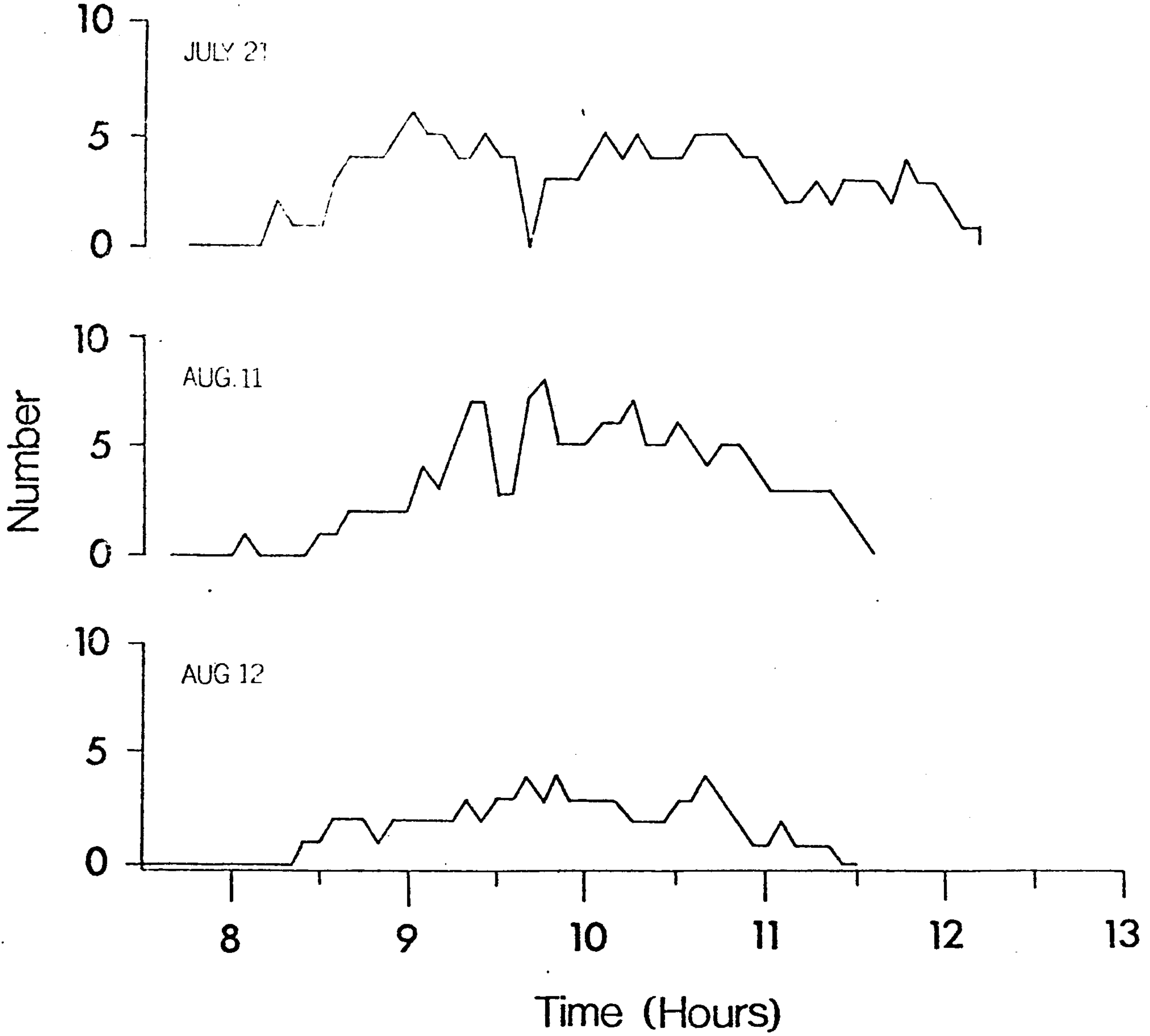

100
%
0
NUMBER BASKING
20
15
10
5
0
8
9
10
11
12
13
14
15
16
TIME (HOURS)

Figure 21. Number of turtles emerged on basking sites at pool 12. Observations made in 1971.


10
JULY 21
5
0
10
AUG. 11
5
0
10
AUG 12
5
0
Number
8
9
10
11
12
13
Time (Hours)

The pattern of atmospheric basking apparently is related to daily insolation. Many turtles at pool 12 responded to the first sunlight by emerging to bask out of water. Rarely, a turtle would emerge before the sun struck the basking sites. The pool was in partial shade after 1300 hours and entirely shaded by 1530 hours in summer months (Figures 19-21). Most turtles terminated atmospheric basking before the occurrence of shade on the pool; they may use shade on nearby cliffs and other objects as cues to end atmospheric basking, because the turtles usually returned to the water before their bodies were in shade.

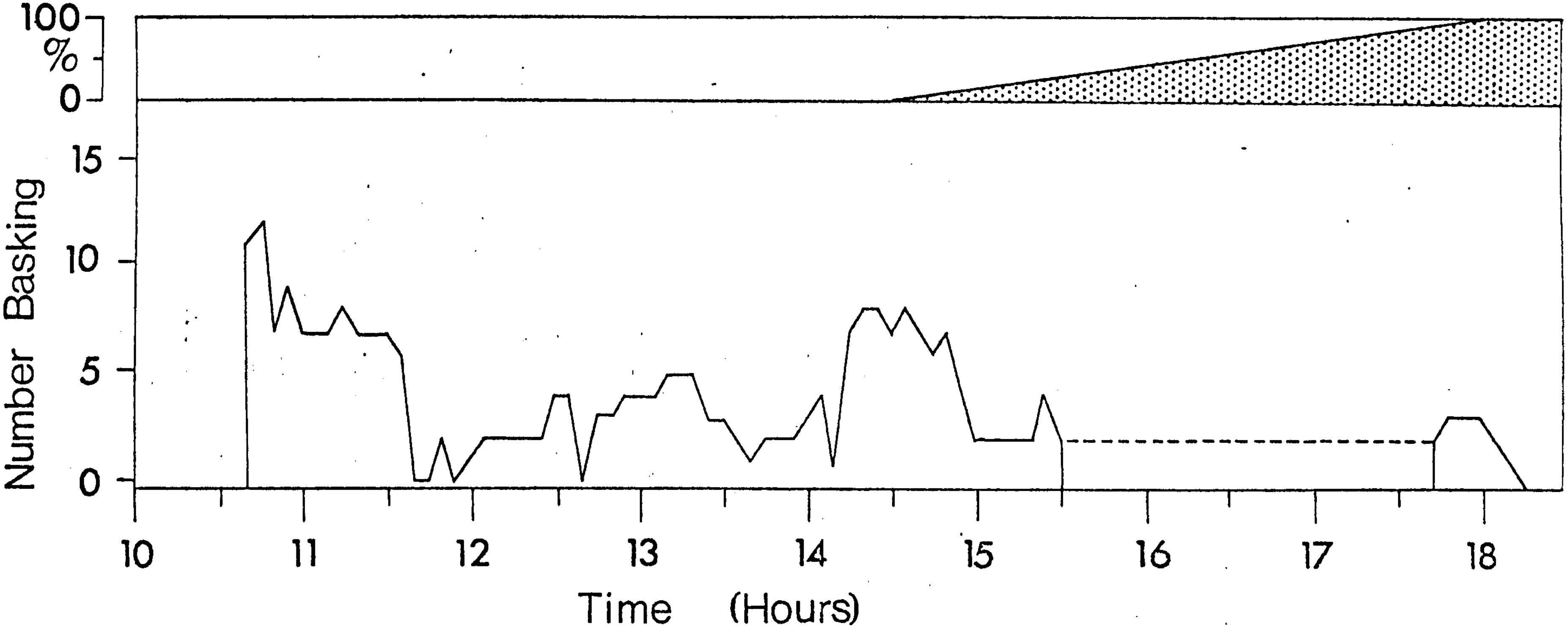
The turtles may respond to other physiological or environmental factors which lead to termination of atmospheric basking. Pool 12 animals seem to be synchronized to the daily regime of sunlight at this particular area. The motivation to sun appeared to be lessened as the day progressed perhaps because of increased water temperatures. These and other factors may all be important, but it appears that shading had a marked effect and examination of patterns of atmospheric basking at other pools may better define the influence of shade.

In pool 27 there were also a large number of turtles which used rocks for sites of atmospheric basking. On June 30, 1970, at 0730 hours I saw 8 and at 0930 hours there were 19 animals basking in the sun. I estimated that the sun struck pool 27 at about 0730 hours in the summer months and turtles emerged soon after sunlight was on the rocks. Sunlight was on pool 27 about 45 minutes before it was on pool 12. The difference is due to the position of the pools; pool 12 is on a north-south axis whereas pool 27 is on an east-west axis. Further, pool 12 receives sun later because of a high mountain ridge to the east. The orientation of the pools and location of surrounding terrain and trees markedly influenced the times and duration of insolation.

Turtles engaged in atmospheric basking later in the day at pool 27. On June 29, 1970, I observed 18 turtles at 1230 hours and 12 at 1300 hours. On August 14, 1970, 7 turtles were sunning at 1345 hours. In contrast, few or no animals were emerged after 1200 hours at pool 12. On August 24, 1970, the greatest number of turtles basking out of water was 12 at 1045 hours (Figure 22). No observations were made prior to 1040 hours. After this peak number around 1045 hours, there was a decrease in basking turtles until about noon when the number out of water began to increase again. Unlike turtles at pool 12, the number of animals engaged in atmospheric basking at pool 27 rose to 6-8 turtles between 1415 and 1450 hours and some continued until late afternoon (Figure 22). Shade began to cover parts of the pool at about 1500 hours, and this again appeared to result in cessation of atmospheric basking.

At pool 24 there was direct sunlight only from 1000 to 1200 hours, and it was during this time that turtles emerged. Once out of water the turtles occasionally remained in partial or full shade. In the afternoon the water temperatures were 24° - 27° and no turtles were observed to emerge.

Figure 22. Number of turtles engaged in atmospheric basking at pool 27 on August 23, 1970. See Fig. 19 for explanation of graph.


100
%
0
15
10
5
0
Number Basking
10
11
12
13
14
15
16
17
18
Time (Hours)

At Sheill Gulch the turtles emerged to sun at about 0800 hours, shortly after the sun rose over the mountains. Atmospheric basking continued until about noon when partial to full shade variously covered the pool due to nearby, overhanging foliage. In the afternoon sunlight occasionally came through the tree canopy. I observed turtles basking out of water in full sun, partial sun, and full shade within the span of an hour and the animals remained on the basking sites during these changing conditions. Some of these turtles were present for long periods of time.

There were no apparent differences in the patterns of atmospheric basking between July, August, and early September. Physical factors such as the duration of sunlight each day appeared to markedly influence the number of turtles out of water. Shade apparently terminated most atmospheric basking. Hayfork *Clemmys marmorata* appear to be opportunistic in their basking habits and emerge soon after direct sunlight is available in the morning. After about 1200 hours, the motivation to engage in atmospheric basking may be lessened due to increased water temperatures, but if insolation is available some animals may emerge at any hour of the day. The height of atmospheric basking clearly is in the morning hours, usually about 0900 to 1000 hours.

Atmospheric Basking of Individual Turtles

To my knowledge, there have been no previous studies of the individual behavior of freshwater turtles while basking out of water nor any effort to relate such behavior to changes in environmental factors. Boyer (1965) investigated the effects of several physical and biological factors on sunning turtles, but these observations were on captives or groups of wild turtles. In the preceding section it was shown that present knowledge about atmospheric basking in freshwater turtles is based on counts of the number of animals out of water in relation to time of day or air temperature. Such information is worthwhile for comparative purposes, but provides data on only part of the overall basking behavior of freshwater turtles.

Individual responses of freshwater turtles need study. Do turtles that emerge early in the day bask longer than animals emerging later? And, if so, why do they spend a longer time out of water? What is the duration of basking for turtles which voluntarily terminate basking as compared to those which terminate basking by any means in nature? Do individual periods of basking vary seasonally? Do they vary between different habitats? And what environmental conditions influence the duration of atmospheric basking?

To shed light on these questions, I recorded periods of atmospheric basking in unrestrained pond turtles during the summer and early fall and at different pools. In 1970, I spent parts of 8 days at pool 12, 5 days at pool 27, and 5 days at pool 24 (Tables 12-14). In 1971, parts of 3 days were spent at pool 12 (Table 13) and 5 days at Shiell Gulch (Table 14).

Table 12. Duration of atmospheric basking in turtles at pool 12 in 1971 grouped by the hour of emergence. N = number of animals; $\bar{X}$ = mean; S.D. = standard deviation; R = range of individuals periods.

Date and Time	Voluntary			All Observations		
	N	$\bar{X}$ S.D.	R	N	$\bar{X}$ S.D.	R
1970:						
July 6, 23, 24, 26						
0800-0859	25	68.2 ±29.0	4-120	42	51.1 ±32.6	1-120
0900-0959	29	39.9 ±20.1	5-89	53	36.2 ±20.1	1-89
1000-1059	56	24.0 ±15.2	2-69	101	18.9 ±13.9	2-69
1100-1159	73	16.0 ±9.4	2-46	117	15.6 ±9.6	1-46
1200-1259	36	11.6 ±5.1	1-24	49	10.4 ±5.4	1-24
1300-1359	2	15.0	13-17	5	11.2 ±4.7	5-17
July 31						
1000-1059	29	17.8 ±36.1	1-200	32	16.7 ±34.5	1-200
1100-1159	30	8.4 ±9.0	1-42	37	7.5 ±8.5	1-42
1200-1259	25	9.3 ±7.2	2-29	26	9.1 ±7.1	2-29
1300-1359	7	10.7 ±12.7	2-37	8	9.5 ±12.2	1-37
Sept. 3, 4, 9						
0800-0859	3	74.3 ±21.5	52-95	3	74.3 ±21.5	52-95
0900-0959	6	45.7 ±6.4	39-57	8	44.6 ±6.5	36-57
1000-1059	18	36.9 ±29.3	5-92	21	36.2 ±29.9	5-92
1100-1159	8	27.6 ±25.8	2-84	20	15.1 ±19.6	1-84
1200-1259	8	30.3 ±19.5	5-55	11	35.0 ±33.8	5-55
1300-1359	4	30.0 ±32.8	5-78	10	25.1 ±22.3	3-78
1400-1459	2	23.0	5-41	2	23.0	5-41

Table 13. Duration of atmospheric basking in turtles at pool 12 in 1971 and pool 27 in 1970 grouped by the hour of emergence. N = number of turtles; $\bar{X}$ = mean; S.D. = standard deviation; R = range.

Date and Time	Voluntary			All Observations		
	N	$\bar{X}$ S.D.	R	N	$\bar{X}$ S.D.	R
1971: Pool 12						
July 19, Aug. 11, 12						
0800-0859	9	49.9 ±16.0	24-74	24	23.4 ±25.2	1-74
0900-0959	15	30.3 ±18.5	4-60	36	18.0 ±17.6	1-60
1000-1059	27	16.9 ±10.5	5-43	49	13.6 ±11.8	1-54
1100-1159	10	14.5 ±8.4	4-30	15	13.1 ±9.0	4-30
1970: Pool 27						
July 29, Aug. 4, 24, 25, 28						
1000-1059	7	36.3 ±22.3	4-67	10	34.1 ±21.8	1-67
1100-1159	20	21.3 ±14.5	2-55	40	17.1 ±14.0	1-55
1200-1259	8	23.0 ±10.5	11-40	16	17.6 ±12.2	2-40
1300-1359	5	15.6 ±6.6	9-25	10	17.1 ±8.9	3-32
1400-1459	12	31.2 ±21.8	2-85	13	29.2 ±22.1	2-85
1700-1759	3	22.3 ±2.5	20-25	3	22.3 ±2.5	20-25

Table 14. Duration of atmospheric basking in turtles at pool 24 in 1970 and Shiell Gulch in 1971 grouped by the hour of emergence. N = number; $\overline{X}$ = mean; S.D. = standard deviation; R = range.

Date and Time	Voluntary			All Observations		
	N	$\overline{X}$ S.D.	R	N	$\overline{X}$ S.D.	R
1970: Pool 24						
July 7, 10, 12, 15, 18						
0900-0959	1	16.0		3	67.7 ±73.7	16-152
1000-1059	3	41.0 ±17.4	26-60	9	42.4 ±20.4	6-70
1100-1159	3	76.3 ±64.4	31-150	5	60.8 ±50.3	31-150
1971: Shiell Gulch						
July 4, 5, 7, 8, 10						
0800-0859	5	94.6 ±24.6	52-112	6	79.2 ±43.8	2-112
0900-0959	3	91.0 ±94.0	22-198	10	45.6 ±58.5	1-198
1000-1059	10	53.8 ±42.1	10-127	16	49.4 ±48.4	1-159
1100-1159	1	10.0		2	51.0	10-92
1200-1259				2	23.0	4-42
1300-1359	3	83.3 ±54.4	39-144	7	58.0 ±42.0	12-144
1400-1459	1	61.0		2	65.0	61-69

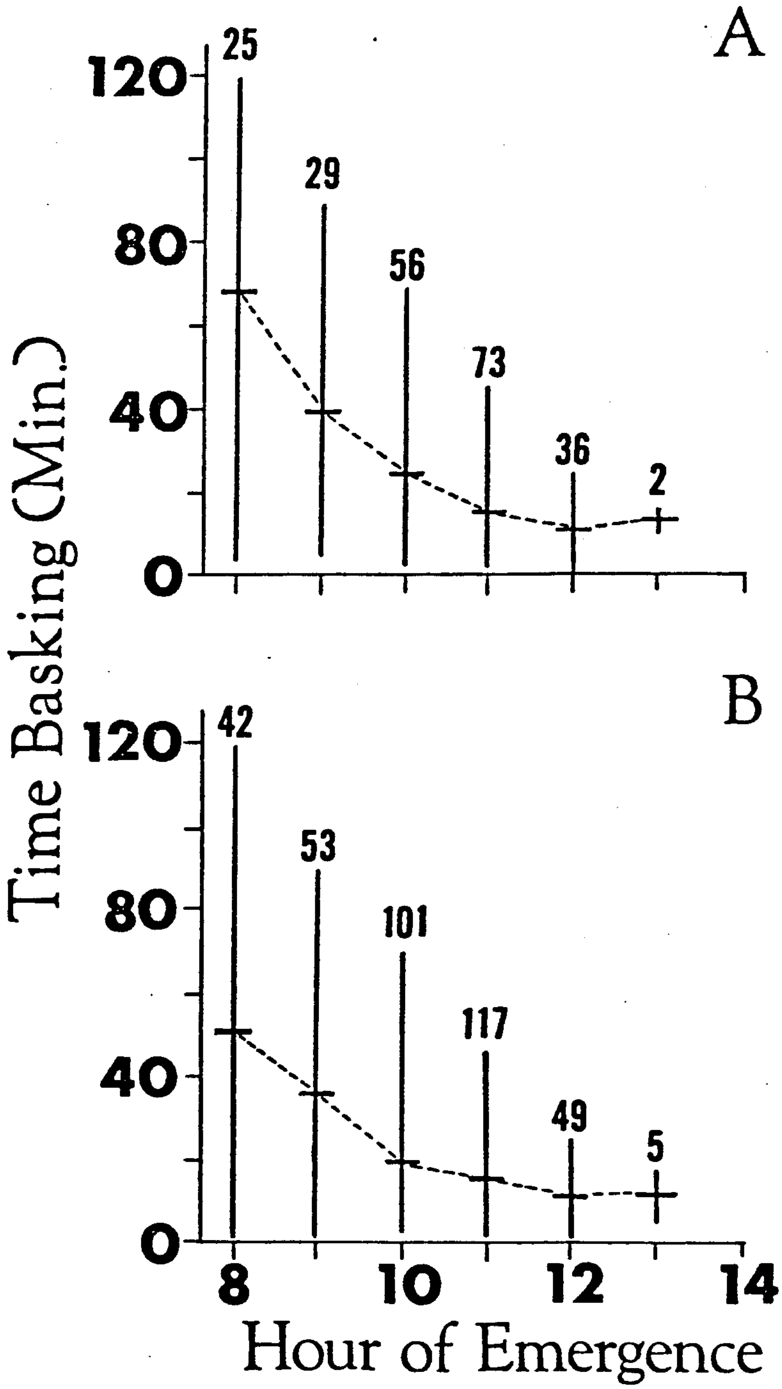
Duration of Basking in Relation to Hour of Emergence

To find out if there were differences in duration of atmospheric basking in turtles emerging at various times during the day, I recorded the length of individual basking times in relation to their hour of emergence, i.e. turtles which emerged between 0800 and 0859 hours, 0900 and 0959 hours, etc. I differentiate between those turtles which voluntarily terminated basking and animals that ended basking by any means.

At pool 12 the average length of time of atmospheric basking decreased in individuals emerging from 0800 hours to 1100-1400 hours (Tables 12 and 13). The trend is clear for turtles that returned to the water voluntarily. On July 31, 1970, the turtles displayed unusual behavior due to irritation from diesel fuel in the creek (see Appendix) and the duration of atmospheric basking was much lower than comparable hours on other days (Table 12). Excluding these times of water pollution by petrochemicals, it was found that turtles which emerged early in the day at pool 12 basked longer than those which emerged at later hours. The durations of atmospheric basking at other pools differ (Table 13 and 14) and are discussed later.

My most extensive records were made on July 6, 23-24, and 26, 1970, and these observations were examined in detail. Figure 23 depicts the decrease in the ranges and means of hourly records from 0800 to 1200 hours. The average duration of atmospheric basking decreased from 68.2 minutes for those turtles emerging 0800-0859 hours to 11.6 minutes for animals emerging 1200-1259 hours and which terminated basking voluntarily. The means were 51.1 and 11.2 minutes, respectively, for all the observations.

Figure 23. Length of time (in minutes) pond turtles engaged in atmospheric basking in relation to the hour during which they first emerged. Vertical lines represent ranges in duration of basking and horizontal lines the means. Number of turtles observed during each hour is indicated above the vertical lines. Data recorded July 6, 23-24, and 26, 1970. A. Turtles that voluntarily terminated basking. B. Animals that terminated basking by any means.


A
B
Time Basking (Min.)
Hour of Emergence
120
80
40
0
8
10
12
14
25
29
56
73
36
2
42
53
101
117
49
5

Although the average and range of times decrease each hour (Figure 23), the individual responses of these turtles are not shown. To examine such behavior, the distributions of atmospheric basking periods in relation to the hour of emergence for turtles that voluntarily terminated basking and for all the observations are shown in Figure 24. There are wide variances in the data from 0800-0859, 0900-0959 and 1000-1059 hours, but it is apparent that individual turtles spent less time engaged in atmospheric basking as the day progressed. The mean values and standard deviations of data are given in Table 12. Except for the small sample at 1300-1359, the mean and standard deviation steadily decrease in value starting at 0800 hours. Since the means and variances tended to be proportional a logarithmic scale was used to analyze these data (Bartlett, 1947; Edwards, 1965).

On a logarithmic scale, the data for each hour are less scattered than on an arithmetic scale, and examination of the log distributions showed that the data approximated normal distributions. With these log values each hourly group was compared using a t-test (Figure 25). Observations for adjacent hours from 0800 to 1100 hours are significantly different from each other ($p < 0.01$). It is apparent that under the stated habitat conditions pond turtles reduced their times of atmospheric basking as the day proceeded.

Influence of Different Terminations

Presumably the chief function of atmospheric basking is to elevate body temperatures to facilitate metabolic processes. Ideally, a turtle would get maximum return on this behavior if it could bask undisturbed and as long as desired.

Figure 24. Distribution of individual records of atmospheric basking obtained July 6, 23-24, and 26, 1970, at pool 12. Intervals are five minutes each. Hour of emergence is indicated to the right of each hourly graph. Histograms represent total of all observations and dark histograms are for those turtles that voluntarily terminated basking.

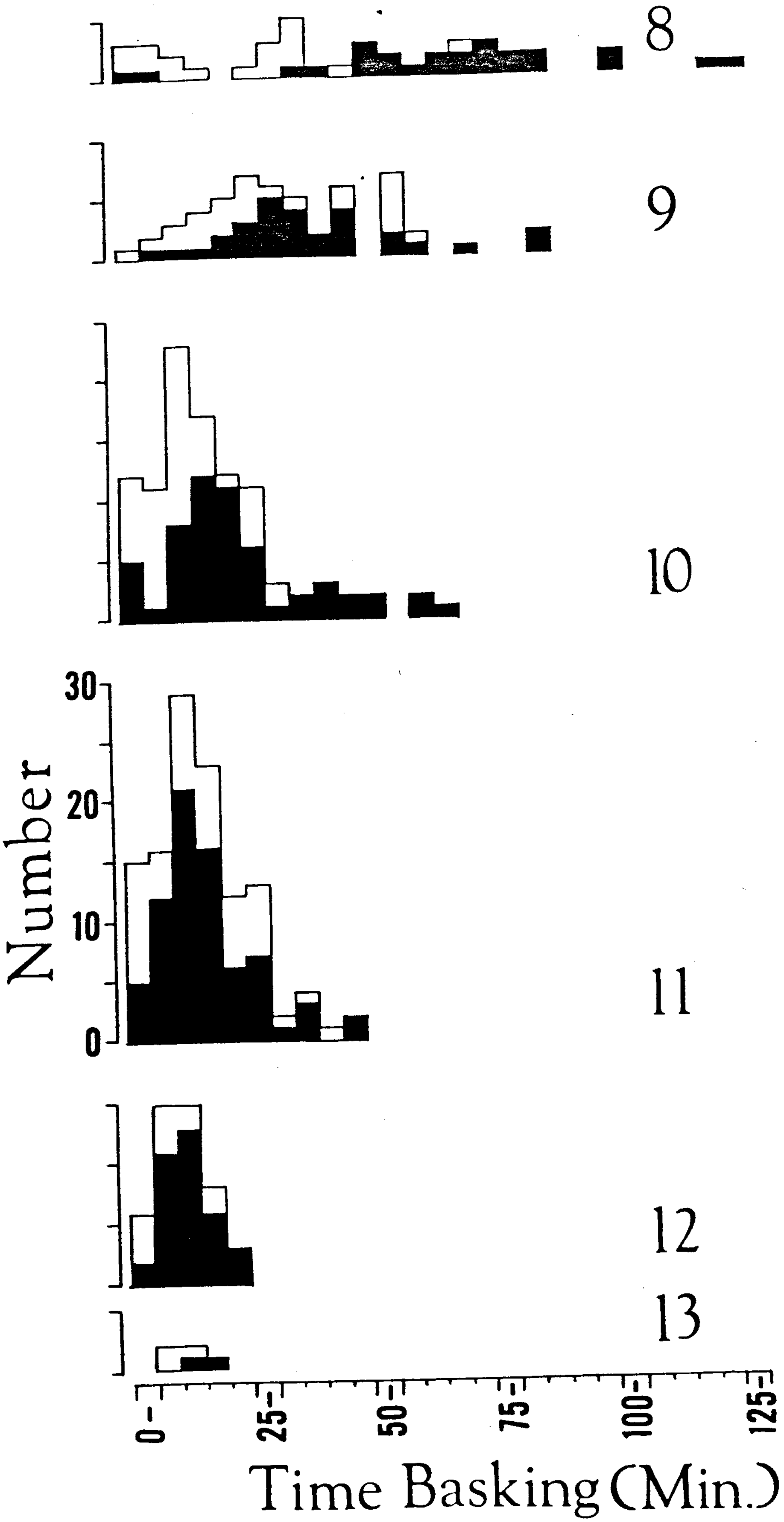
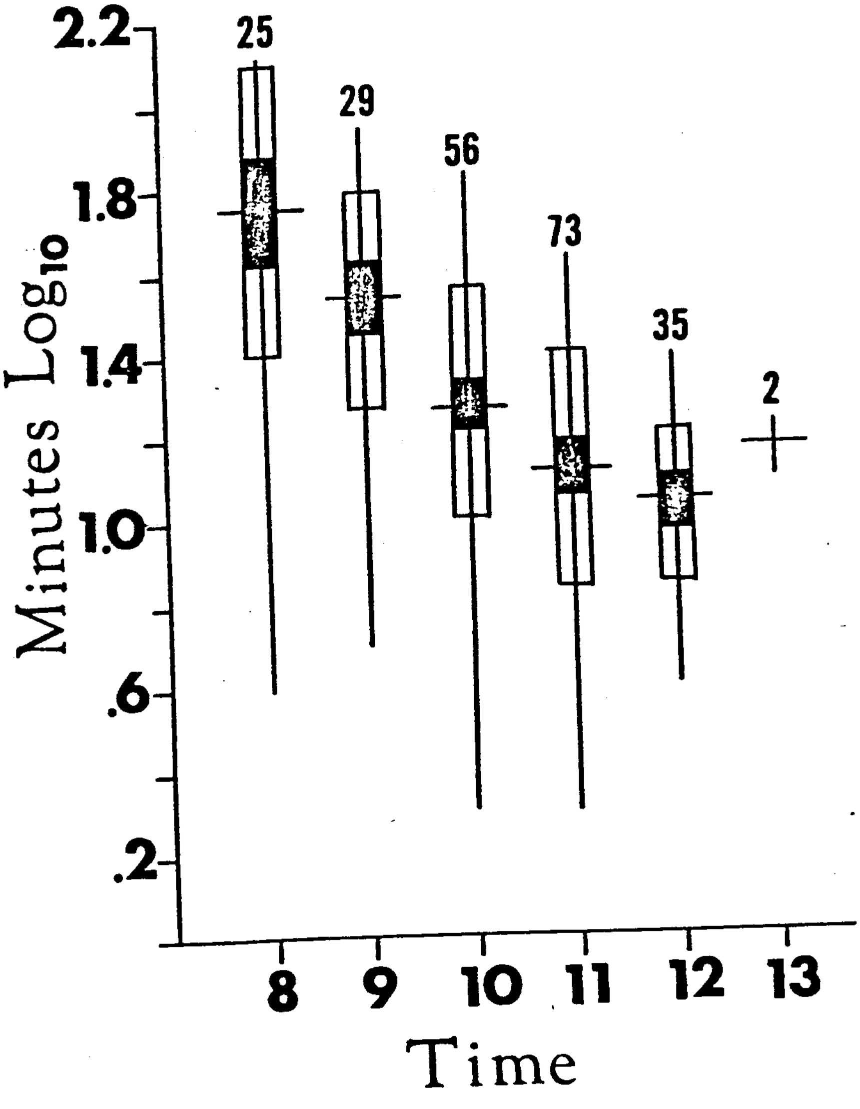

8
9
10
11
12
13
Number
30
20
10
0
0
25
50
75
100
125
Time Basking (Min.)

Figure 25. Comparison of hourly times of emergences on a logarithmic scale. Vertical lines are ranges in atmospheric basking times; open rectangles are one standard deviation on either side of the mean; horizontal lines are means; and dark rectangles indicate 95% confidence intervals on either side of the mean. Sample size is indicated above the vertical line.


2.2
1.8
1.4
1.0
.6
.2
Minutes Log_{10}
25
29
56
73
35
2
8
9
10
11
12
13
Time

In nature, however, this is seldom possible because of the constant threat of predation, events that frighten turtles (such as landslides, falling branches, etc.), and antagonism of other turtles seeking the limited basking sites available. I compare the different terminations to indicate what may be optimal for metabolic needs (voluntary termination of basking) with what is actually realizable in nature (all observations). The former basking times obviously will be longer, but on a population basis it is not known how much of basking is shortened because of threats and other disturbances. At times such disturbances may override the basking urge and its apparent thermoregulatory role, causing a marked decrease in the length of atmospheric basking on a population basis.

The average basking times for those that voluntarily terminated basking were greater than for all observations, except for a few hours (Table 12-14). Excluding records on July 31, 1970, when the creek was polluted by diesel fuel (see Appendix), the duration of atmospheric basking apparently was decreased by an average of 6.2 minutes per turtle on a population basis. During certain hours the duration of atmospheric basking was decreased from 17.1 to 26.5 minutes per turtle due to the influence of threats and other disturbances.

The duration of atmospheric basking for turtles voluntarily terminating basking is statistically different from those animals terminating basking due to some disturbance (Table 15). Further, there is a marked difference between the average lengths of times of turtles voluntarily terminating basking and those that terminated basking by any means(all observations). Disturbances apparently have

Table 15. Comparison of differences in means for the duration of basking periods. Test of significance is for turtles that voluntarily terminated basking and those that were disturbed. Observations from July 6, 23-24, and 26, 1970, at pool 12.

Time	All turtles		Vol termination		Disturbed turtles		Vol-Dist. difference	t-value
	N	$\bar{X}$	N	$\bar{X}$ S.D.	N	$\bar{X}$ S.D.		
0800-0859	42	51.1	25	68.2 ±29.0	17	26.0 ±18.3	42.2	5.79*
0900-0959	53	36.2	29	39.9 ±20.1	24	31.8 ±19.5	8.1	1.48
1000-1059	101	18.9	56	24.0 ±15.2	45	12.8 ±8.9	11.2	4.58*
1100-1159	117	15.6	73	16.0 ±9.5	44	15.0 ±10.0	1.0	0.54
1200-1259	49	10.4	36	11.6 ±5.2	13	7.1 ±4.8	5.5	2.84*
1300-1359	5	11.2	2	15.0	3	8.6 ±4.0	6.4	-

* → significant difference $p < 0.05$

an effect on the duration of atmospheric basking times, and, where possible, this behavior should be recognized in order to avoid confusion between the natural patterns of atmospheric basking and times of voluntary basking periods. Clearly, observations on atmospheric basking should include the effects of extrinsic factors because these may significantly alter the duration of basking times.

Seasonal Changes

The annual activity cycle of Hayfork Creek pond turtles is relatively short. Searches on March 30, 1970, and May 9, 1971, yielded no turtles, but on May 29 in 1970 and 1971 there were many turtles in the creek. This evidence suggests that the turtles emerge from hibernation in mid or late May. They were abundant throughout the summer months, and were common as late as Sept. 12, 1967, Sept. 14, 1969, and Sept. 16, 1968. On October 29, 1971, no turtles could be found. They probably leave the stream between late Sept. and late October. Light snowfall occurs in the area from November through February. On Oct. 29, 1971, there was ice along the edges of shallows during the morning hours (up to 1030 hours). The creek does not freeze over in the winter, but has cold waters near freezing. Spring time temperatures in the area are mild during the day, but the creek is cold due to its high mountain source. For example, on May 29, 1971, the water temperature 10 cm deep was 13.5° at 1100 hours and 15.5° at 1600 hours.

There is insufficient data to define basking periods in late May and in June. Table 16 shows the differences between turtles in July and early September, 1970, which voluntarily terminated basking.

Table 16. Comparison of the duration of atmospheric basking by time of year. Data for pool 12 recorded in 1970. Voluntary terminations.

Time	July 6,23-24, and 26		Sept. 3,4, and 9		t-value
(Hours)	N	$\bar{X}$	N	$\bar{X}$	
0800-0859	25	68.2 ±29.0	3	74.3 ±21.6	-
0900-0959	29	39.9 ±20.1	6	45.7 ±6.4	1.28
1000-1059	56	23.9 ±15.2	18	36.9 ±29.3	1.79
1100-1159	73	15.9 ±9.5	8	27.6 ±25.8	1.27
1200-1259	36	11.6 ±5.2	8	30.3 ±19.5	2.69 *

* - significant difference at $p < 0.05$

There was little difference between these months, and there appears to be no relationship between duration of basking and time of year for the Hayfork turtles.

Influence of Local Habitat Conditions

The physical conditions at Hayfork Creek vary greatly between pools and over relatively short distances. In this situation it appears that Clemmys marmorata is opportunistic in its atmospheric basking habits.

The configuration of the pool, associated vegetation, and nearby cliffs affected the amount and duration of solar radiation received at a particular site. The habitat conditions influenced the basking times and patterns of turtles because direct sun was the primary motivation for emergences of turtles at the pools studied. Available direct sun varied from two hours at pool 24 to 11 hours at pool 27 and atmospheric basking occurred most frequently when direct sun was available (Figures 19-22). However, at pools with some shade (pool 24 and Shiell Gulch) turtles remained out of water longer (Tables 13 and 14), perhaps because they could escape the high temperatures from direct sun. Some turtles may be habituated to the daily light regime at certain pools because I saw animals occasionally emerging early in the morning a few minutes before the site was in full sun. These turtles emerged on sites that received sun earlier than other places in the pools.

Turtles basked on rocks, logs, soil, and clumps of grass; their rates of heat gain may differ depending upon the nature of these substrata. The location and slopes of these basking sites may also influence the duration of atmospheric basking.

Habitat conditions affect atmospheric basking in Clemmys marmorata and the turtles apparently alter their behavior at different pools. Thermoregulatory responses in different habitats are discussed in the following sections.

Behavior During Atmospheric Basking

The individual behavioral responses of turtles during atmospheric basking have received little attention. Boyer (1965) reported that variations in heat absorption in turtles, resulting from differences in the angle of incidence of the sun's rays, may occur either as a result of accidental positioning or active orientation. He observed many P. scripta making deliberate changes in position of 90° to 180° in a horizontal plane. The majority of turtles in the genus Pseudemys will assume basking positions with the posterior end in the same half of the compass as the sun and control of body temperature may be exercised by selection of substrate, by choosing partly submerged sites, and by basking in shaded locations (Boyer, 1965). Moll and Legler (1971) found that the slider, P. scripta, in Panama assumed a characteristic posture during atmospheric basking. The neck was fully extended in gradual dorsal curve and the head was often rotated to one side. Limbs not used as holdfast organs were fully extended, partially pronated, and raised from the basking surface. Orientation of the body appeared to expose the maximum possible surface of the carapace to the sun. In the terminal phases of basking in one test animal, the turtle became more restless than it had been, changing its orientation more often and moving its head and neck about in an attitude of circumspection. The turtle moved to the edge of the basking site and dipped its head (eyes submerged or not) into the water several times for periods of perhaps two seconds. This behavior heralded the termination of atmospheric basking.

Orientation and Posture

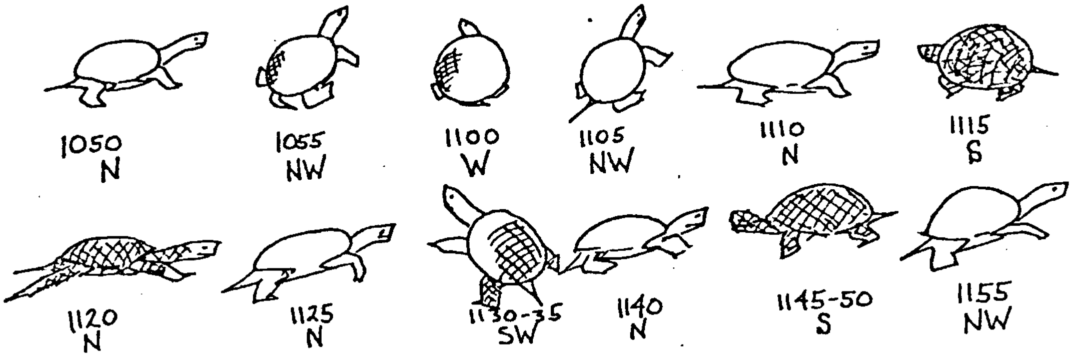
Pacific pond turtles selected atmospheric basking sites that usually provided good exposure to the sun. Rock and bank surfaces chosen were often those that sloped toward the sun during the basking periods. This slope resulted in the posterior part of the shell being in the same half of the compass as the sun. However, once dry most turtles seemed to position themselves in almost any direction that allowed them to maintain their perch. At Hayfork Creek there was no definite behavior among turtles to orient the shell with posterior parts facing the sun.

The orientation and posture of pond turtles were closely studied in 1970-71. Behavioral responses during atmospheric basking are illustrated in Figure 26. Atmospheric basking posture of a turtle is shown in Figure 27.

Orientation of the shell to maximize exposure to solar radiation may occur in sunning turtles, but present evidence does not confirm this observation. Usually the posterior part of the carapace in sunning _C. marmorata_ was directed toward the sun, but it is not know whether this was intentional or a result of the slope of the sunning sites themselves. Occasionally the anterior end was positioned toward the sun and pond turtles frequently moved about while basking out of water (Figure 26). Parts of the body may be exposed to the sun or other sources of heat while other parts are being cooled in the shade of the shell or that cast by

Figure 26. Orientation and posture of an adult female C. marmorata during atmospheric basking at pool 24. Time is at 5 minute intervals and the compass direction that the turtle faced are indicated below sketches (re-drawn from field notes). Cross hatching indicates area of turtle in shade. The sun shone from the southeast during the period of observation. The same animal is shown on each day.

July 11, 1970



July 12

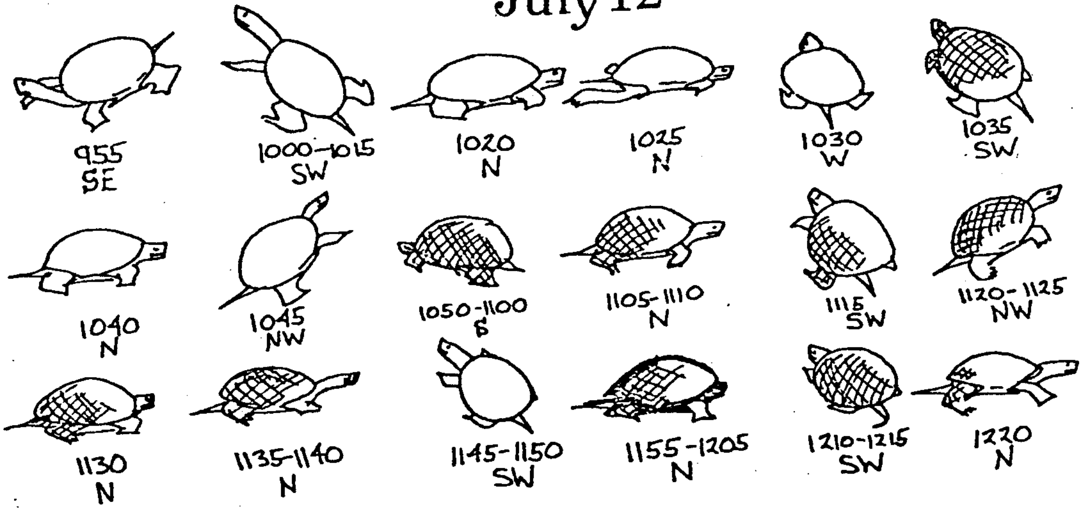


Figure 27. Posture of an adult female C. marmorata while sunning. Note extension of neck and legs. Turtle facing north. Photograph taken August 12, 1971, at pool 12, Hayfork Creek.

objects in the environment. Orientation to the sun and shifts in position may alter the rates of heat gain and loss during atmospheric basking, and such behavior could serve as a fine tuning device in thermoregulation.

The postures of the animals change during atmospheric basking. A typical sequence is as follows. On emergence a turtle extends its neck, tail, and limbs. Often the neck and head are held high (Figures 26 and 27). During this time the animal usually is in direct sunlight. When the shell and body dry in about 10 minutes time, the turtle partly retracts the neck and limbs, and may occasionally shift position. After 20-30 minutes the turtle generally is completely withdrawn into its shell; such withdrawal may frequently be interrupted by shifts in position on the basking sites. Tearing was noted in some turtles. Lastly, once a pond turtle presumably reaches a body temperature near its thermal preference it usually returns to the water or employs some thermoregulatory behavior to maintain the preferred level. When terminating atmospheric basking it usually turns towards the water and slowly moves to the edge of the basking site. Here the head is almost always dipped one or more times. This dipping may cool the head region to reduce rapid thermal changes, prepare the animal for diving, and alert the turtle to the presence of underwater predators before it submerges.

Dunking Behavior

Pond turtles frequently interrupt periods of atmospheric basking by entering the water. This rapidly cools the animals and probably serves as a thermoregulatory function. I present here an analysis of this behavior which may be referred to as dunking.

It is depicted in Figures 28 and 29. Dunking usually occured in a characteristic sequence. A turtle slowly moved into the water after atmospheric basking and then floated or slowly paddled around on the surface. It remained in water for 1-3 minutes, rarely longer. The animal moved back to the basking sites and emerged for further atmospheric basking. Occasionally a turtle moved into the water with out wetting the upper part of the carapace, but almost always submerged the head, neck, and legs.

The average and range of the duration of atmospheric basking was longer for the first few periods than latter ones (Figure 30). Most turtles had two to four periods of atmospheric basking; the maximum number was six. It appears there is a decrease in duration with each successive basking period.

The means and standard deviations of data by period were: first - 49.1 ± 26.2, second - 25.3 ± 14.2, third - 15.2 ± 10.2, fourth - 18.5 ± 10.8, fifth - 8.4, and sixth - 12.5 minutes. There were few observations for the last two periods, and standard deviations were not calculated. The means and variances tended to be proportional and a log transformation of the data was done. Using a t-test, there was a significant difference ($p<0.01$) between periods one and two, and two and three, but not between periods three and four. The first period of atmospheric basking in the dunking sequence was statistically different ($p<0.01$), i.e. longer in duration, when compared to all following periods, and, likewise, the second period was longer in duration than all following periods.

Figure 28. Examples of dunking behavior in C. marmorata. Vertical scale indicates degree of terrestriality, i.e. 100% represents a turtle that is completely out of the water, 50% means it is half in the water, and 0%, submerged. Abbreviations: t = turtle left basking site because it was threatened or attacked by another turtle; s = turtle frightened off basking site.

a) Medium-sized turtle, July 26, 1970; b) adult female, August 12, 1971; c) adult, July 26, 1970; d) medium, July 26, 1970; e) medium, July 24, 1970; f) medium, August 12, 1971; g) medium, July 21, 1971; h) adult, July 26, 1970; and i) medium, July 4, 1971.

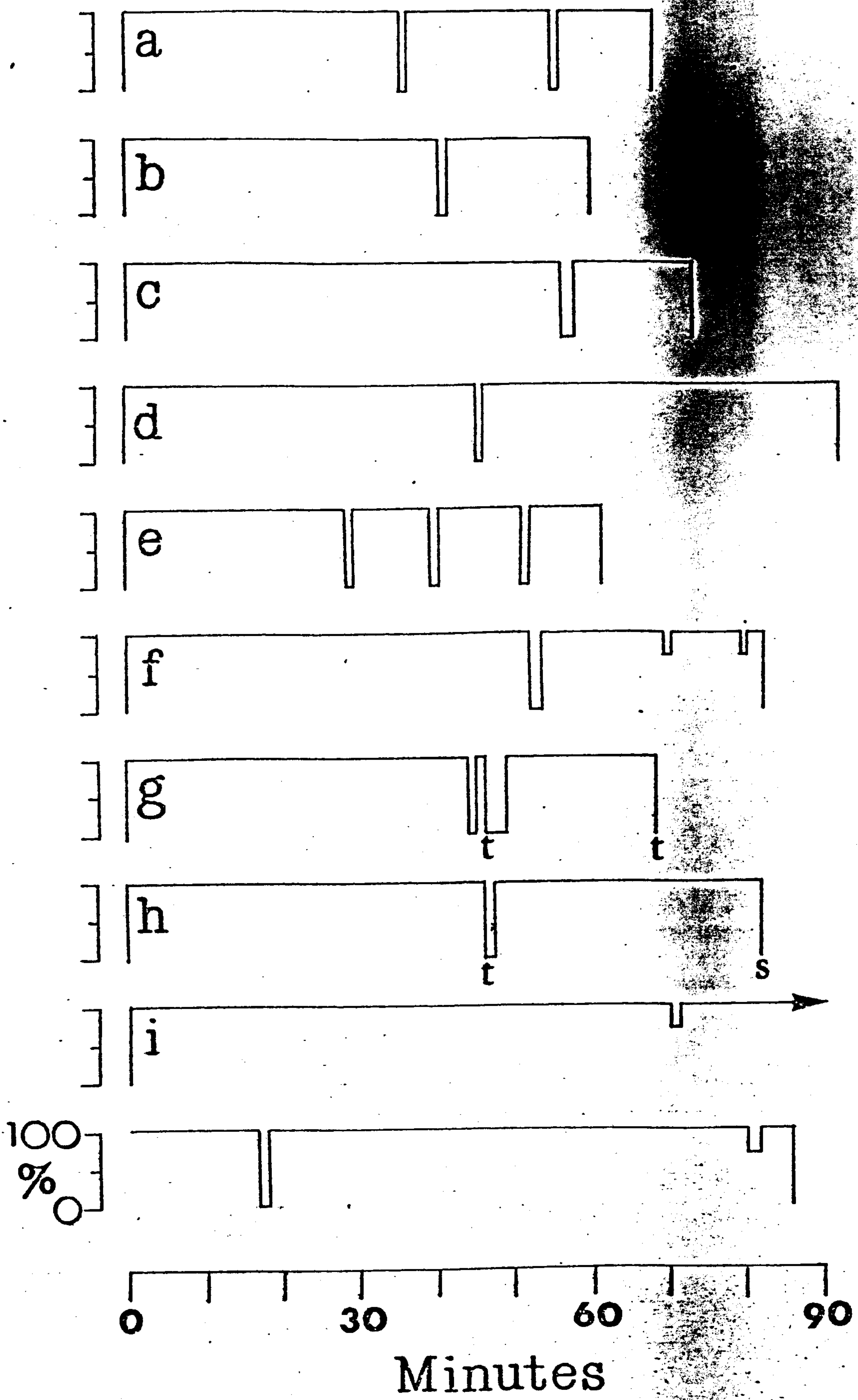

a
b
c
d
e
f
g
t
t
h
t
s
i
100
%
0
0
30
60
90
Minutes

Figure 29. Dunking behavior in C. marmorata. See Fig. 28 for explanation of graphs.

a) Medium-sized turtle, July 10, 1971; b) adult, July 26, 1970; c) medium, July 4, 1971; d) medium, August 12, 1971; and e) medium, September 9, 1970.

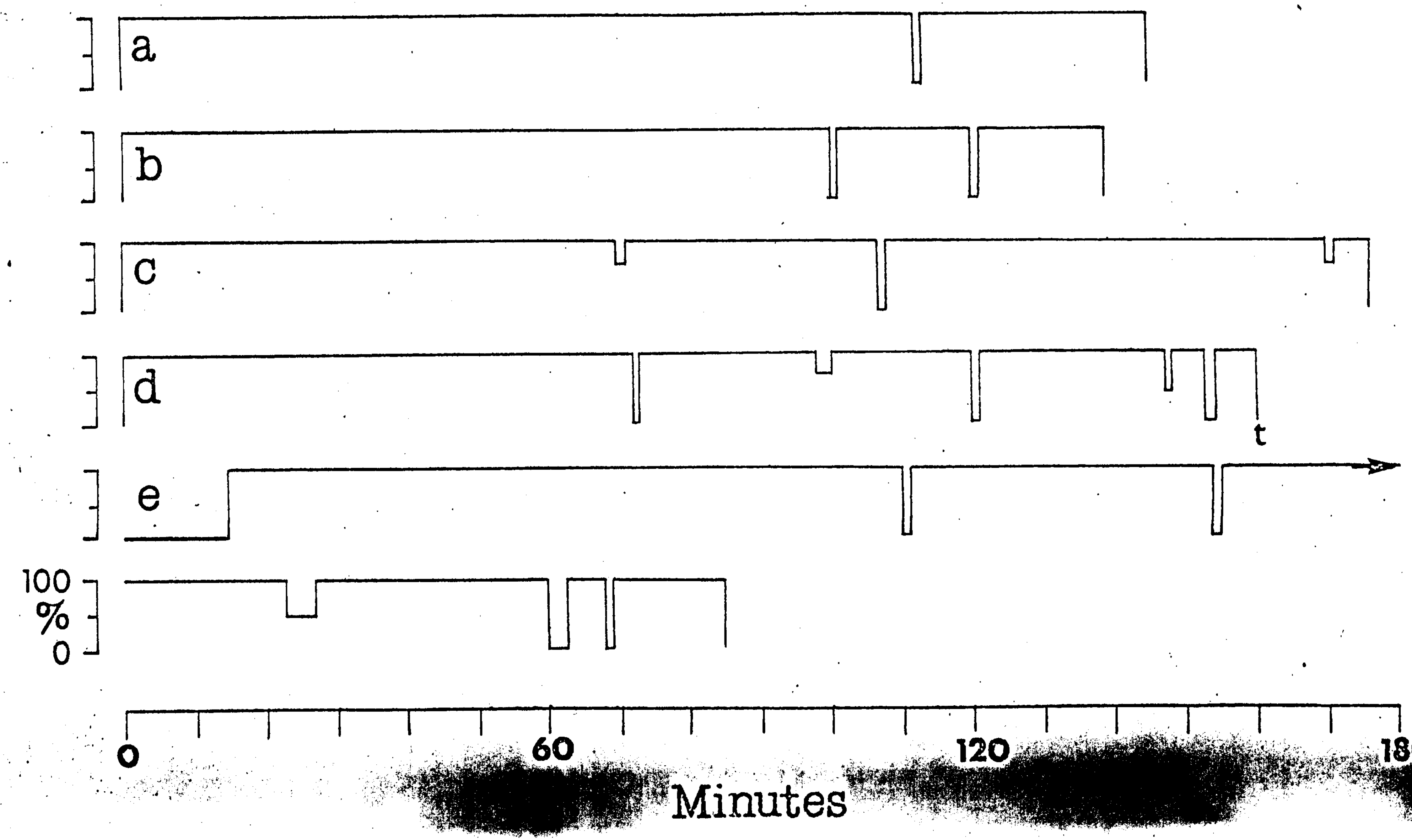
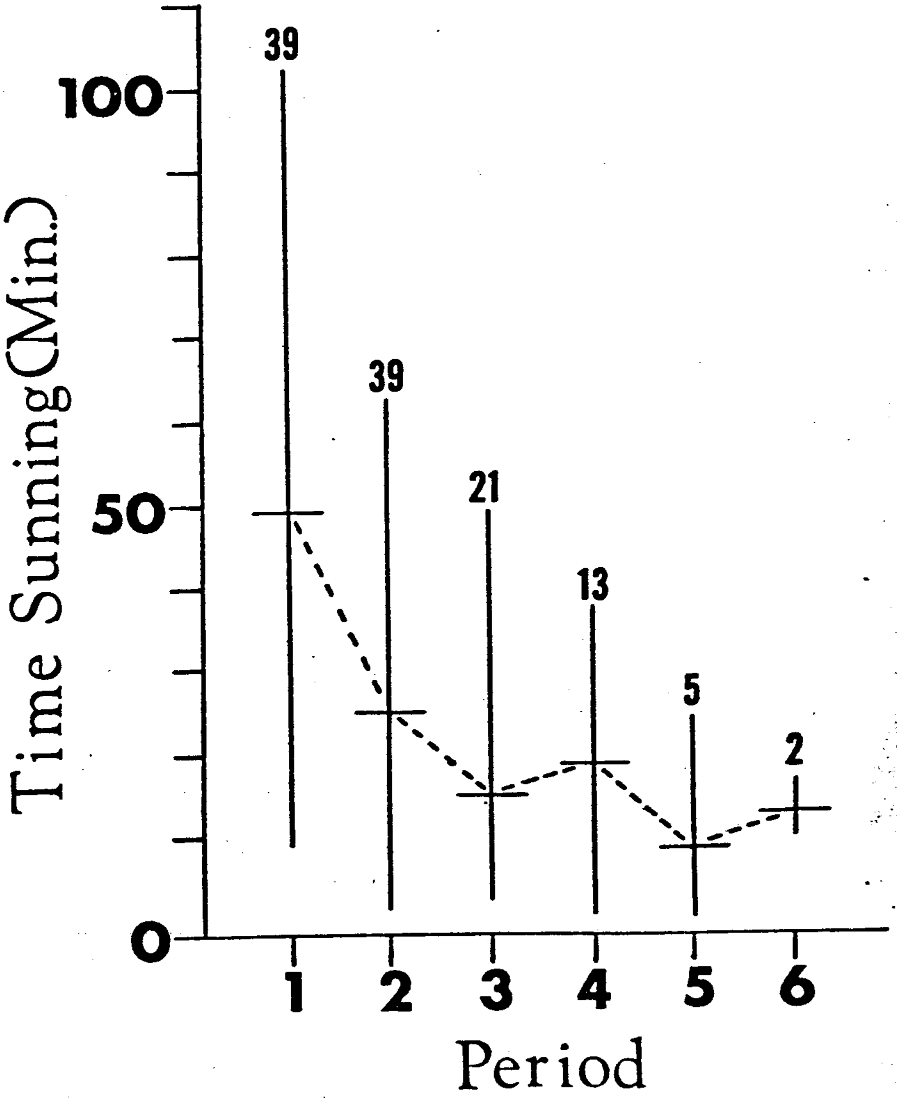

a
b
c
d
e
t
100
%
0
0
60
120
180
Minutes

Figure 30. Comparison of the atmospheric basking periods in <u>C. marmorata</u> (sunning only) that displayed successive dunking behavior. Vertical lines are ranges, horizontal lines are means, dashed lines connect means, and numbers at top are sample sizes.


Time Sunning (Min.)
100
50
0
39
39
21
13
5
2
1
2
3
4
5
6
Period

Partly Wetting the Body

Turtles were observed to place part of the shell or, at times, one or more appendages in the water while engaged in atmospheric basking. Often a turtle would emerge and leave the hind limbs and posterior part of the shell in water for long periods. Others were completely dry and then moved to areas where part of the body contacted water, such as the sides of the shell, or the forelimbs were dangled in the water and the head was occasionally dipped (Figure 31).

Use of Shade

Examples of turtles using shade during atmospheric basking are shown in Figure 32. The varying amounts of shade on these animals was not entirely due to environmental factors, but rather these turtles actively sought the shade at certain times. Usually animals increased the amount of shade on the body the longer they were out of water.

Several pools were partially shaded during the day by cliffs, over-hanging vegetation, and nearby trees. At pool 24 and Shiell Gulch direct sun was available for only a few hours each day and turtles occasionally engaged in atmospheric basking in partial shade.

Figure 31. Partly wetting the body during atmospheric basking in C. marmorata. See Fig. 28 for explanation of graphs. a) Adult, July 26, 1970; b) adult, May 29, 1971; c) medium, July 25, 1970; d) medium, September 3, 1970; e) medium, September 3, 1970; and f) large medium, September 3, 1970.

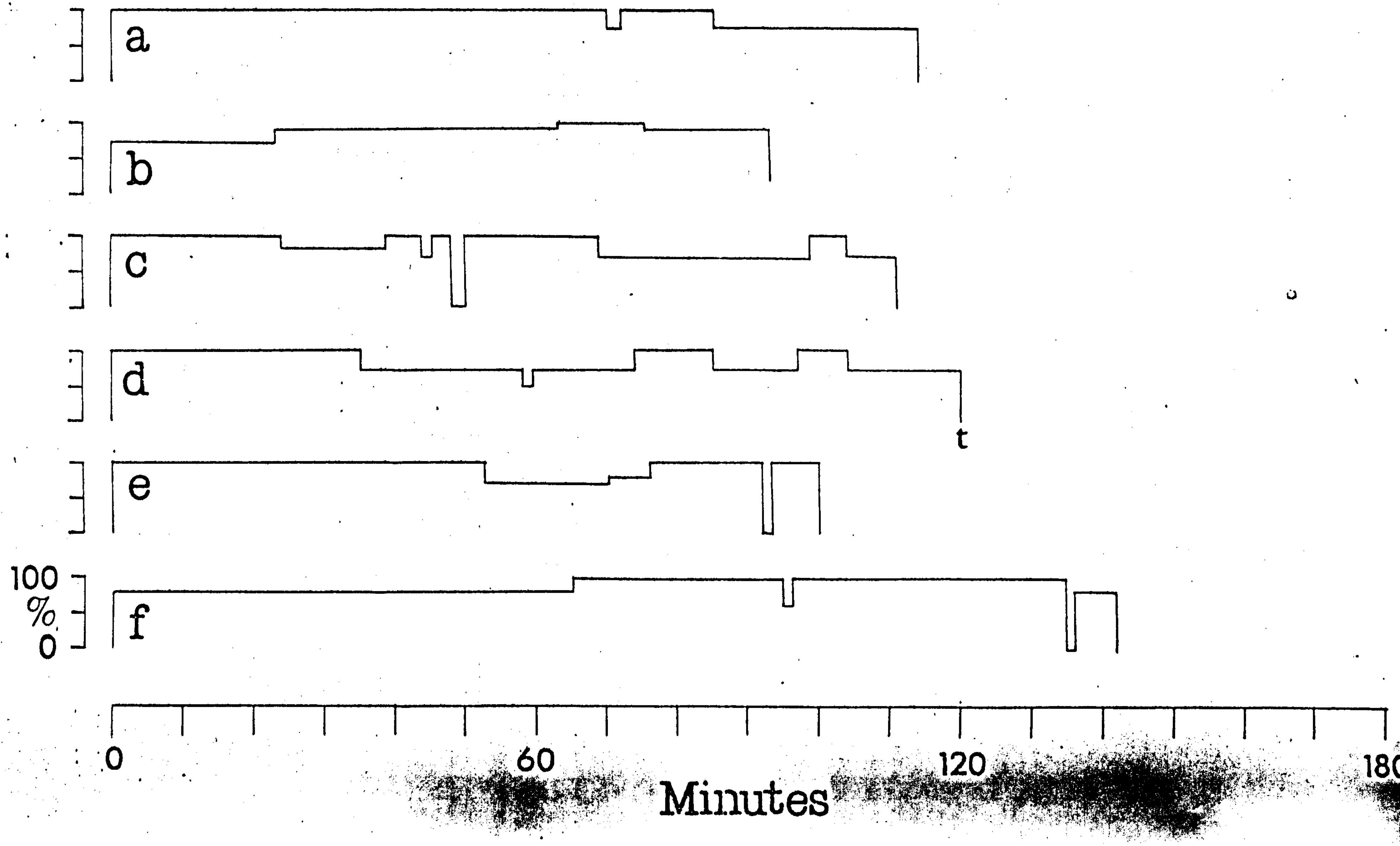
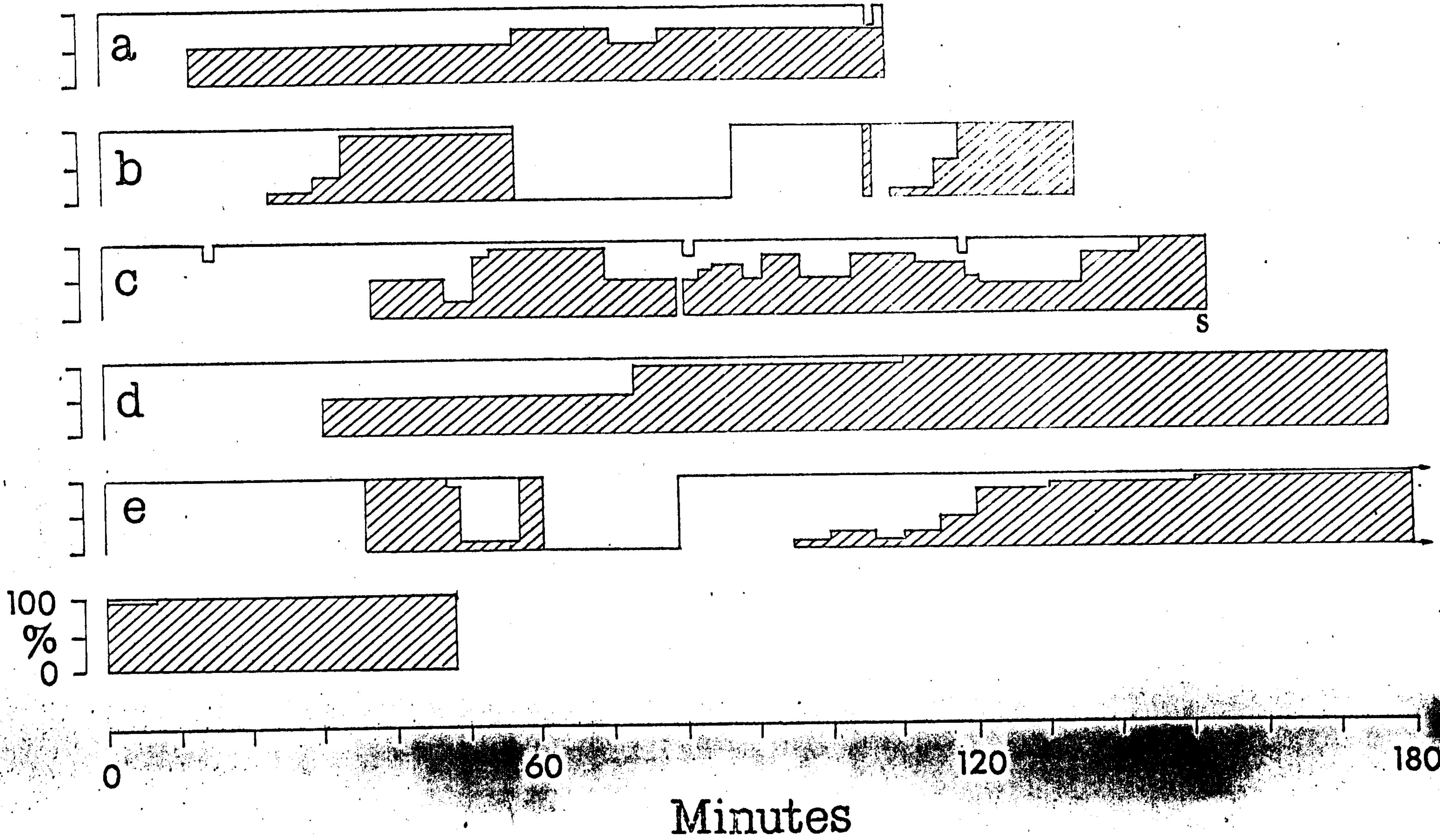

a
b
c
d
t
e
f
100
%
0
0
60
120
180
Minutes

Figure 32. Use of shade by C. marmorata. See Fig. 28 for explanation of graphs. Stippled areas indicate the percent of the body in shade. a) Adult, July 29, 1970; b) medium-sized turtle, July 7, 1970; c) adult female, July 12, 1970; d) medium-sized turtle, July 31, 1970; and e) adult male, July 18, 1970.


a
b
c
s
d
e
100
%
0
0
60
120
180
Minutes

Combination of Behavioral Responses

Orientation of the body, changes in posture, dunking, partly wetting the body, and use of shade are not exclusive categories of behavioral response. Rather, they are employed during atmospheric basking, presumably for thermoregulatory control, singly or in varying combinations, depending on local environmental conditions. Some examples of combined responses are depicted in Figure 33. As shown, a turtle may use exclusively one behavioral response for an extended period of time, such as dunking behavior, and then later shift to another, like partly wetting the body. Orientation and posture changes are not shown in Figures 28-29 and 31-33, but concurrent to other responses these were actively employed.

Comparison of Responses

Continual observations were made on many individuals for 30 minutes or more of atmospheric basking. I compare those animals basking over 30 minutes as this eliminates numerous short periods during which there probably was little or no thermal stress. Many of these turtles had a single basking period, whereas others used one or more behavioral responses during atmospheric basking. (Fig. 34).

The maximum time for any turtle to remain out of water with a single basking pattern was 125 minutes. Maximum times of atmospheric basking for displaying the previously described behavioral responses were: dunking behavior, 246 minutes; partly wetting the body, 198 minutes; using shade, 210 minutes; and combination of responses, 271 minutes. Obviously, the turtles employing behavioral reponses remained out longer than turtles simply emerging for one basking period.

Figure 33. Combination of behavioral traits employed during atmospheric basking in *C. marmorata*. See Fig. 28 for explanation of graphs. Stippling indicates amount of the turtle in shade. a) Adult, July 26, 1970; b) medium-sized turtle, September 9, 1970; c) large medium, July 4, 1971; d) medium, July 8, 1971; and e) medium, July 8, 1971.

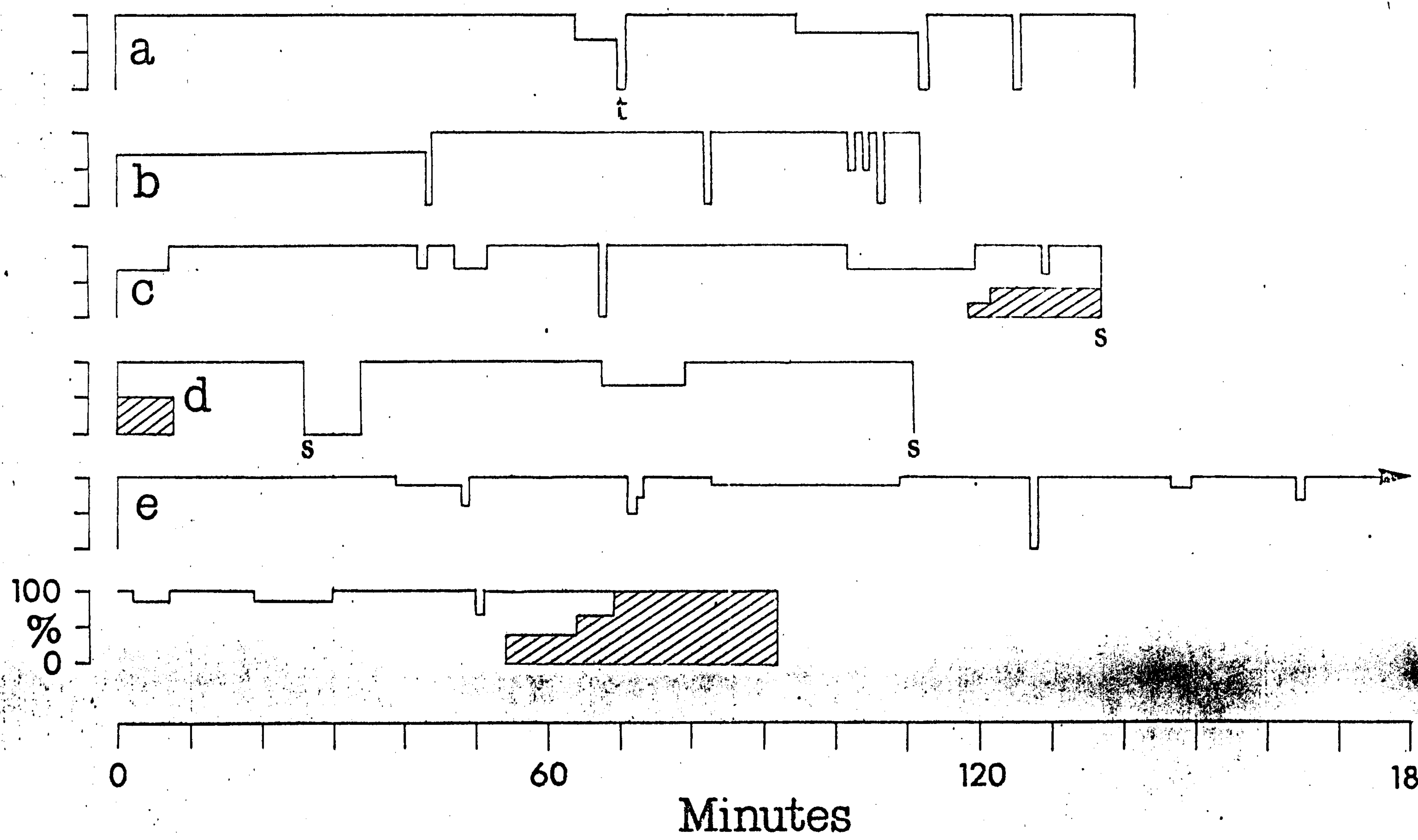
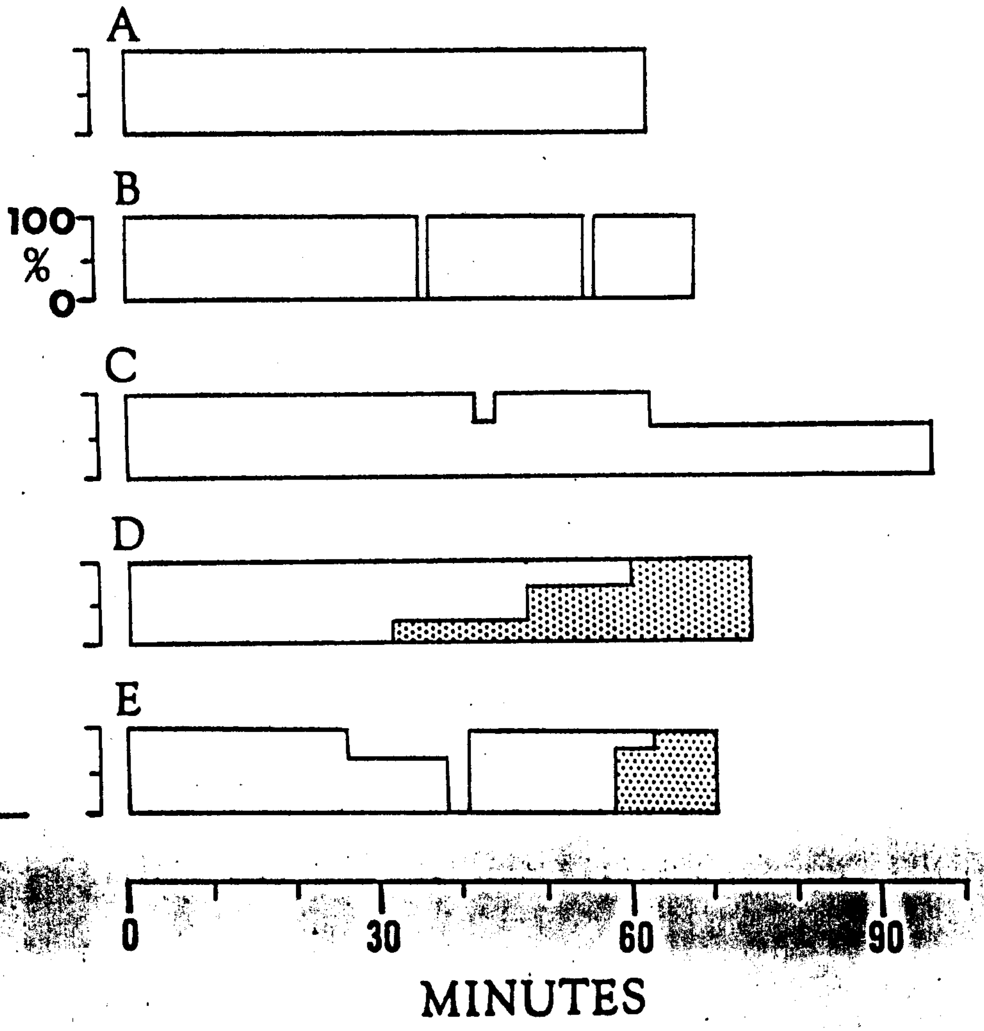

a
t
b
c
s
d
s
s
e
100
%
0
0
60
120
180
Minutes

Figure 34. Durations of different behavioral responses during atmospheric basking for turtles observed for longer than 30 minutes. Vol. represents those turtles voluntarily terminating basking; All stands for duration of basking for turtles terminating basking by any means (all observations); N is the number of turtles observed; and $\overline{X}$ is the mean in minutes. See Fig. 28 for explanation of graphs. A. Single basking period. B. Dunking behavior. C. Partly wetting the body. D. Using shade. E. Combination of behavioral responses.

VOL		ALL	
N	$\overline{X}$	N	$\overline{X}$
50	53	82	49
47	81	77	73
9	90	15	91
11	95	16	91
22	119	31	112



It is apparent in Figure 34 that the turtles with behavioral responses engaged in atmospheric basking longer than those with a single basking period. The average duration of atmospheric basking in the former group was 96 minutes for voluntary terminations of basking and 92 minutes for all observations, which is about twice that of those turtles with a single basking period ($\overline{X}$ = 53 minutes and 49 minutes, respectively). Further, of 139 turtles which voluntarily terminated basking, 89 (64.0%) used one or more of the described behavioral responses. There were a total of 221 turtles that terminated basking by any means, and of these 139 (62.2%) employed some behavioral response. In other words, most of the turtles remaining out of water longer than 30 minutes employed some response (dunking behavior, etc.) which apparently permitted them to engage in further basking behavior.

Aquatic Basking

Although freshwater turtles spend the greater part of their daily activities in aquatic environments, little is known about basking underwater or on the surface. Cagle (1950) reported that Pseudemys scripta in North America at times may float on the surface when resting, and juveniles enter shallow water where they often aggregate in large numbers. Reasons for this behavior were not given. Sexton (1959) found large number of Chrysemys picta spending most of their summer days on top of mats of foating aquatic vegetation; here the turtle could forage and often about half of the carapace was out of the water. Temperatures taken in August showed that the surface air temperature of the water in such plant beds was within 1°C of air temperature whereas water on the bottom was 3°-9°C. Presumably turtles on top of the mats could select the warmer waters and be exposed to direct sun. Brattstrom (1965) suggested that Chelydra serpentina and Sternotherus odoratus selected water temperatures near their preferred body temperatures. This evidence indicates that freshwater turtles select warm parts of aquatic habitats, but the importance of this behavior in daily activities in unclear.

Moll and Legler (1971) termed "aquatic basking" for those times when turtles were basking at the surface of bodies of water. The turtles were motionless with limbs fully extended and part of the carapace protruded out of the water. Such behavior usually occurred on top of beds of aquatic, floating vegetation. It was common in juvenile and sometimes used by adult P. scripta in Panama.

Basking on the surface was noted only once in Hayfork Creek Clemmys marmorata. An adult female was observed on the west shore of pool 12 where she rested in shallow water with part of an algae mat draped over her carapace. About half of the carapace was out of the water. She remained stationary for 2 hours, except for occasional movements caused by the head coming up through the algae, presumably raised for air. Surface basking in pond turtles was rare. C. marmorata were not observed resting on the surface, even where algae mats were available. Turtles were seen slowly swimming and occasionally floating with the current, but the shell was usually entirely wet and this behavior seldom lasted more than a few minutes.

Unlike the usage proposed by Moll and Legler (1971), I do not restrict the term "aquatic basking" to just those times when turtles rest on the surface with part of the shell out of the water. Rather, I propose that "aquatic basking" refer to all times of heat gain while animals are predominantly underwater, including resting on the surface with or without the carapace exposed to air and when the animals seek warm water.

Documentation of aquatic basking behavior in pond turtles is principally based on field observations and collecting of turtles during the summers of 1960-62 and 1967-71. Hayfork Creek C. marmorata mostly hide at night and during most of the afternoon during summer months. Field experience indicated that their distribution in the creek may be influenced by environmental factors such as temperature of the water.

Pond turtles apparently selected warmer parts of the aquatic environment. The stream temperatures varied. In some pools, cold springs flowed into the pools or deep water was cooler than that on the surface due to thermal stratification. For example, at pool 6 in July, 1970, the surface water temperature (10cm deep) was 24°C whereas at 3 m deep in a "cold pocket" the water was 16°C. In summer the surface waters during the afternoons and evenings were about 1 to 3°C warmer than at 1 m deep, and below 1 m the water cooled rapidly. Pond turtles in the creek were often concentrated in protected shallows such as under large rocks, logs, and undercut banks. Turtles in these situations were noticeably warmer than those in deep parts of pools. Also, it was often found that turtles were crowded in shallow, protected sites even when there were extensive areas of cover available on the bottom of pools. This evidence suggests that pond turtles may select these sites because they afford warmer environmental conditions. A different hypothesis may be advanced that these sites provide the turtles with access to air without requiring that the animals expose themselves to real or potential predation. Energy would be conserved there since a turtle hiding on the bottom of pool would occasionally need to surface for air. If the latter is the primary motivation for seeking shallow, protected areas, the turtles never-the-less are exposed to the warmer waters.

In July, 1971, several turtles were found under mats of algae in shallow water where water temperatures were 24°-28°C in late afternoon. In addition to warm water under these mats, the turtles were camouflaged by the vegetation, had easy access to air, and there appeared to be an abundance of food (insects, tadpoles) in the vegetation mats. Presence of turtles in such situations may be due to one or more of these factors, but occurrence in shallows provides the animal with exposure to warmer waters than available in other parts of its aquatic environment (deep parts of pools, cold springs). Pond turtles may select these shallow waters primarily for thermal reasons.

Pond turtles engaged in aquatic basking on summer nights. They are in the water (T_a = 17°-22°) from 1800 hours until about 0800 hours. During this time the water is warmer than the air (T_a = 8°-12°). At night they apparently select the warmest environmental temperatures, i.e. the stable aquatic medium. During the day they appear to select warm parts of the aquatic environment as a major source of heat for many hours.

Discussion and Summary of Thermal Ecology

Thermoregulation by means of behavior is characteristic of all reptiles thus far studied. Basking in the sun plays a dominant role in the lives of diurnal lizards and snakes, whereas nocturnal reptiles rely largely upon the heat of the substratum as a source of body warmth (Bogert, 1949; Brattstrom, 1965; Templeton, 1970).

The present study indicates that <u>Clemmys</u> <u>marmorata</u> behaviorally regulates its body temperature within a relatively narrow activity range and appears to prefer temperatures between 24° and 32° during summer months. Selection of appropriate temperatures occurs both within and between terrestrial and aquatic environments. The pond turtle is able to increase a cool body (T_b = 17°-18°) up to the voluntary maximum (T_b about 32°) by sunning itself for only about 30 minutes and then to regulate its T_b out of water by a number of behavioral responses. It remains in water at night when it is colder on land than in the water, also an important thermoregulatory strategy. It thus elevates its body temperature (T_b between 24° and 32°) for many hours day and night. Telemetry data showed that many behavioral responses were correlated to changes in T_b; the Pacific pond turtle, and probably most freshwater turtles, accurately regulate their T_b when there is opportunity to select appropriate temperatures.

Boyer (1965) concluded from his extensive studies on <u>P. scripta</u> that the most important function of basking in the sun was to elevate the body temperature in freshwater turtles. Moll and Legler (1971) reported that data collected in the field in Panama on this species and in the laboratory also suggest that raising the body temperature is the main function of basking in tropical freshwater turtles; but they state, too, that basking is a complex phenomenon which probably accomplishes all or most of the functions attributed to it (e.g., thermoregulation, drying, Vitamin D synthesis). Most recently, Spray and May (1972) list several possible explanations for why turtles "bask" and their data support the hypothesis that the chief purpose of basking is intermittent thermoregulation, since the ability to heat rapidly and to decrease cooling rates, even to some extent in water, gives turtles more time at a relatively high temperature.

Clearly, the field evidence for Clemmys marmorata shows that the animal regulates its body temperature at relatively high levels when possible and studies on other freshwater turtles (Moll and Legler, 1971; Spray and May, 1972) strongly support Boyer's hypothesis that elevation of body tmperature is the most important function of basking behavior. Other functions of basking (elimination of parasites, drying of the integument, and synthesis of Vitamin D) are discussed in detail by Moll and Legler (1971); some or all of these may be derived from atmospheric basking as secondary benefits.

Evidence that basking is primarily for elevation and maintenance of body temperature is supported by the following observations:

1. Many physiological functions in turtles are temperature dependent. Although turtles may occasionally be active at low temperatures, maximal efficiency of physiological processes is closer to that of "preferred" body temperatures.

2. Clemmys marmorata and presumably other freshwater emydid turtles thermoregulate by behavior, selecting temperatures available in the sun, on land, or in the water. These turtles remain at an elevated body temperature for most of the day, which suggests the importance of basking in the lives of these turtles.

3. Freshwater turtles rapidly gain heat in air and may have means to reduce cooling in water. Rapid heat loss is expected to occur when a freshwater turtle returns to cool water. Since the rate of heat loss is markedly faster than the rate of heat gain, it might seem that the overall effort of atmospheric basking is inefficient and that turtles emerge for some other purpose than elevation of body temperature. However, this is a simplistic model and unrepresentative of free-living turtles. Heat conservation mechanisms appear to function during diving. The heart rate slows to a minimum rate as soon as a turtle submerges (Belkin, 1964) and the cardiac output may fall to 5% of the predive value (White and Ross, 1966). This serves to reduce the rate of circulation of blood and loss of heat through the extremities. Weathers and White (1971) demonstrate physiological thermoregulation in freshwater turtles by showing that there is peripheral vasodilation during heating and vasoconstriction during cooling.

4. Clemmys marmorata may repeatedly bask out of water in the course of one day and regulate its body temperature by employment of several behavioral responses; atmospheric basking in this species permits it to obtain a relatively high T_b during the cool morning hours and by the time this behavior is terminated the water temperatures have risen from about 17° to 25°-27°.

5. Clemmys marmorata apparently avoids temperatures over 34° and often terminates basking out of water at about 32°. This is below the lethal point (about 40°C). If this species were to maximize its synthesis of Vitamin D, drying of the skin, and elimination of parasites, it would seem that it would have high tolerance to heat so it could remain in the sun for long periods of time. Rather, C. marmorata returns to the water when T_b approaches 32°-34° or employs thermoregulatory responses to lower its T_b, such as moving into shade.

Thus, the rates of heating and cooling in freshwater turtles appear to maximize the attainment and maintenance of an elevated body temperature. Thermoregulatory strategies include selection of appropriate temperatures available on land or in the water. Behavioral responses of individuals probably modify the rates of heating and cooling, serving as fine tuning mechanisms in its thermoregulatory repertoire. Elevated body temperatures apparently are for maximal efficiency of physiological functions and are obtained via complex basking strategies and responses.

Atmospheric basking denotes times of heat gain out of water, including basking in direct sun, partial sun, or full shade. Hayfork Creek pond turtles engaged in atmospheric basking presumably to elevate their body temperatures above that of the aquatic environment. Atmospheric basking occurred during the day when air temperatures were markedly higher than those in the water, and was most frequent in the morning hours. Most behavior thought to be important as a cooling mechanism involved complete or partial returns to the stream.

Daily patterns of atmospheric basking in summer were studied at several different pools, and these data revealed the following:

1. Foraging and movements may start as early as 0630 hours, and turtles usually emerge for atmospheric basking with the first sunlight (0730 to 1000 hours, depending on the local environmental conditions).

2. In most situations the species basks in greatest numbers during the morning hours with peak times about 0900 to 1000 hours.

3. The daily light regime greatly effects the pattern, since direct sun appears to initiate atmospheric basking and shade terminates it.

4. There seems to be less motivation to bask later in the day, perhaps due to increases in water temperature (T_a = 24°-28°) during afternoon hours.

5. Turtles appear to be opportunistic in their atmospheric basking behavior, principally due to the heterogenous nature of the habitat at Hayfork Creek.

6. There were no apparent differences in the basking patterns between July, August, and early September.

Analysis of the individual attributes and periods of atmospheric basking indicated several new relationships. First, turtles that emerge early in the morning engage in atmospheric basking longer than those emerging later in the day. At pool 12 there was a significant difference ($p<0.05$) between hourly groups of data from 0800-0859 (average duration of basking = 68 minutes) hours until 1200-1259 hours (average = 12 minutes). Shorter times of atmospheric basking as the day progressed probably reflect higher body temperatures of emerging turtles (due to prior basking) and increases in ambient temperatures (both air and water). Second, turtles may voluntarily terminate atmospheric basking, which represents the preferred duration of exposure to external heat, or be disturbed. These differences needed to be recognized in order to determine the duration of undisturbed basking times, which were markedly longer than those for disturbed turtles. Extrinsic, independent factors may greatly alter the times of atmospheric basking in nature. Third, there was no apparent difference between the duration of basking in July and early September. Lastly, local environmental conditions appeared to greatly affect the duration of atmospheric basking, and turtles appeared to be opportunistic in the basking habits.

Pond turtles were observed to orient with the posterior part of the shell directed toward the sun, but there was insufficient evidence to decide if this was due to selection or merely a result of the slope of basking sites. The turtles often shifted positions while basking out of water and basking appears to be an active process. Postures varied with time since emergence. Recently emerged turtles protruded the head and appendages, presumably to maximize the surface area exposed to the sun or other heat source. Later, the appendages were withdrawn into the shell. Measurements have not been made of the effect of appendage exposure on rates of heat gain and loss. However, present evidence suggests that the orientation and posture changes in freshwater turtles during atmospheric basking serve as ways to regulate body temperature. Frequently synchronized with changes in orientation and posture were other behavioral responses during atmospheric basking.

Periodic return to the water was one of the most common behavioral responses and there may be repeated returns by an individual turtle. Whether partly or entirely submerged during such dunking behavior, the turtle doubtless lost heat in the water and upon subsequent emergence probably had a reduced heat gain for several minutes due to heat loss from evaporation of water from the body. It is suggested that dunking behavior is a major thermoregulatory mechanism to cool the body and to regulate body temperature near preferred levels. Further, the first periods of dunking behavior were longer in duration that later intervals. The first basking periods were usually in the morning hours when ambiant conditions were cooler and, presumably, it took longer for animals to reach their preferred temperature levels. When a turtle terminates atmospheric basking its body temperature is expected to drop rapidly in water, but in dunking behavior the time in water usually was only 1-3 minutes. On second or later emergences the turtle probably had a higher T_b (body temperature) than on its first emergence. Ambient temperatures rose as the day progressed. Turtles would thus bask for shorter periods of time lest the animal surpass the upper limit of temperature for normal activity.

Wetting the body may also be an effective way to regulate body temperature, since varying amounts of the body could be placed in water to obtain the desired body temperature. Use of shade was observed, too. This permits an animal to remain out of water for extended periods of time and, presumably, maintain an elevated body temperature without the discomfort that would occur if exposed to direct sun. Again, a thermoregulatory function is suspected.

Periodic returns to the water, partial wetting of the body, and use of shade are not exclusive categories of behavioral responses. Rather, they are all involved in apparent cooling of pond turtles and often used in combination. Turtles employing behavioral responses during atmospheric basking remained emerged longer than those with a single basking period; these turtles likely maintained the body temperature at an elevated level for many hours every day.

Aquatic basking refers to those times of heat gain that take place principally underwater. A major part of such behavior in pond turtles appears to be involved in the selection of warm waters in protected shallows and remaining in water during times when air temperatures are less than those available in the aquatic environment. Pond turtles apparently use the stream as a retreat from cool air temperatures between about 1600 hours (late afternoon) until 0800 hours (morning), which comprises about two-thirds of each summer day. Present evidence indicates that aquatic basking is an important thermoregulatory strategy and, overall, may be as vital to the lives of freshwater turtles as atmospheric basking.

This study indicates that basking behavior is a complex and important process, and one of the major features of the daily activity of pond turtles. Such behavior probably plays a vital role in the ecology of freshwater turtles, particularly those which frequently leave the water to engage in atmospheric basking. Present evidence suggests that basking in Clemmys marmorata is operative day and night during summer months, resulting in elevated body temperatures for bodily functions during most hours of each day. The turtles appear to actively select particular environmental temperatures and behaviorally regulate their body temperatures.

Aggressive Behavior

Social relationships in turtles are poorly understood and, except for mating behavior, there is little evidence of interaction during their daily activities.

Moll and Legler (1971) reported that sliders (Pseudemys) can be regarded as solitary. Members of the same species apparently seek each other only for the purpose of mating. Further, they stated that the presence of more than one individual at the same time and place (when feeding, basking, or nesting) can be regarded as fortuitous or at least not resulting from social or gregarious tendencies.

On the other hand, Ernst (1971) stated that the painted turtle, Chrysemys picta, is not solitary like many turtles. Instead, it is most often found in large aggregations, especially near favorable sunning sites, because of mutual attraction of turtles to areas with favorable environmental contitions.

Except for courtship and mating behavior, none of these authors believed that aggregations of freshwater turtles were due to any attraction between individuals. They attributed any associations to congregations at favorable basking, feeding, or nesting sites.

The Pacific pond turtle aggregated in large numbers at pools with cover and sunning sites (see Home Range). It is not known whether the turtles were attracted to each other.

Fighting, threats, and other aggressive activities are well known components of the social behavior of many lizards, but evidence of aggression in other reptile groups is scant. Among the turtles and tortoises of the large family Testudinidae, aggressive behavior has been reported as common only among the terrestrial gopher tortoises (Gopherus). Combat between male gopher tortoises is frequent in nature and captivity, but aggression among females and sexually immature individuals in uncommon (Weaver, 1970). Box turtles (Terrapene) are mainly terrestrial but aggressive interactions appear to be rare in nature except for some biting during courtship (Legler, 1960; Stickel, 1950). However, Boice (1970) found that captive Terrapene compete for food. He suggested that it is possible that field studies of Terrapene are incomplete and that aggressive behavior has not been noted because researchers expect turtles to be asocial. This attitude seems to exist also for freshwater turtles.

Although the aquatic Testudinidae is a diverse and species rich assemblage, there is only one report of aggression in this group. Babbitt (1932) observed a pair of male pond turtles, Clemmys guttata, engaged in combat on land for over half an hour. Ernst (1971) found that the painted turtle, Chrysemys picta, even when crowded, appeared to treat conspecifics as inanimate objects and no fighting, aggressiveness, or display of territoriality was observed. No instances of fighting were observed among P. scripta during extensive field studies by Moll and Legler (1971).

Reports of aggression in other families of turtles are meager. There are five known cases of aggressive interactions among captive turtles, mostly concerned with biting between males or behavior related to sexual activity, and one report of aggression between two male musk turtles, Sternotherus minor, that occurred under natural conditions (Jackson, 1969).

Jackson (1969) stated that present knowledge suggests that agonistic behavior may be of more general occurrence among terrestrial turtles than among aquatic forms and that the difference is perhaps more apparent than real, owing to the greater difficulty encountered in making observations on the aquatic species.

Aggression in Free-living Pond Turtles

Clemmys marmorata is a wary species of turtle, but by using blinds it was possible to observe animals during daily periods of activity at pools 12 and 27. Data were collected on 12 days in July, August, and early September of 1970 and 1971, during the non-breeding season. Incidental notes were taken on other days.

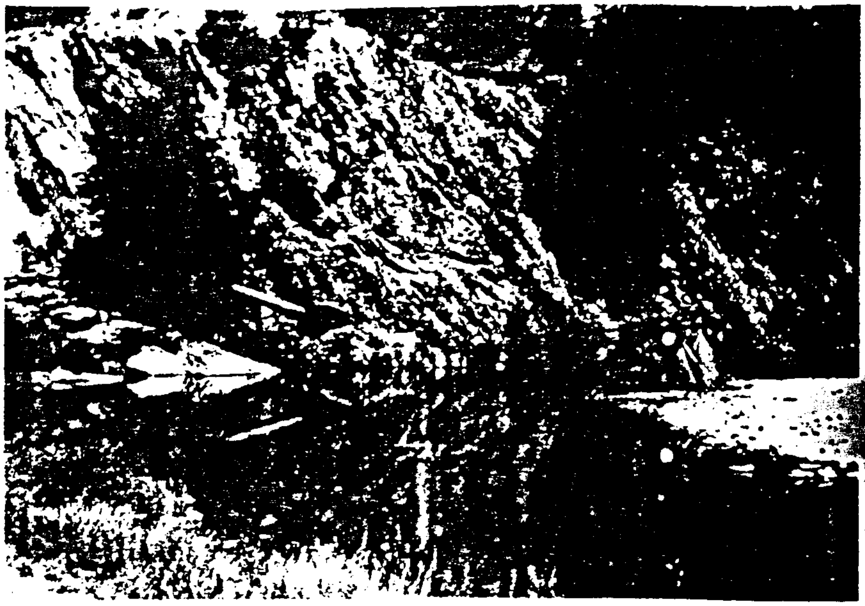
Turtles were watched through binoculars and behavioral actions noted or described on a tape recorder. Observation posts were blinds built about 30 m from sites used for sunning by the turtles. These posts overlooked the pools. No turtles were frightened by my presence in these quarters.

From the vantage points above the pools I saw the behavior of unrestrained individuals. A "bushman" blind was constructed across from the sunning sites in pool 12 during the summer of 1971 (Figure 35). On August 11 and 12 a Nikon camera with a 300 mm telephoto lens was used to obtain photographs of aggressive behavior.

Description of Aggressive Behavior

Between 1058 and 1103 hours on September 3, 1970, I observed pond turtles fighting. An adult male swam behind a large medium-sized turtle for about 2 m. Then he swam around in front of the smaller turtle and bit at the anterior part of the shell. During

Figure 35. Blind built at pool 12 where turtles were photographed on August 11 and 12, 1971. Top: Looking north with blind to the right. Large rocks at left were favored sunning sites. Bottom: Camera view of sunning sites on large rocks on opposite side of pool.



a second bite he appeared to nip the leg of the medium-sized animal, which caused it to momentarily withdraw into its shell. After this brief encounter the smaller one faced the adult and bit him on the foreleg. The adult temporarily withdrew his head, but soon approached the smaller animal and bit at it twice without making contact. The latter turned and swam about 1 m; the adult followed. Again the male swam around to the front and they faced each other on the surface with the anterior edges of the shells out of water. Each lunged at the other twice without contact. Suddenly the medium-sized turtle turned and rapidly swam upstream for about 4 m until it was hidden in a mat of algae. The adult followed for about 3 m, but apparently gave up pursuit when the smaller animal moved into the algae mat. This was the only aggressive behavior observed between pond turtles while they were in the water.

Several kinds of aggressive behavior were seen during atmospheric basking. The most common was an open mouth gesture, which consisted of one turtle opening its mouth widely, and usually stretching the neck, directly toward another (Figure 36). The mouth was held open from 1 to 10 seconds, mostly less than 5 seconds. The recipient of this gesture usually responded by turning away or crawling to a new position. Rarely, it would return the gesture (Figure 36). A few turtles simultaneously had their mouths open toward one another. The open mouth gesture was not preceded by any apparent signal. In one case, an adult female sunned next to a medium-sized turtle without any interaction for over 5 minutes; the smaller animal started to protrude its head from its shell when suddenly the female opened her mouth toward the medium-sized turtle, whereupon the latter immediately withdrew its neck (Figure 37). In another instance, two adult males sunned near each other for about 5 minutes when one presented an open mouth gesture toward the other without any response on the part of the latter individual; after 5 minutes more, the same turtle turned toward the other, but this time opened its mouth widely and then bit the other animal on the shell (Figure 38). Biting in pond turtles was uncommon and all of these attacks were preceded by an open mouth gesture.

A few cases of ramming, pushing, or avoiding another turtle were not associated with an open mouth gesture or any other apparent signal. However, the open mouth gesture itself seldom failed either to evoke a response on the part of the recipient of to be followed by an attack, or another gesture, by the first turtle. During 37 hours of observations I saw a total of 145 aggressive acts: 111 (76.5%) open mouth gestures, 11 (7.5%) attacks involving biting, and 24 (15.0%) instances of pushing or ramming another turtle. Of the 122 open mouth gestures (including 11 that were followed by attacks), 89 (72.9%) resulted in a nearby turtle avoiding the gesture by returning to the water, turning the body away, or retracting the appendages. Subtle responses could not be detected and open mouth gestures probably more often result in some action by the recipient than noted here. Most open mouth gestures resulted in a response by the recipient.

Aggressive acts occurred between the sexes, members of the same sex, and between adults and medium-sized turtles. Adults directed a total of 85 aggressive acts toward other turtles whereas medium-sized individuals engaged in 60 such actions. Chi-

Figure 36. Open mouth gestures. Top: Adult female directing open mouth gesture toward medium-sized turtle, which is in the process of turning away. Bottom: Smaller turtle with open mouth gesture as adult female began to crawl past it. Photographed August 11, 1971.

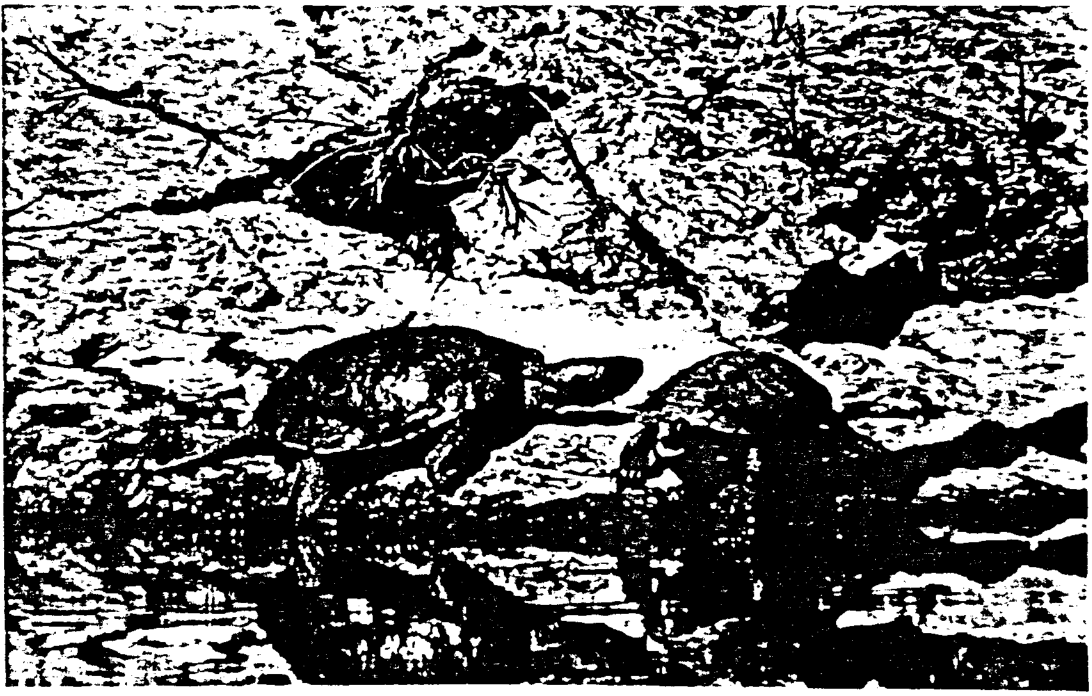
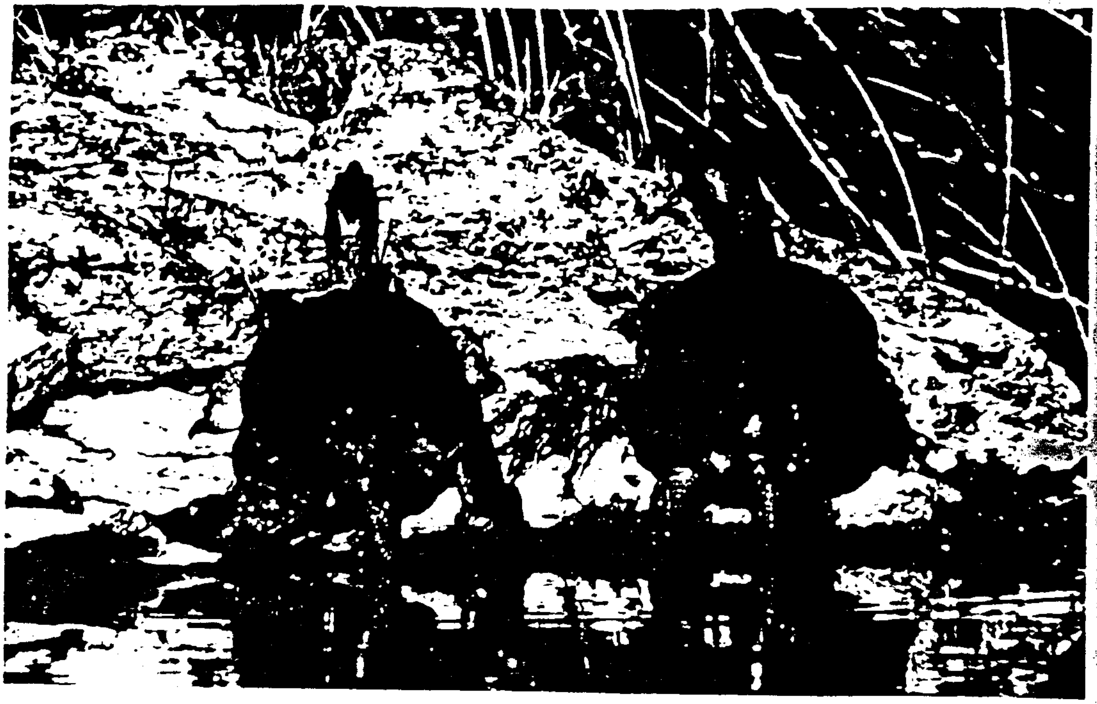


Figure 37. Open mouth gestures. Top: Adult female sunning next to medium-sized individual without any apparent interaction. Bottom: When smaller turtle started to protrude its head out of its shell, the adult female directed an open mouth gesture toward it, which resulted in immediate withdrawal of the head. Photographed August 11, 1971.

Figure 38. Open mouth gestures, and biting in Clemmys marmorata. Top: Two adult males sunning near each other; turtle on the right is directing a partial open mouth gesture toward other animal. Turtles are recently emerged as shells are wet. Bottom: Same adult males shown with adult on the right biting other turtle following an open mouth gesture (about 5 minutes after the photo above). Photographed August 12, 1971.



square tests were performed to determine if these actions occurred in a random manner or had direction (Table 17). The overall difference between the observed and theoretical expected frequencies was not significant even at $p < 0.10$. However, this does not indicate the proportion of adults and immatures involved in the aggressive acts. During summer about 35% of the Hayfork population is composed of medium-sized turtles and the remainder (65%) are adults. Also, at pool 12 I observed about 1 medium-sized turtle sunning for each two adults. Assuming the proportion of immatures and adults were the same as in the entire population, I calculated corrected frequencies of expected values (Table 17). In other words, since there were more adults in the population than immatures, it was expected that mature animals would be involved in more aggressive acts. The difference between these values and the observed frequencies was high ($\chi = 55.2$, $df = 1$), and is a significant difference ($p < 0.001$). Or, after correction for age composition, aggressive acts were not randomly distributed between test cells (i.e. adult-adult, adult-medium, etc.). Tests of each cell against the remainder of the frequencies revealed that all of them were significantly different ($p < 0.01$): adults directed less aggression towards other adults than expected but more aggression toward immatures; medium-sized individuals directed less aggression towards adults and more towards other immatures than expected on the basis of chance alone.

Table 17. Frequencies of aggressive actions observed in *Clemmys marmorata* at pool 12, Hayfork Creek.

	Recipient						
	Adult			Medium			
Instigator	Obs.	Exp.[1]	Exp.[2]	Obs.	Exp.[1]	Exp.[2]	Total Obs.
Adult	35	32	61	50	53	33	85
Medium	19	22	33	41	38	18	60
Total	54			91			145

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[1] Theoretical frequencies of expected values.

[2] Corrected frequencies of expected values based on population composition (35% medium-sized turtles and 65% adult turtles).

Factors Effecting Aggressive Behavior

Observations on 7 days from 0800 to 1300 hours at pool 12 provided information on the number of aggressive acts per hour and indicated some of the factors inducing aggression. Most atmospheric basking occurred between 0900 and 1159 hours, but most agressive acts were between 1000 and 1159 hours (Table 18). There was an increase in aggression from 0800-0859 hours (actions per turtle = 0.51) to 1100-1159 hours (0.88) and 1200-1259 hours (0.81). Table 19 indicates the number of aggressive acts in relation to the number of emergences and to the total number of movements on or off the basking sites. The number of aggressive acts increased during the day when compared to the number of emergences per hour, but hourly differences were slight in relation to the total number of movements. These relations are shown in Figure 39. However, it is not clear if these behavioral traits are correlated to aggressive acts. Therefore, I plotted the number of aggressive acts per hour of each day against the average number of turtles basking and number of movements (Figure 40). I calculated the correlation coefficients (r) for these sets of data. There is not significant correlation ($p < 0.05$) between the number of aggressive acts and the number of turtles basking per hour. The relation ($r = 0.352$) is a weak one. However, there was a correlation ($p < 0.01$) between aggressive acts and number of movements ($r = 0.542$). This is still far from being highly correlated (+1 is perfect positive correlation). It appears that both the number basking and moving may influence aggressive acts, but the latter apparently is more important.

Table 18. Hourly comparisons of the total number of aggressive interactions (A) and average number of turtles basking simultaneously (B) during the time period.

Date	0800-0859		0900-0959		1000-1059		1100-1159		1200-1259	
	A	B	A	B	A	B	A	B	A	B
1970										
July 24	0	10.8	4	10.7	8	14.7	7	13.3	6	5.9
July 26	5	9.5	5	23.4	11	20.0	6	13.6	0	2.0
Sept. 3					4	13.4	7	9.4	6	5.7
Sept. 9	0	1.3	2	4.1	4	5.0	1	2.5	0	1.2
1971										
July 21	6	2.3	10	3.7	13	4.5	15	2.7	1	1.3
Aug. 11	1	0.9	4	4.9	2	5.2	0	2.2		
Aug. 12	1	0.9	3	2.8	3	2.7	3	0.5		
Total	13	25.7	28	49.6	45	65.5	39	44.2	13	16.1
Average/Day	2.2	4.3	4.7	8.3	6.4	9.4	5.6	6.3	2.6	3.2
A / B	0.51		0.56		0.69		0.88		0.81	

Table 19. Hourly comparisons of the total number of aggressive interactions (A), total number of emergences out of the water (E), and total number of movements of turtles on and off sunning sites (M).

Date	0800-0859			0900-0959			1000-1059			1100-1159			1200-1259		
	A	E	M	A	E	M	A	E	M	A	E	M	A	E	M
1970: July 24	0	13	24	4	33	64	8	53	109	7	40	85	6	27	59
July 26	5	29	35	5	20	40	11	45	95	6	31	74	0	0	4
Sept. 3							4	14	37	7	14	31	6	7	17
Sept. 9	0	3	3	2	6	10	4	7	14	1	4	11	0	4	10
1971: July 21	6	16	26	10	11	24	13	22	48	15	12	21	1	0	3
Aug. 11	1	3	4	4	20	37	2	21	44	0	2	7			
Aug. 12	1	4	6	3	5	9	3	6	9	3	2	4	—	—	—
Total	13	68	95	28	95	184	45	168	356	39	105	233	13	38	93
Average/Day	2.2	11.3	15.8	4.7	15.8	30.7	6.4	24.0	50.9	5.6	15.0	33.3	2.6	7.6	18.6
A /E		0.19			0.29			0.27			0.37			0.34	
A /M		0.14			0.15			0.13			0.17			0.14	

Figure 39. Comparison of the number of aggressive acts (A), emergences (E), submergences (S), and total number of movements on or off basking sites (T) by hour of occurrence.

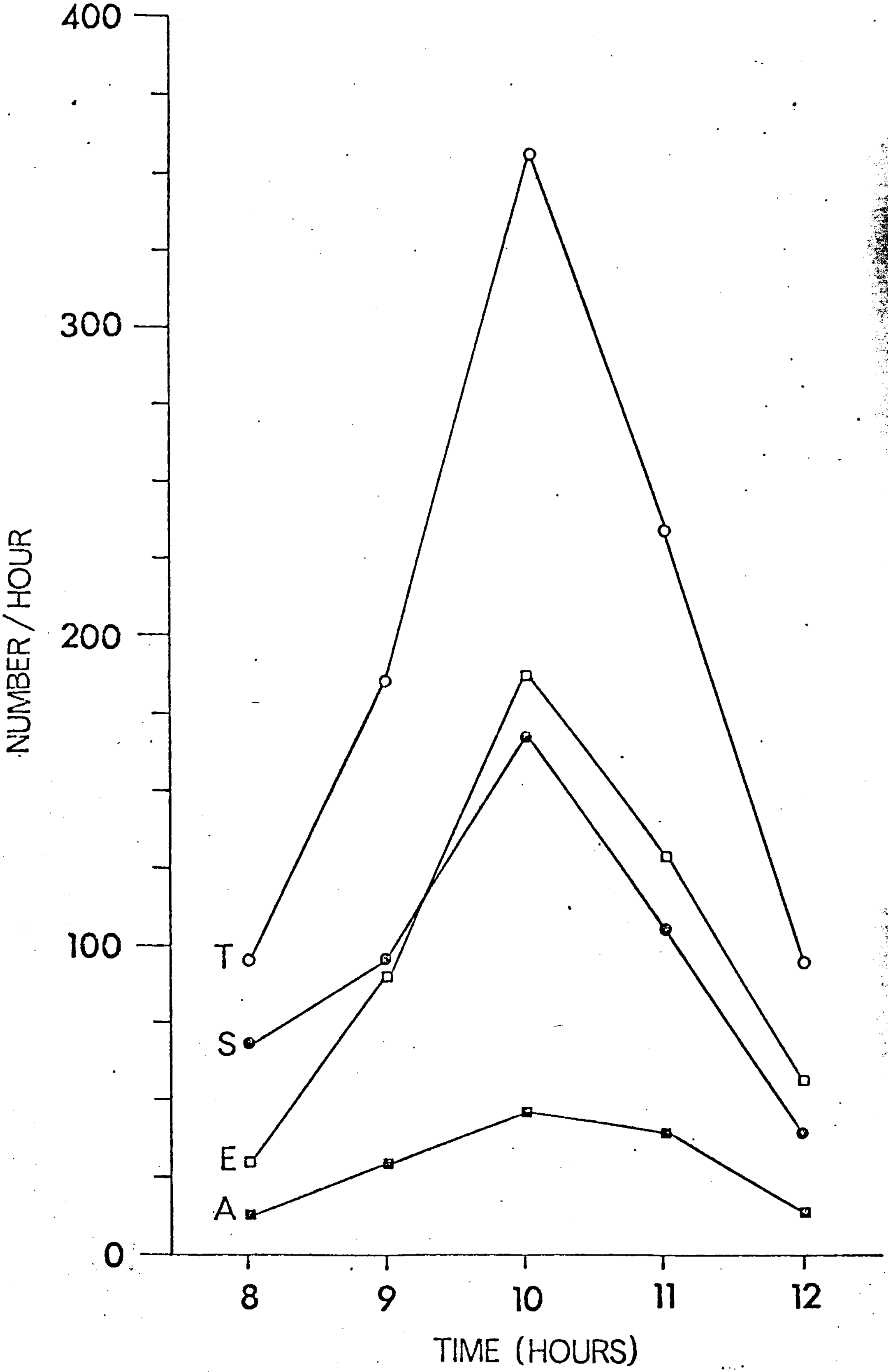
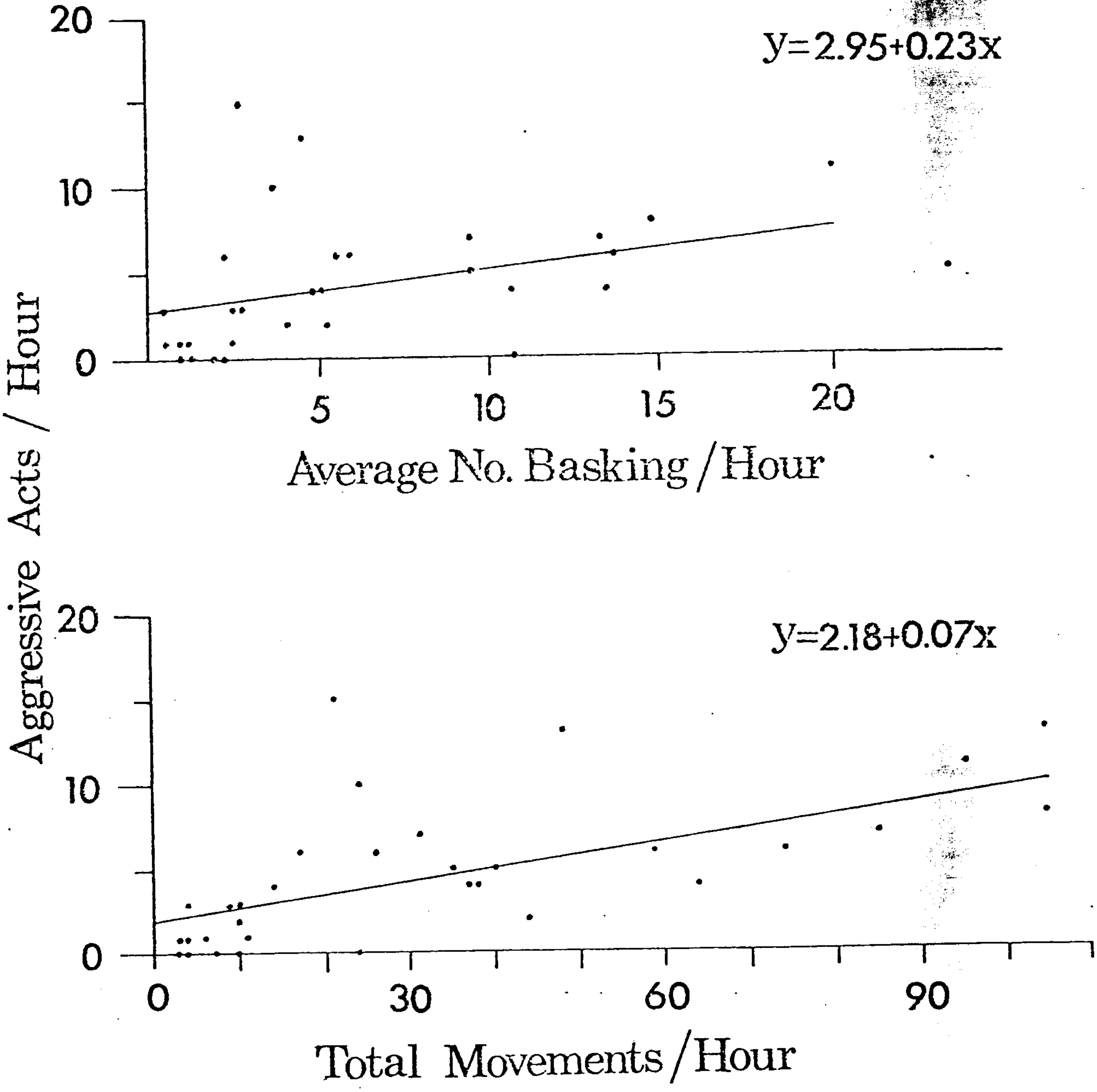

400
300
200
100
0
NUMBER / HOUR
T
S
E
A
8
9
10
11
12
TIME (HOURS)

Figure 40. Relation of aggressive actions per hour to the average number basking, number emerging, number submerging, and total number on or off the basking sites per hour.


y=2.95+0.23x
20
10
0
5
10
15
20
Average No. Basking / Hour
Aggressive Acts / Hour
y=2.18+0.07x
20
10
0
0
30
60
90
Total Movements / Hour

Movements of turtles on or off basking sites appear to influence the aggressive level in Clemmys marmorata. It was repeatedly observed that an emerging turtle instigated or was the recipient of an open mouth gesture, ramming, or attack. This may occur because such an animal upsets the spacing of turtles already on the basking site and occasionally must literally force itself onto the site. Turtles returning to the water usually turned and moved slowly toward the water, but occasionally had to move through areas congested with other turtles. This latter situation often evoked aggressive responses.

Other factors may influence the level of aggression in freshwater turtles. Perhaps the effects of crowding influence aggression. In general there is more aggression with increased number of turtles engaged in atmospheric basking (Table 18), but of equal importance is whether these turtles are spaced widely or clumped together. In many cases, most of the turtles emerged to sun on a few preferred sites and these areas would soon be crowded while nearby sites were unoccupied. It seemed that these crowded individuals performed most of the aggressive actions. However, I also observed aggression when there were only 2 turtles basking on a particular site (Figures 36-38). Crowding may influence aggression, but its role was not clearly determined in my studies.

Previous encounters may have some influence on aggression. Freshwater turtles may have "chaining of aggression" i.e. an animal threatened or attacked will undertake an aggressive act toward a different individual. I saw an adult bitten on the leg by a medium-sized turtle and the adult slid off the sunning site into the water. It swam to a new site and on emergence gave an open mouth gesture (about 8 seconds in duration) toward a sunning immature turtle, which immediately vacated the site. The adult crawled out of the water and with its mouth widely opened proceeded toward another immature turtle on the site, which also left. Afterwards the adult returned to the water. This sequence of events occurred in less than 3 minutes. Overall, though, previous encounters appeared to constitute a minor role in determining aggressive activity.

Lastly, thermal influences may play a role. There was a steady increase in air and water temperatures from 0800 up to 1300 hours. Environmental temperatures effect the duration of atmospheric basking, since pond turtles usually return to the water when body temperatures approach preferred levels. Temperatures are probably important determinants of the rate of movements on and off basking sites. The turn-over rate of turtles is greater at the times of day when ambient conditions are high, and the increased movements undoubtedly results in more frequent shifting of turtles and aggressive actions. Also, the turtles may be more aggressive at higher temperatures since most reptiles are more active when warm and activities are probably carried out faster.

Function of Aggression

Aggressive behavior during periods of aquatic activity was rare. Occasionally one turtle followed another but usually such pursuit was terminated after 1 or 2 minutes without any interaction. One fight was seen between an adult male and a large medium-sized turtle (a young male or female). I suggest that this encounter occurred because the adult male provoked the smaller individual by an attempt at courtship. Turtles observed swimming underwater usually passed one another without any apparent aggressive interaction. The paucity of aggression in water may be related to the low frequency of contact between individuals because crowding was not observed during periods of aquatic activity (foraging, swimming, resting on the bottom). In some pools pond turtles were crowded under cover where there may be aggressive acts. However, I was unable to observe such behavior. It will require scuba equipment or an underwater viewing chamber to study turtles in these locations.

Aggression was relatively frequent among turtles during times of atmospheric basking and consisted of open mouth gestures, biting attacks, and ramming or pushing. The open mouth gesture is regarded as a threat in that it preceded hostile behavior and was responded to accordingly by conspecifics. Threat signals of this form are common throughout the vertebrates. An open mouth threat is generally considered a ritualization of an intention to bite. In many species in which this behavior occurs the visibility of the signal is enhanced by vivid markings in or around the mouth. In _Clemmys marmorata_ the open mouth threat exposes the yellow edging of the jaws and the bright pink to reddish interior of the mouth and tongue. The result is a conspicuous flash of color on an otherwise cryptically colored animal. Freshwater turtles have color vision (Ernst and Hamilton, 1969; Hailman and Jaeger, 1971). Presumably _C. mamorata_ respond both to the opening of the mouth and to the display of color.

My observations were made in the non-breeding season and encounters involved both immatures and adults, as well as members of the same sex, which suggests that the described aggression is probably not related to courtship. Rather, it appears to be used to settle disputes over preferred basking sites and promote spacing of turtles engaged in atmospheric basking.

Certain rocks and logs in the stream were preferred basking sites. These were usually near deep water for quick escape from terrestrial enemies, accessible to the turtle (i.e. not too steep of an incline), and large enough to rest the body out of water. These sites were the first to be occupied each morning, and many turtles were often crowded together on them during the daylight hours. Unlike some emydid turtles, Pacific pond turtles were never seen stacked upon each other during times of atmospheric basking. Instead, they were usually spaced out and separated by at least a few inches. Rarely were turtles seen with their shells in contact. Maintenance of space around an individual may insure that it receives available sunlight without being pushed off the basking site or shaded by a turtle on top. Aggressive actions may promote this spacing.

Conclusions

Other than a few prior notes concerning events associated with courtship and mating, there is scant evidence of aggressive behavior in freshwater turtles. In fact, Moll and Legler (1971) found no agonistic behavior in the slider, Pseudemys scripta, and, likewise, Ernst (1971) reported an absence of fighting, aggression, or territoriality in the painted turtle, Chrysemys picta. However, I suspect previous investigators were not aware of aggressive acts. Although not defined as such, there is a suggestion of aggressive actions (open mouth threat) in the following statements made by Moll and Legler (1971):

"Opening the mouth widely or gaping is a well-known behavioral phenomenon in reptiles; it is usually associated with exposure to heat... It probably serves the same thermoregulatory function that panting does in mammals, i.e. cooling by evaporation from the mucous membranes of the mouth and pharynx... Nearly all of the P. scripta which were observed basking under natural conditions at Juan Mina gaped at some stage in their basking, some beginning to gape when the shell was scarcely dry. ...It is clear however that some turtles begin to gape long before deep-core body temperatures achieve a plateau of discomfort or anything close to a lethal maximum temperature. Possibly gaping is triggered by thermal discomfort in any part of the body (in this case the shell) and has nothing directly to do with temperatures of vital organs. Whether or not gaping (at least in its initial stages) can be regarded as a cooling mechanism is a moot point."

Their arguments admittedly do not lend support for gaping as an efficient thermoregulatory mechanism in turtles. I suggest that the gaping behavior seen in emydid turtles may sometimes be open mouth gestures. Investigators need to observe the responses of nearby turtles when gaping is taking place in order to assess whether this behavior is an aggressive signal or used for some other purpose. Gaping in Clemmys marmorata is regarded as an open mouth threat, and, sometimes, to stretch the jaw muscles momentarily.

This study clearly shows that aggressive behavior is an important part of the daily activities of the Pacific pond turtle, and it provides the first detailed documentation of such behavior in any freshwater turtle. Further studies may demonstrate a comparable level or, perhaps, even a higher incidence of aggression in other aquatic and semi-aquatic turtles. Hayfork Creek *Clemmys marmorata* showed little aggression while engaged in aquatic activities but other populations may respond differently and, perhaps, other species may be aggressive in the aquatic environment. There was a relatively high level of aggression in *C. marmorata* during times of atmospheric basking when animals were often crowded on suitable basking sites. Such situations may evoke encounters.

Of the turtles and tortoises in the family Testudinidae, aggressive behavior is now known among the gopher tortoises, *Gopherus*, in captivity and in nature (Weaver, 1970), captive box turtles of the genus *Terrapene* (see Boice, 1970), possibly in the painted turtle, *Chrysemys picta* in the field (Babbitt, 1932), and among Pacific pond turtles, *Clemmys marmorata*, under natural conditions (data presented here). Excluding times of courtship when males fight one another, gopher tortoises do not appear to display a higher level of aggression than Pacific pond turtles. I did not observe *C. marmorata* for extended periods during the mating season and cannot comment on their courtship actions. However, I suggest that *C. marmorata* and, perhaps, other aquatic emydid turtles (*Pseudemys*, *Chrysemys*, etc.) may eventually prove to have aggressive activities equal to or higher than the gopher tortoises. Both the aquatic and terrestrial turtles may compete for limited food, shelter, and other resources in their environments, and aggressive actions may be important in the distribution of these resources between individuals.

Since there is such limited information on aggressive behavior in freshwater turtles, additional quantitative studies are greatly needed to explain the role and importance of such behavior in their lives. Further, workers should explore the possibilities of social hierachies and territoriality in freshwater turtles, presently unknown in these animals.

My study revealed that adult Clemmys marmorata directed more aggression toward medium-sized turtles than toward other adults, whereas medium-sized animals were more aggressive toward their own group than toward adults. Hence, juveniles were more likely to be recipients of aggression than were adults. This may reflect reduced aggression between adults due to recognition of individuals or subtle signals that result in avoidance of aggression. These behavioral interactions need to be examined in closer detail than was possible in my study. Juveniles may be intimidated by the size of larger turtles and, therefore, are more often aggressive toward animals of their own size.

My observations also indicate that the relative frequency of aggression during atmospheric basking was higher in late morning than earlier. Several factors may directly or indirectly affect this level of aggression, but it appeared that movements of turtles on or off the basking sites had the most important influence. Moving animals seemed to cause most of the aggressive actions, probably because the spacing of turtles on a basking site was often altered by an individual emerging or submerging. Aggressive acts in Clemmys marmorata may promote spacing and settle disputes over atmospheric basking sites.

Adaptive Strategies

The present study indicates some of the adaptive features of Pacific pond turtles that apparently have resulted in their widespread occurrence and abundance from southern British Columbia to northern Baja California, from sea level to 1830 m (6000 ft) elevation, and in diverse aquatic communities (streams, rivers, ponds, lakes, and estuaries).

The estimated density of turtles was about 214 animals per kilometer (333 per mile) of stream or about 214 per hectare (85 per mile), including parts of the stream seldom occupied by animals. This constitutes a relatively large biomass of vertebrate life in an aquatic community. In both numbers of individuals and biomass the turtles comprise a large proportion of the reptiles in western North America. The pond turtle is an omnivore and a scavenger (Bury, in prep.). Their non-selective, opportunistic diet permits these turtles to live in many regions.

Pond turtles apparently prefer certain environmental features in stream communities, such as pools with cover, depth (over 1 m), and large size. However, they are not as restricted to specialized conditions as are, for example, some of the other freshwater turtles in North America.

Most of the pond turtles appeared to use the same home ranges over several years. There is no evidence of territorial defense and this may permit animals to reach high densities in areas with favorable basking, hiding, nesting, and feeding condtions. Males appear to roam farther than females or juveniles. Adults are capable of long range travels (up to 300 m per day) and may move over land or in water. Adults are long-lived and individuals may move relatively long distances during their lifetimes. These factors may account for the widespread distribution of the species in western North America during interglacial periods.

Pond turtles are able to achieve an elevated body temperature by behavioral selection of environmental conditions and this may permit the animals to live in many areas. Preferred temperatures (about 24°-34°C) may be maintained over many hours by a number of basking responses. Turtles apparently select temperatures from the relatively stable aquatic medium or thermally variable conditions in air.

Overall this species appears to be social since animals are found in aggregations. However, aggressive acts were observed during atmospheric basking and such behavior may promote spacing. Perhaps aggression serves to distribute turtles so that excess numbers do not occur in one area, thereby depleting available resources.

Pacific pond turtles appear to be generalized and adapted to live in a variety of aquatic communities. In many remote areas, they are abundant and probably play a major role as a predator and scavenger. They have successfully invaded many waters over a wide geographic and altitudinal range.

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Appendix

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