THE UNIVERSITY OF MANITOBA

ACTIVITY TIME ALLOCATION AND DIVING BEHAVIOR IN THE WESTERN PAINTED TURTLE, Chrysemys picta bellii

by

NATHALIE GAMACHE

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ABSTRACT

This research examines the diving biology of Chrysemys picta bellii. Since C. p. bellii is highly aquatic, the ability to control buoyancy would facilitate its locomotion at depth. Eight turtles, equipped with pressure-sensitive radio-transmitters, were tracked during summer and fall 1988 to assess diving ability and characteristics during submergence when feeding, resting and traveling. In addition, visual observations of terrestrial activities such as traveling and thermoregulating helped establish activity time allocation for individual turtles. During summer, turtles spent > 60 % of a diel cycle in water, feeding pattern was bimodal and occurred at depths > 3m. Submerged resting was restricted to darkness and occurred in shallow water (< 1.5 m). Dive duration varied with type of activity, ranging from a few seconds to several hours. Surface interval (< 180 s) was independent of dive duration, suggesting maintenance of aerobic metabolism during submergence. Thermoregulation occupied > 60 % of daylight period. In autumn, thermoregulating time was reduced greatly and only one feeding event occurred in late afternoon. The rest of the diel cycle was spent resting underwater. Extrinsic factors such as air and water temperature influenced timing of activities.

In the laboratory, determination of frequency and duration of dives and surfacing bouts revealed that turtles submerged > 80 % of the time in normoxic and hypoxic water. In hypoxia, lower activity level,

increase in surfacing bout duration and a reduction in surfacing frequency attest to the importance of aquatic O_2 input in this species. Turtles initiated dives at neutral buoyancy (0.9982 $g \cdot ml^{-1}$), which allowed passive descent, and reached bottom at negative buoyancy. Gas loss resulted in increased negative buoyancy during submergence, causing turtles to struggle during ascent. Uptake of dissolved O_2 by turtles averaged 2.86 $ml \cdot kg^{-1} \cdot h^{-1}$, and CO_2 loss to water averaged 12.75 $ml \cdot kg \cdot^{-1} \cdot h^{-1}$. The CO_2 output was equivalent to gas loss observed during voluntary submergence. Chrysemys picta bellii, which makes extensive use of the aquatic milieu in the field, alters lung volume at the onset of a dive to reduce buoyancy at depth and takes advantage of aquatic respiration to optimize submergence duration.

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CHAPTER I - ACTIVITY TIME ALLOCATION

INTRODUCTION

Their abundance, wide geographical distribution, exploitation of several habitat types, and performance of various activities on land have allowed the ecology of freshwater turtles to be studied extensively. However, few studies have examined the general ecology or activity patterns of freshwater turtles (Cagle 1950, Sexton 1959, Ernst 1972, Ernst and Ernst 1973), and although cyclic locomotion activity was studied in the laboratory (Hutchison and Kosh 1964, Brett 1971, Graham and Hutchison 1978), only Obbard and Brooks (1981) examined diel activity patterns of turtles in the field, both in water and on land. Such study increases knowledge of general ecology of a species, but also provides information about specific aspects of their activities, habitat utilization, and allows the relationship between extrinsic factors and such characteristics to be examined. Furthermore, several recent field studies of submerged activity in reptiles (Eckert et al. 1986, Rubinoff et al. 1986) and mammals (Le Boeuf et al. 1986, Dolphin 1988, Feldkamp et al. 1989), using tracking devices, have provided for the first time, information on activity patterns of animals which spend most, or all of their time in the aquatic milieu.

This study was undertaken to describe general patterns of activities and to examine aspects of the diving biology of Chrysemys picta bellii in the field. This information was gathered from turtles equipped with

depth-sensitive radio-transmitters which allowed establishment of diving profiles during various activities, and when coupled with visual observations of activities performed by turtles on land, provided an insight on activity time allocation in C.p.bellii. Characteristics of activities such as feeding, thermoregulating, and submerged resting were established for each turtle, which allowed comparisons between individuals, sexes, and of general trends between summer and autumn. Relationships between extrinsic factors such as air and water temperatures, weather conditions, photoperiod, and activity patterns and characteristics were also examined for each season.

MATERIALS AND METHODS

ANIMALS

Twelve Western Painted turtles Chrysemys picta belli were collected on May 6 and 10, 1988 from Crater Lake, near Pinawa, Manitoba ($50^{o}10'N,95^{o}51'W$). Prior to their return to the field for observations, turtles were housed in a 1970 L tank (1.78 m diameter, 0.80 m deep) with a flow-through water system at 25 C, and a 10 L:14 D photoperiod. A basking stand and a lamp were provided and turtles were fed frozen fish on a weekly basis.

RADIO-TELEMETRY STUDIES

To locate and record depth of diving turtles, pressure-sensitive radio-transmitters (4 cm x 2 cm x 1,5 cm) were manufactured by Advanced Telemetry Systems Inc., of Isanti, Minnesota. These had individual frequencies between 48.020 - 48.090 MHz and emitted pulses with 15m/sec width and had an effective range of 0.5 km. All transmitters were calibrated at the study site prior to attachment. The reception of emitted pulses was affected by the high conductivity of the water, causing it to be interrupted below a depth of 1.50 m, thus vertical positions of turtles below 1.5 m could not be determined. Cork glued to the sides of the transmitters made them neutrally buoyant. Transmitters were anchored to the carapace by implanting 4 self-

Table 1. Identification, characteristics, and activity periods of turtles with transmitters used during the field study in 1988.

Turtle	Sex	Date of Collection	Colour	Carapace Dimensions (cm) Length	Weight	Body Weight Dry (g)	Period monitored	Condition at end of monitored activity period
A	o	May 6-10	Yellow	18.5	13.5	763.5	May 31 - August 10	Fallen transmitter
B	o	May 6-10	Silver	19.5	15.5	884.5	May 31 - August 5	Transmitter off
C	o	May 6-10	Blue	18.0	12.0	557.5	May 31 - June 30 Aug 25 - Sept 23	Transmitter off Transmitter off
D	o	May 6-10	Orange	17.5	12.5	544.5	May 31 - June 28 July 11 - Aug 22	Transmitter off Transmitter off
E	o	May 6-10	Yellow	----	----	507.3	Sept 27 - Nov 25	Hibernation
F	o	August 19	Yellow	----	----	976.9	Sept 1 - Sept 19	Dead
-	o	August 19	Red	----	----	869.8	Sept 1 - Sept 13	Dead
G	o	August 19	Red	----	----	690.8	Sept 20 - Nov 25	Hibernation

tapping stainless steel surgical screws to a depth of 1.5 mm. Transmitters were attached to the screws with thin wire. Dental cement covered the screws, reducing the possibility of entrapment in vegetation. Each transmitter was painted with a distinguishing color enabling individual identification and facilitating visual observations in the field (Table 1). Turtles, so equipped, were kept in the laboratory for 24 h prior to release. Observations suggested that the presence of transmitters did not impair activity or diving ability. Transmitter pulse rate was monitored with a loop antenna (ground use) and a Fieldmaster 10 channel receiver (Advanced Telemetry Systems Inc., Isanti, Minn.) connected to a battery operated cassette recorder.

On June 1, 1988, four transmitting and eight non-transmitting turtles were released in a pond located on the grounds of Canada Lafarge Inc., on McGillivray Boulevard, Winnipeg, Manitoba. The pond, approximately 475 m x 80 m with a maximum depth of 3.75 m, developed following excavation for clay 27 years ago. It was bordered by aquatic vegetation with extensive beds of submerged vegetation. Aquatic invertebrates, tadpoles and small fishes constituting prey for turtles were abundant.

To facilitate visual observations, turtles were restricted to the north portion of the pond by installing a net across a narrow channel. Four basking stands were placed near shore. Pulse rate recording and visual information were collected on top of a 12 m cliff overlooking the

pond. Pulse rates recorded on 120 min Concertape cassettes were subsequently analyzed in the laboratory. Daily replacement of batteries, and hourly replacement of cassettes, hourly may have caused a small portion of information to be lost, possibly affecting estimates of dive and emergence duration in some cases. This should be considered as a possible source of error when interpreting results, especially during feeding and submerged resting dives.

Variables recorded included weekly, water temperature (± 1 C; at surface, 1.5 m and 3.0 m depth), weekly, dissolved O_2 at surface, conductivity (once in June), daily, water level (± 1 cm), and hourly, air temperature (± 1 C) recorded during observations. Changes in wind and weather were noted at time of occurrence.

After release, turtles were allowed 7 d to become familiar with the pond. Observations and recordings commenced on June 8, 1988 and were obtained on transmitting and non-transmitting turtles for a total of 50 d during the summer. Transition to autumn was arbitrarily selected to be August 30, 1988, because examination of accumulated information revealed noticeable changes in activity patterns after that date in the only turtle retaining an active transmitter. This date was chosen to delimit two seasonal activity periods for purpose of analysis only.

For the comparative analysis between seasons, three additional

turtles were collected in Crater Lake in mid August, held in the laboratory, fitted with transmitters as above and released in the pond in September 1988 (Table 1). Information was gathered over 26 d on the latter animals along with one actively transmitting turtle remaining from the summer period and eleven non-transmitting others.

ACTIVITY TIME ALLOCATION

To determine activity time allocation of each turtle, the ratio of cumulative time spent in each activity over the total period of observation was calculated for each hourly interval of the 24 h cycle, for summer and autumn. Results were averaged for each hourly interval and used to determine time allocated to particular activities for individual turtles over the course of a day and during different seasons.

Five main activities were identified during the study and were defined as follows:

FEEDING A series of dives of variable duration, characterized by steep ascents and descents to depths in excess of 1.5 m, interspersed by brief surfacing bouts. Surfacing bouts are episodes during which turtles are partially emerged at the surface of the water. In a single feeding event, turtles utilized very restricted areas, repeatedly diving within a 5 X 5 m for periods sometimes > 2 h.

THERMOREGULATING Activity during which turtles emerge out of water to warm by exposure to ambient heat (atmospheric) or submerge in water under patches of dead vegetation to cool or avoid extreme heat (aquatic).

REFRESHING Brief (1-3 min) aquatic submergences interrupting basking during periods of intense warmth. Turtles resumed basking after a few minutes, normally at the same site.

TRAVELING Horizontal movement of variable distance accomplished by a series of shallow dives (0.3-0.6 m) at slow to moderate speed (aquatic), or displacement over land, from one area of the pond to another (terrestrial).

RESTING A series of dives to depths between 0.3 and 1.5 m close to shore, long in duration, interrupted by brief surfacing bouts, during which a turtle remains inactive. Resting occupied most of night time period during summer and autumn but also occurred in daylight, especially in autumn.

Comparison of the percentage of time was made for each type of activity between summer and fall. Since information was not available for the period extending from 2100 h to 0700 h during the fall, summer data were blocked in two categories (0700 h - 2100 h ; 2100 h - 0700 h) to allow comparison of daytime results between seasons.

FEEDING

For feeding activity, pulse recordings were obtained from six turtles for a total of 61 h and 21 min in the course of the summer, and from three turtles for a total of 13 h and 11 min during the fall. Underwater observation sessions with snorkeling equipment served to gather information on feeding. Since information on feeding in the fall was restricted to a few hours for some turtles, frequency of occurrence and time allocation were not assessed for individual turtles or for the group during that period. Correlations between emergence time and dive duration were assessed by individual turtle because of the significant differences in dive duration and emergence time between 2 individuals during the fall.

BASKING

Telemetric and visual information on basking activities was collected over 38 d during the summer, for a total of 178 h and 35 min of observations. In the fall, information from 9 d totalled 36 h and 09 min of observation.

NOCTURNAL RESTING

Three turtles observed on four separate nights yielded a total of 36 h and 35 min of information as follows:

NIGHT	DATE	TURTLE
1	July 7-8	A
2	July 9-10	A
3	July 21-22	D
4	August 29-30	C

Data obtained on turtle "D" is reported in this section but has not been incorporated in nocturnal resting data analysis. Inclusion of the information resulted in the rejection of the hypothesis of homogeneity of variance.

Statistical differences were considered significant when $p \leqslant 0.05$. Significant differences are indicated by an asterisk (*) in tables and figures. Where applicable, Scheffe's or Tukey's multiple range tests were used to accomplish pairwise comparisons to supplement and substantiate analyses of variance.

RESULTS

ACTIVITY TIME ALLOCATION

During the summer, activities appeared to be influenced by temporal and climatic factors, and the manner in which they were performed appeared to reflect turtles' individuality. There was no difference between turtles in the percentage of time allocated to activities in the summer (Table 2). In the fall, similar proportions of time were allocated to thermoregulating, traveling, and refresher dives, but significant differences between turtles occurred in resting and feeding activities (Table 3).

During summer, the proportion of time allocated to particular activities changed markedly in a diel cycle. The first feeding bout was initiated after sunrise by all turtles. Feeding peaked between 0700 h and 0800 h and gradually decreased over the morning. Additional feeding periods occurred in late afternoon and early evening (Fig 1A). Onset of atmospheric thermoregulation corresponded with the decline in matinal feeding. Frequency of thermoregulation increased throughout the morning and peaked around midday, when most of the time was devoted to aquatic or atmospheric thermoregulation. Patterns of thermoregulatory activities were similar among turtles, although males appeared to end earlier. Nocturnal resting usually commenced at dusk and extended over the night. Resting occurred infrequently during the

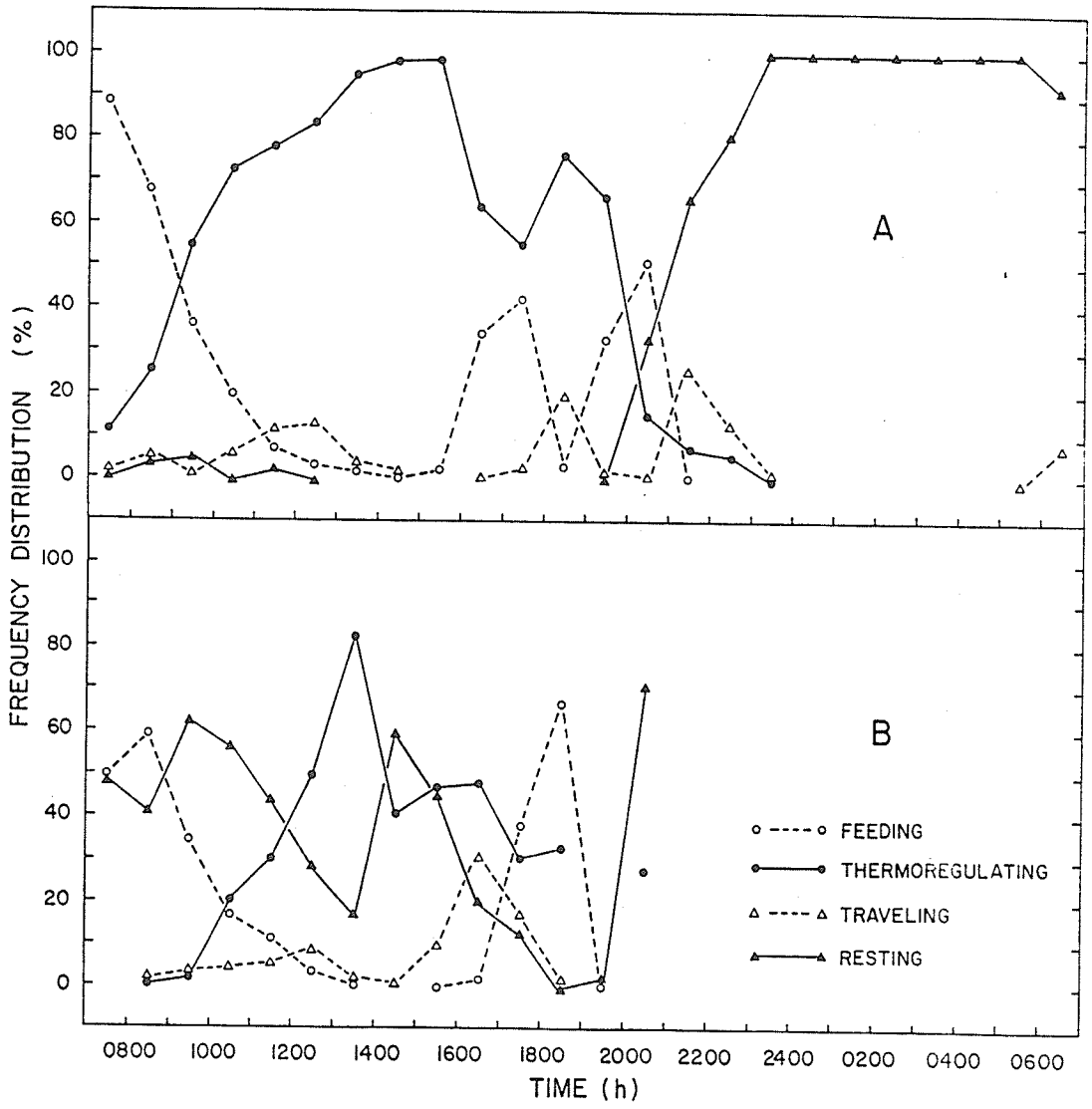
Table 2. Time allocation (%) for each activity performed during summer 1988, between 0700 h and 2100 h, per individual turtle. Includes ANOVA among turtles for each activity type.

Activity	Turtle A	B	C	D	p
Feeding	13.9	29.7	37.4	28.7	> 0.30
Thermoregulating	84.3	65.6	52.6	50.1	> 0.05
Traveling	0.9	3.3	7.1	5.6	> 0.20
Refreshing	1.0	0.7	0.7	0.3	> 0.70
Resting	0.0	0.8	2.3	15.4	$\leqslant 0.01$

Table 3. Time allocation (%) for each activity type performed during fall 1988, between 0700 h and 2100 h, per individual turtle. Includes ANOVA among turtles for each activity type.

Activity	Turtle C	E	F	G	p
Feeding	0.0	56.8	20.6	13.7	< 0.01
Thermoregulating	43.5	39.4	26.3	32.3	> 0.70
Traveling	12.6	1.4	14.8	1.1	> 0.20
Refreshing	0.0	0.8	0.3	0.0	> 0.30
Resting	43.9	1.6	38.0	52.9	< 0.01

Figure 1. Average activity time allocation in a diel cycle during summer 1988 (A) and fall 1988 (B).

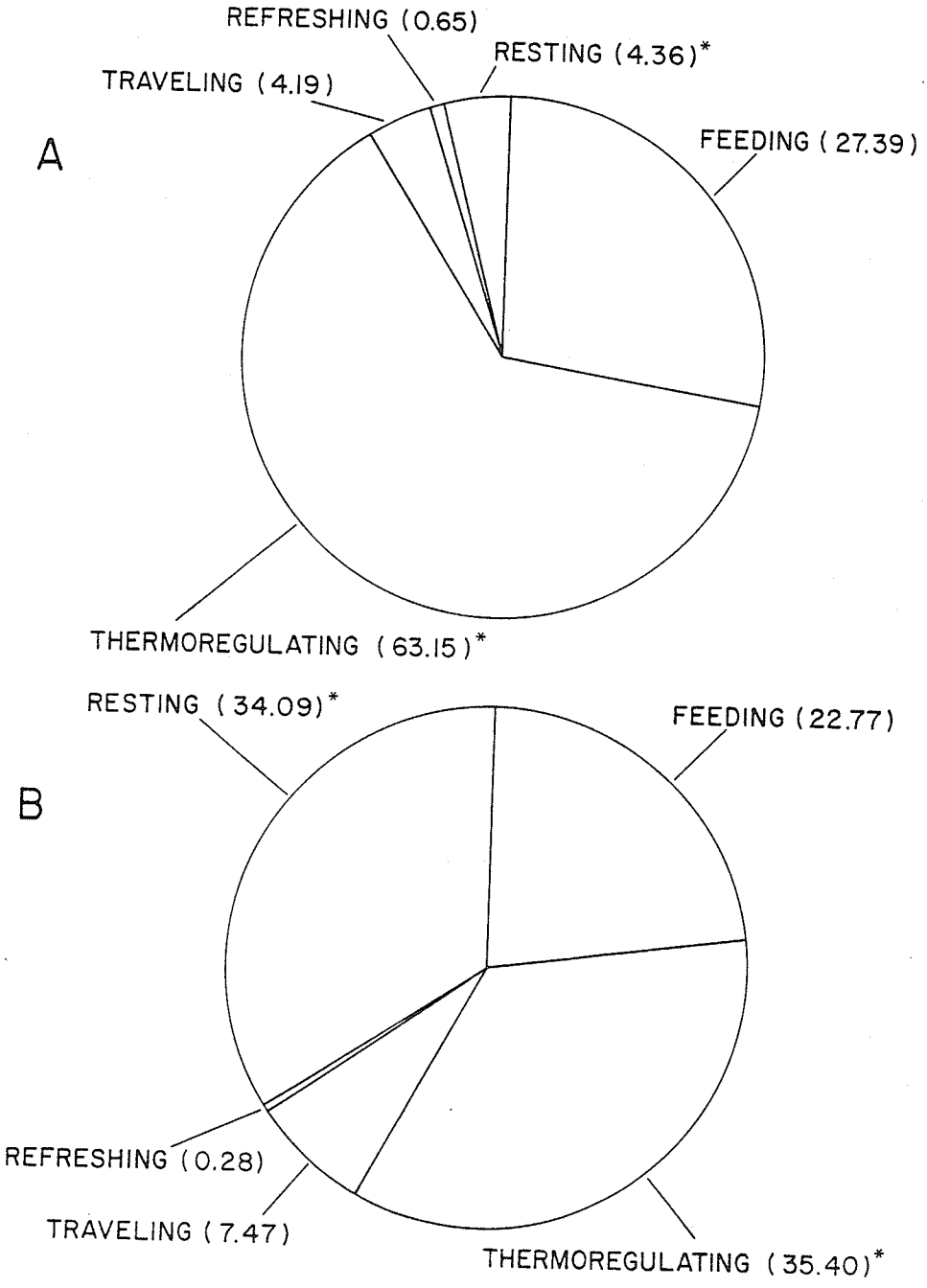

FREQUENCY DISTRIBUTION (%)
100
80
60
40
20
0
A
B
FEEDING
THERMOREGULATING
TRAVELING
RESTING
0800
1000
1200
1400
1600
1800
2000
2200
2400
0200
0400
0600
TIME (h)

day (Fig 1A) and was always associated with brief periods of cloudiness. Individual patterns of nocturnal resting events were also similar among turtles. Peak traveling corresponded with periods of activity transitions (Fig 1A). Refreshing occurred within lengthy atmospheric thermoregulatory episodes.

In autumn, feeding peaked later in the morning and its frequency was not as great as in summer. In late afternoon, only one feeding period occurred (Fig 1B), but at a time comparable to summer. Thermoregulation followed similar trends as in summer but started later in the morning (Fig 1B) and did not reach the same frequency as in summer. In the fall, resting occurred at a much greater frequency during daylight periods than during the summer (Fig 1B). If weather and air temperature permitted, feeding and traveling were initiated, in which case nocturnal resting began at approximately the same time as in the summer. Travel occurred later (Fig 1B), but represented similar time investment (Fig 2A,B). Refreshing involved less time, although a difference in frequency did not occur (Fig 2A,B).

On average, there was a marked decline in thermoregulation time in autumn (Fig 2A,B). In summer, turtles thermoregulated from fifty to over eighty percent of the daylight period (Table 2); in autumn, time for this activity was reduced by nearly half (Fig 2A,B). On average, turtles seem to invest slightly less time on feeding activities during the fall (Fig 2A,B), however examination of individual percentages reveal

Figure 2. Average frequency distribution (%) per activity between 0700 h and 2100 h during summer 1988 (A) and fall 1988 (B). Asterisks represent difference between season for particular activity.


A
REFRESHING (0.65)
RESTING (4.36)*
TRAVELING (4.19)
FEEDING (27.39)
THERMOREGULATING (63.15)*
B
RESTING (34.09)*
FEEDING (22.77)
REFRESHING (0.28)
TRAVELING (7.47)
THERMOREGULATING (35.40)*

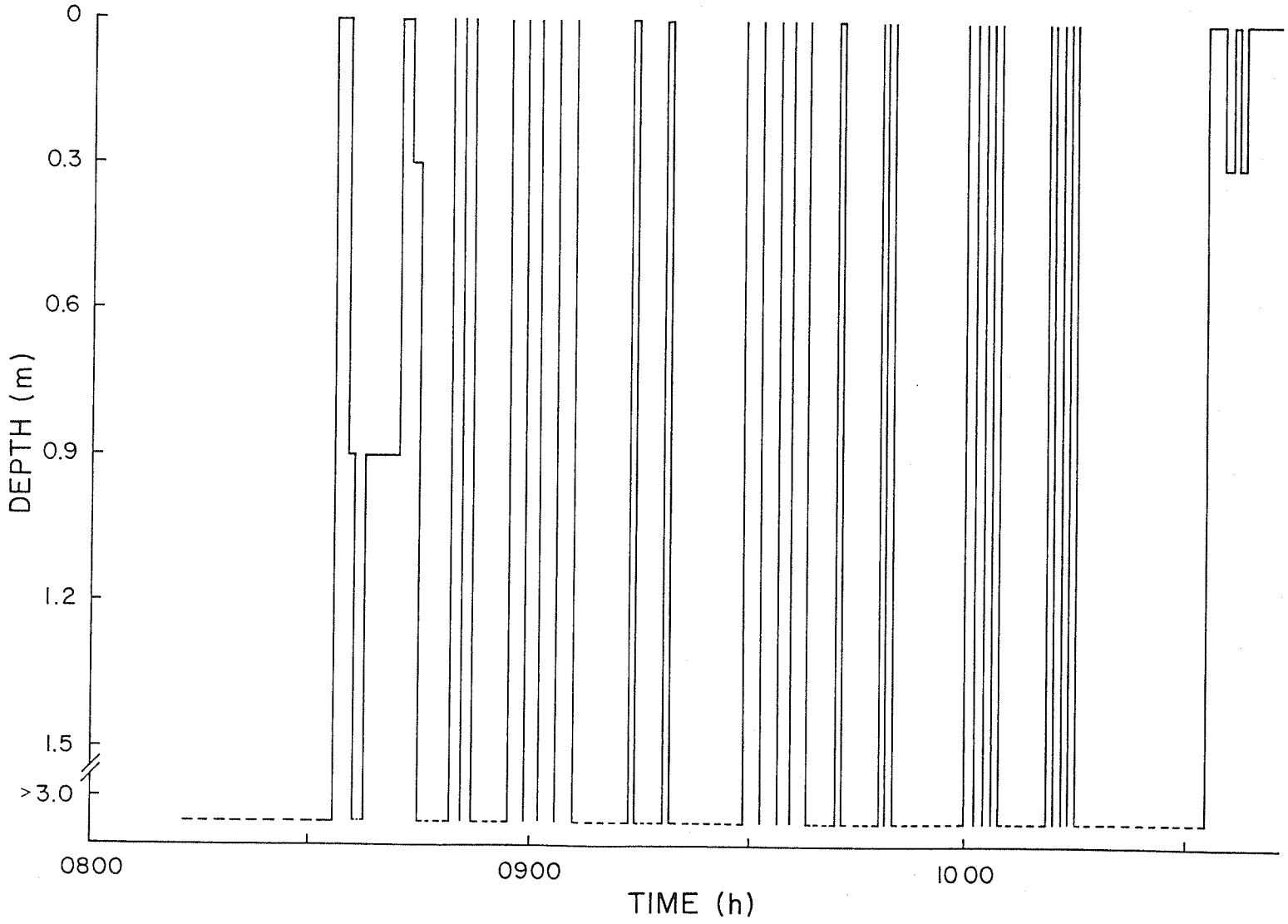
that some turtles actually spent more time foraging in the fall and others were never observed feeding during that period (Table 3). Feeding time expenditure among turtles was more uniform during the summer (Table 2). Daytime resting occupied a significant amount of time in the fall (Fig 2B). Although turtles rested during a few sudden periods of cloudiness in the summer, time investment was minimal (Fig 2A). Traveling and refreshing represented comparable time consumption during summer and fall. During the aestival season, turtles rested for the majority of nocturnal periods (Fig 1A).

FEEDING

During summer, observed maximum duration of morning feeding sessions for four turtles ranged from 144.0 to 288.0 min, and averaged 210.5 min (n=32; S.D.= ± 50.1 min). Six feeding bouts documented during late afternoon indicated duration of individual bouts to vary between 30.0 and 177.0 min, with a mean activity time of 83.0 min (n=6; S.D.= ± 52.9 min).

A typical sequence of feeding dives is illustrated in Fig 3. Evidence obtained from spatial information coupled with a depth profile of the pond established that in areas commonly selected for diving, maximum depth ranged between 2.75 and 3.75 m. Information gathered during brief underwater observation sessions suggests that turtles swim about the densely-vegetated substrate in search of food. Stomach contents extracted from 2 dead turtles found at the study site contained numerous gastropods and some plant matter. With the exception of the variation in number of short, shallower descents preceding deep, longer dives, foraging dive patterns were similar among turtles. Foraging patterns remained similar in the fall but turtles seemed increasingly to limit their food gathering activities to the upper 1.5 m of the water column. By early October, turtles fed only in late afternoon after extensive hours spent basking. If air temperature did not reach 18-21 C, turtles did not emerge for basking and feeding did

Figure 3. Diving profile of turtle B during feeding event on June 29 during summer 1988.


0
0.3
0.6
0.9
1.2
1.5
>3.0
DEPTH (m)
0800
0900
1000
TIME (h)

not occur. The last feeding event was recorded on October 14. After thermoregulating for approximately 4 h, the turtle became active at 1620 h, traveled for 1 h and began to feed. When recording was interrupted at 1910 h, the turtle was still active. Aquatic temperature registered 8°C.

During summer, duration of dives was variable (X=153.2 ± 226.0 s; range 3-3507 s). Differences in mean dive duration were not observed among turtles ($F_{3,684}$=1.03, $p > 0.30$) or between sexes ($F_{1,686}$=1.97, $p > 0.10$). During the fall, dive duration ranged from 2 to 2437 s and averaged 184 s (S.D.= ± 276.8). Significant differences were identified between 2 individual turtles in autumn ($F_{2,166}$=4.52, $p < 0.01$). In the summer, frequency distribution of dives of all turtles into 60 s intervals was strongly skewed with the majority of dives being brief (Fig 4). Comparison among turtles showed frequency distribution to be similar for all intervals ($X^2 > 0.60$) (Appendix 1). Although frequency distribution was skewed, time distribution was similar between intervals (Fig 4) and among turtles ($X^2 > 0.10$) (Appendix 2). Closer examination revealed cumulative frequency percentages of dives < 180 s and < 60 s to be 71.1 and 45.1 % respectively, during the summer period, and 69.2% and 40.2% respectively during the fall. Similarities were revealed for submergence periods < 60 s between sexes during summer ($F_{1,303}$=0.00, $p > 0.90$) and fall ($F_{2,67}$=0.11, $p > 0.80$) but males had greater average dive time than females in dives < 180 s during both summer

Table 4. Frequency distribution (%) of feeding dives < 60 s per 10 s intervals, recorded during summer 1988. n=305.

Interval (s)	Frequency (%)
0 - 9	10.5
10 - 19	23.8
20 - 29	28.5
30 - 39	17.6
40 - 49	10.8
50 - 59	8.8

Figure 4. Mean frequency and time distribution (%) of feeding dives per 60 s intervals, for all turtles, during summer 1988.

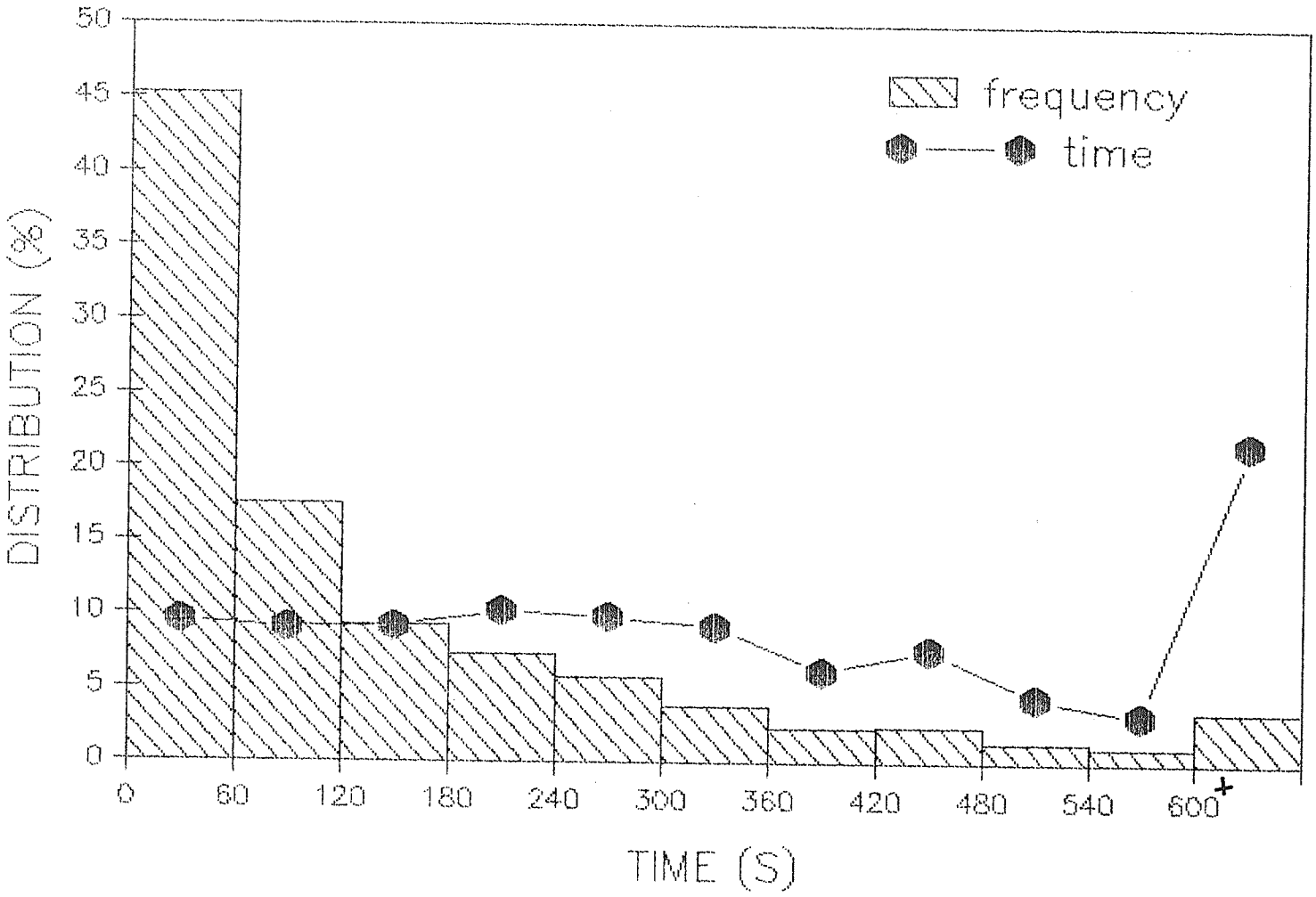
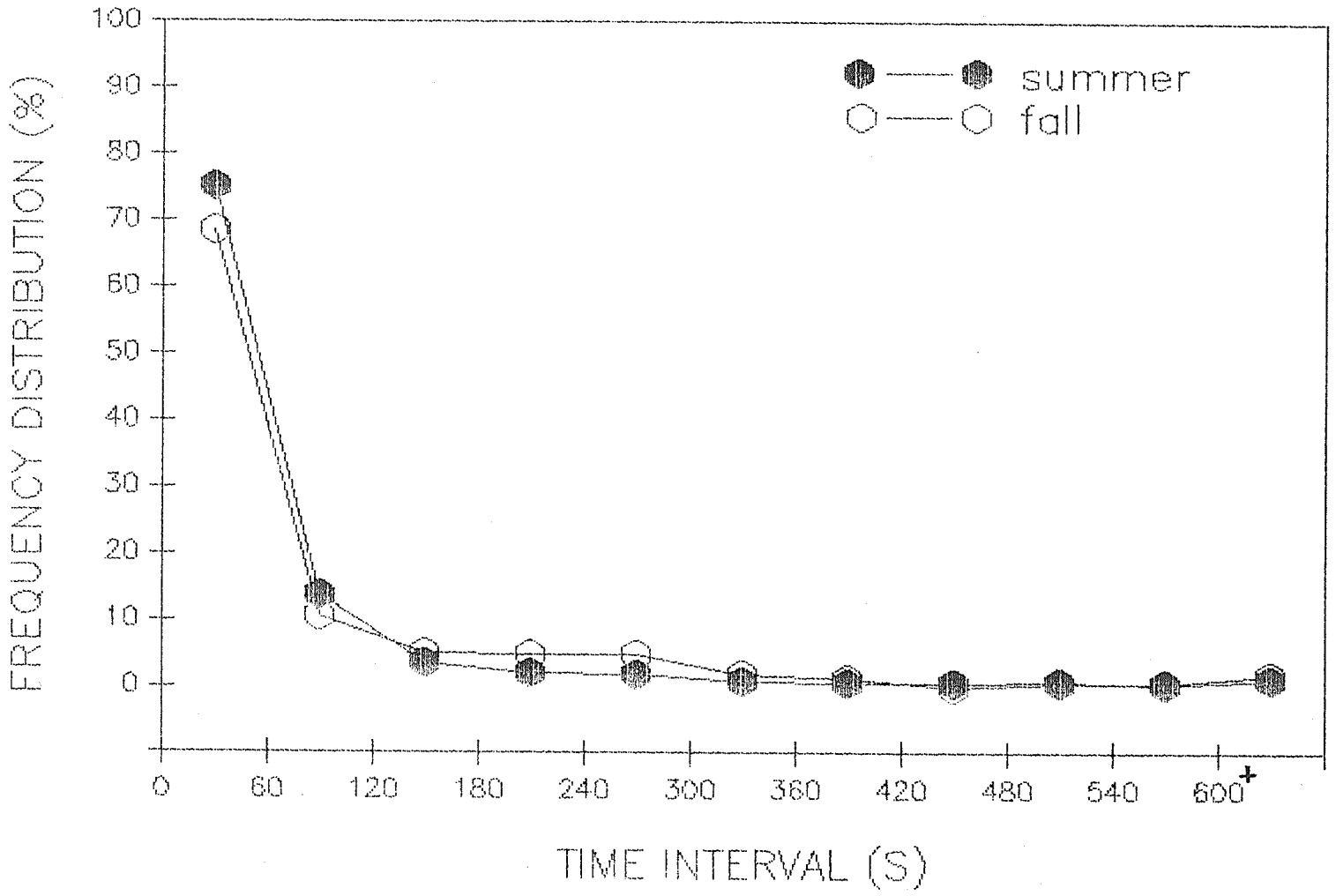

frequency
time
DISTRIBUTION (%)
50
45
40
35
30
25
20
15
10
5
0
0
60
120
180
240
300
360
420
480
540
600+
TIME (S)

Figure 5. Mean frequency distribution (%) of surfacing bouts prior to and subsequent to feeding dives per 60 s intervals during summer and fall 1988.


FREQUENCY DISTRIBUTION (%)
100
90
80
70
60
50
40
30
20
10
0
summer
fall
0
60
120
180
240
300
360
420
480
540
600+
TIME INTERVAL (S)

($F_{1,482}$=4.63, $p < 0.05$) and autumn ($F_{1,115}$=8.24, $p < 0.01$). From aestival results, further distribution of dives < 60 s in 10 s intervals showed over 50.0 % of dives to be in the combined 10-19 and 20-29 s categories (Table 4).

Surfacing bouts preceding and following a feeding dive in summer were usually brief, lasting between 1 and 1296 s, with 90 % of them <180 s (Fig 5). In the fall, duration varied from 1 to 910 s, with surfacings < 180 s totalling 84 % of pre dive and post dive surfacing bouts (Fig 5). Analysis of surfacing bout duration revealed no significant differences among turtles before and after a dive during the summer (Table 5A), but yielded significant differences between 2 turtles for both pre and post dive surfacing bouts in the fall (Table 5B). Comparison between sexes revealed similar results for surfacing bouts subsequent to immersion and indicated dissimilarities prior to a dive in the summer (Table 5A), and both before and after a dive in autumn (Table 5B). In both summer and fall, females were found to have greater average surfacing duration than males. No correlations were found between duration of pre and post dive surfacing bouts and dive length ($P > 0.10$, $r=0.0495$; $P > 0.10$, $r=0.0468$, respectively); duration of surfacing bout was independent of dive length. In the fall, there were no correlations between pre-dive surfacing time and dive duration and a weak positive correlation was found between post-dive surfacing time and dive duration in 1 turtle (Appendix 3).

Table 5. Mean duration of surfacing bouts (s) prior and subsequent to feeding dives during summer 1988 (A) and fall 1988 (B). Data reported per individual turtle and by sex for each season. Standard deviation in parentheses. Number of bouts (n) ranged from 127 to 372. Includes ANOVA among individuals and between sexes.

A. Summer

Surfacing Event		Turtle A ♀	B ♀	C ♂	D ♂	p
Prior to dive	Individual	59.4 (93.3)	80.2 (131.1)	58.8 (112.5)	52.5 (75.0)	> 0.05
	By sex	72.8 (119.2)		56.1 (97.9)		< 0.05
Subsequent to dive	Individual	61.8 (95.8)	79.1 (112.6)	63.4 (120.9)	61.3 (107.1)	> 0.30
	By sex	73.0 (107.2)		62.5 (114.9)		> 0.20

B. Fall

Surfacing Event		Turtle F ♀	C ♂	E ♂	p
Prior to dive	Individual	113.1 (159.2)	73.8 (115.5)	47.0 (49.7)	< 0.05
	By sex	113.1 (159.2)	63.8 (96.8)		< 0.01
Subsequent to dive	Individual	129.2 (176.2)	71.8 (115.8)	49.0 (57.8)	< 0.01
	By sex	129.2 (176.2)	63.1 (97.9)		< 0.01

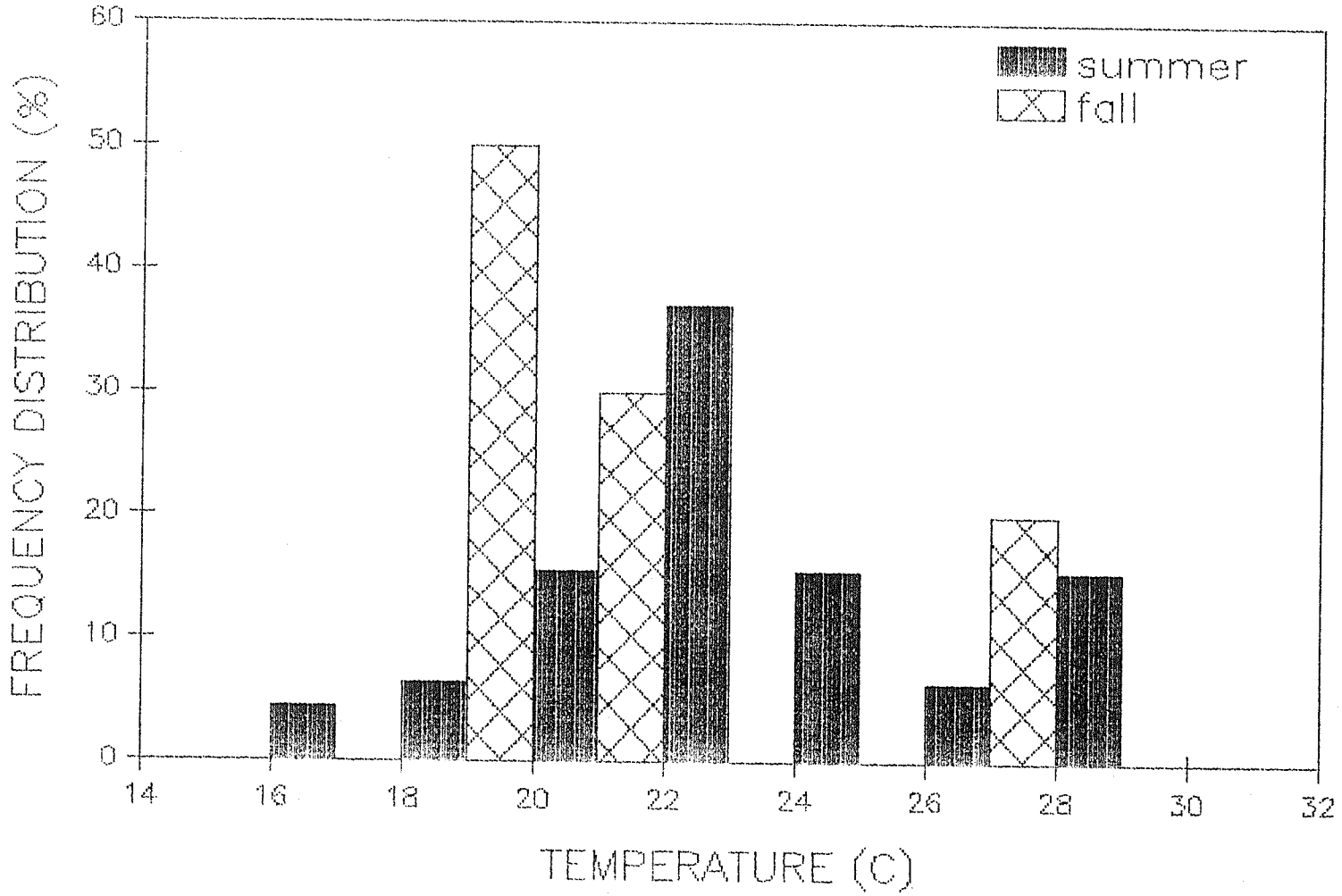
THERMOREGULATING

Shortly after matinal feeding ceased, turtles traveled to a basking area. Wooden stands, areas along the shore, and a patch of dead vegetation on an island in the middle of the pond were frequently used. Availability of sunlight from morning to late afternoon usually characterized the sites chosen. Throughout summer, atmospheric or aquatic thermoregulation occupied most of the diurnal period. Turtles frequently reoriented in relation to the sun and occasionally, atmospheric thermoregulation was interrupted by refreshing when turtles dove in shallow water, only to climb back out at the same site a few moments later.

At onset of atmospheric thermoregulation, temperature averaged 23.4 C (range 16.5-29.5 C; S.D.= ± 3.1 C) with 37.0% of onsets occurring between 22 and 24 C (Fig 6). Over 15.0% of turtles initiated atmospheric thermoregulation between 28 and 30 C (Fig 6). Turtles were observed to retire under patches of dead vegetation along the shore at midday. Turtles used such refuge at a mean air temperature of 27.9 C (S.D.= ± 1.8 C). After spending the warmest part of the day in this manner, turtles frequently resumed atmospheric thermoregulation in late afternoon.

In autumn, atmospheric thermoregulation was initiated at a mean air temperature of 21.0 C (range 18-27 C; S.D.= ± 3.1 C). Eighty percent

Figure 6. Frequency distribution (%) of air temperature (^{O}C) at onset of morning basking episodes during summer and fall 1988.


summer
fall
FREQUENCY DISTRIBUTION (%)
0
10
20
30
40
50
60
14
16
18
20
22
24
26
28
30
32
TEMPERATURE (C)

of total basking onsets occurred between 18 and 21 C (Fig 6). Comparison of temperatures at onset between the two seasons suggested significant differences ($F_{1,54}$=4.81, $p < 0.05$). Contrary to onset time which was progressively postponed in the fall ($p < 0.01$, r=0.7534), temperature at initiation time did not markedly vary with seasonal progression ($p > 0.10$, r=0.4744).

Observations showed that turtles remained at the basking site for prolonged periods of time after sunset in the fall. This phenomenon was not observed during the summer. Aquatic thermoregulation was not observed during the fall, but refreshing occurred.

TRAVELING

Turtles frequently traveled short distances before initiating an activity. For seven turtles, time of travel recorded in a single event averaged 41.0 min per episode (range 3-123 min; S.D.= ± 34.4 min). Temporal investment in the activity was significantly different between sexes ($F_{1,13}$=4.73, $p < 0.05$), with average travel time of 27.0 min (S.D.= ± 25.9 min) for females and 62.0 min (S.D.= ± 36.7 min) for males. Time expenditure for individual travel events showed a high degree of similarity between summer and fall ($F_{1,13}$=0.01, $p > 0.90$).

Distances traveled differed greatly among turtles, ranging from a few meters to nearly 0.5 km. One turtle regularly spent nights at the extreme southern end of the pond and swam 0.45 km to the northern area early in the morning covering this distance in < 1 h.

SUBMERGED RESTING

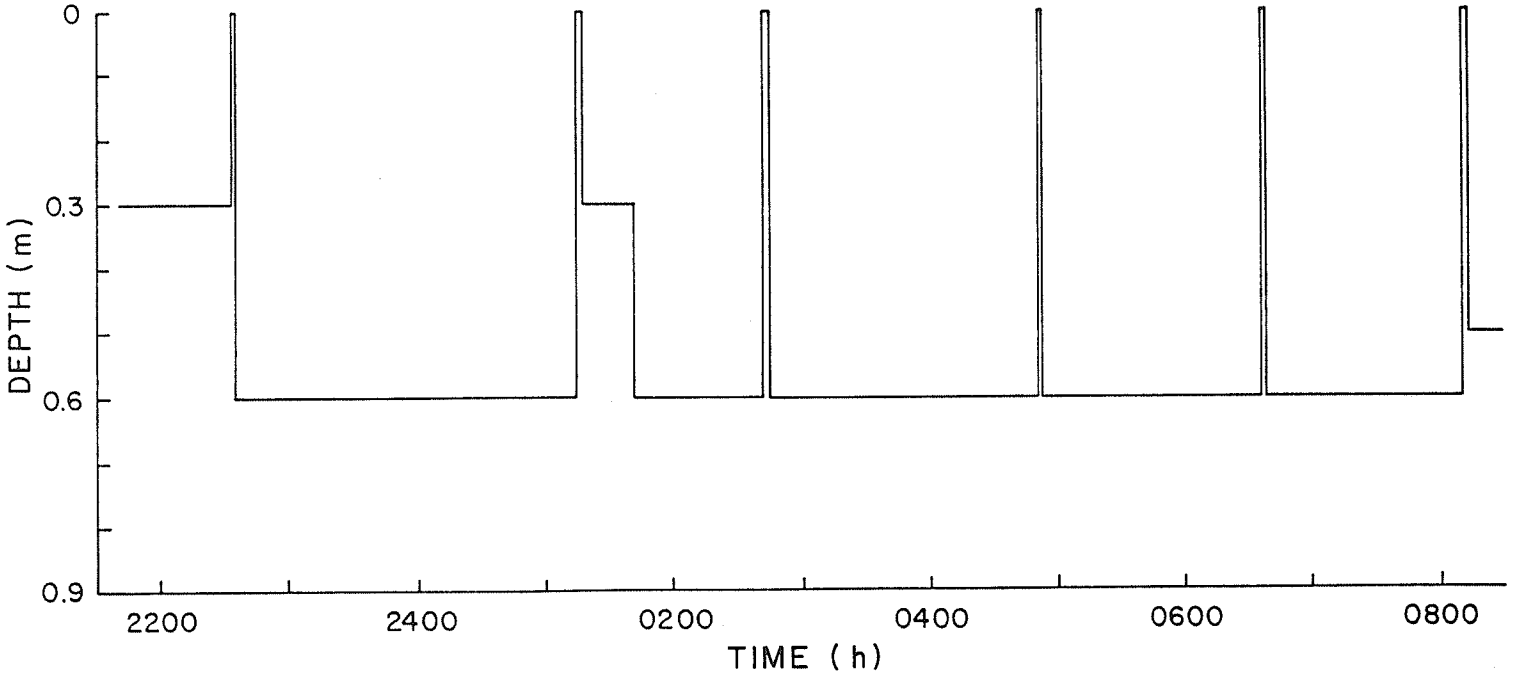
Submerged resting occurred mainly at night and its onset corresponded to nightfall. After locating an area of appropriate depth, turtles slowly descended to that level, initiating a first nocturnal resting dive. Typical sequences of nocturnal resting dives are illustrated in Figs 7 and 8. Dive duration varied greatly among turtles and between consecutive periods of submergence. In addition, the variation in number of surfacing bouts directly influenced the proportion of time spent surfacing, which ranged from 24.0 and 15.0 % for nights 1 and 2, respectively, to 2.1 % for night 4.

Individual dives ranged from 12 s to 9 h 09 min 23 s (Table 6). Comparison among nights 1, 2, and 4 revealed significantly different submergence periods ($F_{3,103}$=364.7, $p < 0.0001$), with males performing much longer dives than the female. Examination of information accumulated on turtle "A" on the nights of July 7-8th and 9-10th showed dive duration to be similar between nights ($F_{1,97}$=1.25, $p > 0.10$). Dives < 60 s duration composed 15.4 and 40.0 % of the total number of dives in turtle "A" during the 1st and 2nd night respectively, and were absent in turtle "C" on the 4th night. Submergence periods < 60 s tended to be clustered and occurred after a surfacing bout, preceding a long dive.

Table 6. Mean duration of nocturnal submerged resting dives per individual turtle, during summer 1988.

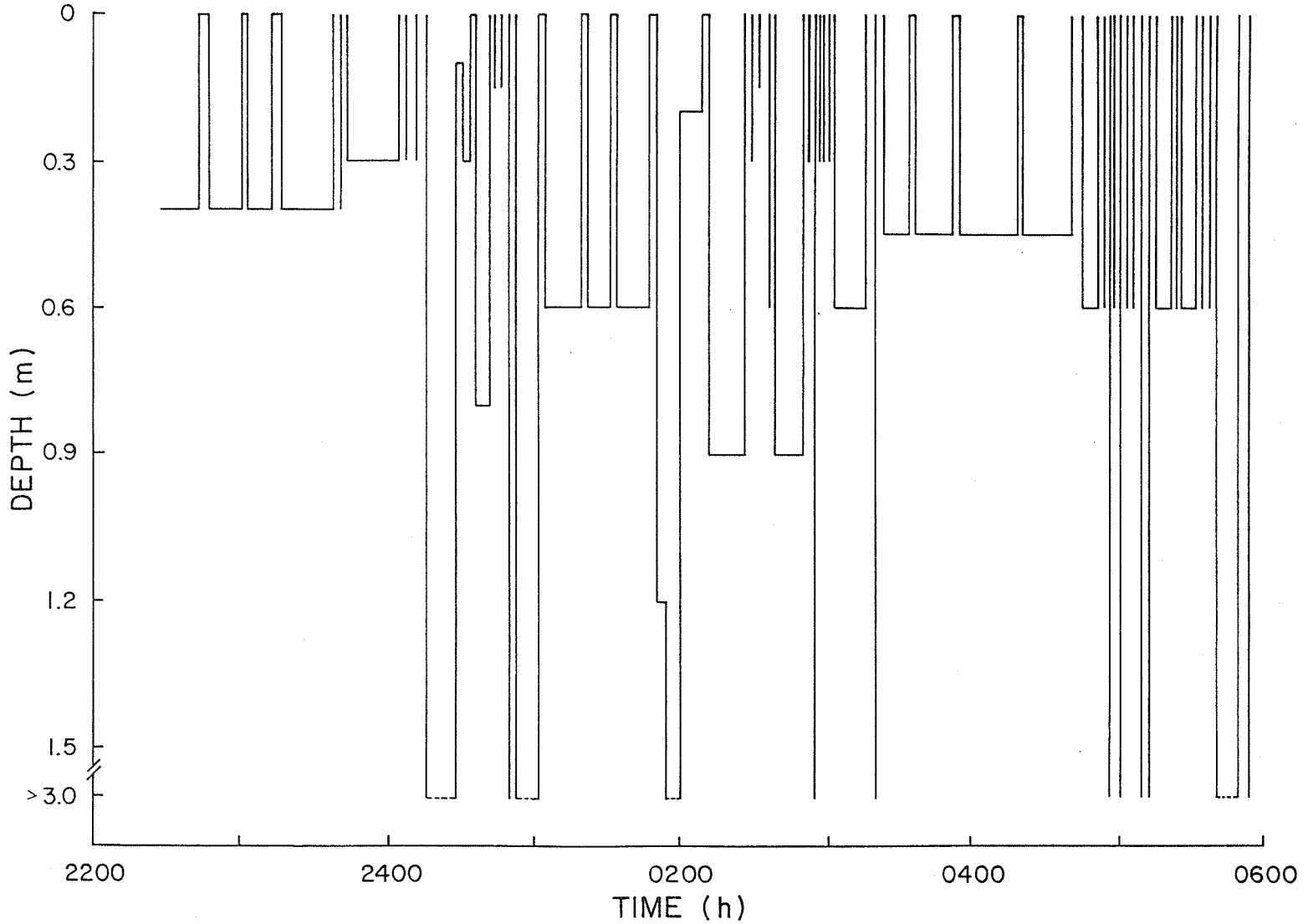
Night	Turtle	Time (min)	S.D. (min)	n
1	A	9.5	8.4	39
2	A	7.1	11.9	60
3	D	296.4	357.8	2
4	C	105.1	20.0	6
X		18.9	57.6	107

Figure 7. Diving profile of turtle C during night 4 on August 29-30 in summer 1988.



Copy. 8.7.89

Figure 8. Diving profile of turtle A during night 1 on July 7-8 in summer 1988.


0
0.3
0.6
0.9
1.2
1.5
>3.0
DEPTH (m)
2200
2400
0200
0400
0600
TIME (h)

Surfacing bouts at night ranged from 11 to 1190 s with 95.2 % < 180 s in duration. Significant differences were established for duration of both pre- and post-dive surfacing bouts between the 1st and 2nd night ($F_{2,100}$=5.06, p <0.01; $F_{2,100}$=5.64, p < 0.005, respectively), but were similar among all other pairs of turtles. There were no correlations between duration of preceding surfacing bouts and submergence times for turtles on nights 1 and 4, but a positive correlation was found for the above on night 2 (Appendix 4) . Surface time was positively correlated with preceding dive duration on nights 1 and 2, but was negatively correlated on night 4 (Appendix 4).

During the fall, diurnal resting dives lasting from 196 s to 3 h 08 min 44 s and averaging 4030.0 s (S.D.= ± 3505.4) greatly exceeded the mean nocturnal diving interval (1131.2 ± 3454.7 s) documented during the aestival period. Significant differences were established for dive duration between the two seasons ($F_{1,131}$=14.65, p < 0.0002).

On October 28, 1988, date of the first snowfall, the surface water of the pond froze, trapping turtles below. Four weekly recordings following this event confirmed complete inactivity and immobility. Transmitting turtles were close to shore, buried 0.30 to 0.60 m below the surface of the ice.

DISCUSSION

ACTIVITY TIME ALLOCATION

In summer, similar proportions of time appeared to be devoted to each daily activity among turtles. Although not statistically significant, there were noticeable differences in time invested in feeding and basking between sexes (Table 2). Females tended to thermoregulate for longer periods of time, postponing late afternoon feeding events. Males interrupted thermoregulation earlier, initiating feeding immediately after emergence from their refuge. Since onset of nocturnal resting occurred at similar time in both sexes, this resulted in a net reduction in late afternoon feeding time for females. Several factors may be responsible for the extended basking period in females and consequent reduction in available foraging time. Spray and May (1972) showed that in turtles, both heating and cooling rates decreased with increasing body weights. Since radio-tagged females in this study were much larger than males (Table 1), this would not only result in a slower rise to preferred body temperature at initiation of basking in the morning but would also cause excess body heat to require longer period of time to dissipate during aquatic basking, hence retarding time at which turtles could become active. Hutchison et al. (1966) also established a correlation between body size and critical thermal maxima (CTM) in painted turtles, with larger turtles having a lower CTM than smaller ones. Since all larger turtles in their study were gravid females,

Hutchison et al. (1966) noted that the differences might not be due to mass effect alone but to the lower heat tolerance of gravid females for physiological reasons. Because all turtles thermoregulated aquatically prior to afternoon foraging events in the summer, high ambient temperature still present at the time may have prevented females from leaving the cooler refuge to forage. Although a slower rate of cooling in females could benefit digestive activities, such an effect was not observed in Chrysemys scripta (Parmenter 1981).

During summer, the first feeding event was always initiated immediately after cessation of nocturnal resting periods (Fig 1A). Although this contradicts reports from Boyer (1965), Ernst (1972), Ernst and Ernst (1973) who placed basking as the initial matinal activity, Cagle (1950) reported Chrysemys scripta troostii to feed in early morning and Brett (1971) and Obbard and Brooks (1981) demonstrated C. scripta and Chelydra serpentina respectively, to be most active from dawn to morning. In the present study, frequency of feeding in C. p. bellii peaked before 0800 h but sometimes extended until late morning early in the season. Average feeding duration usually lasted ~2 h. A second feeding event occurred in late afternoon, following basking. Similar occurrences were reported in C. p. bellii (Ernst and Ernst 1973) and C. s. troostii (Cagle 1950), and Brett (1971) also noted activity level in C. scripta to increase in late afternoon under laboratory conditions. In summer, feeding events occupied an average 17 % of the total diel cycle (Table 7). Twenty-seven percent of the daylight period

Table 7. Mean time allocation (%) per activity for all turtles in a diel cycle, during summer 1988. Standard deviation in parentheses.

Activity	Time Allocation % (S.D.)
Feeding	16.6 (24.9)
Thermoregulating	37.8 (38.4)
Traveling	4.2 (7.3)
Refreshing	0.4 (0.8)
Resting	41.0 (46.8)
Total observation time (h)	239.5

(0700-2100) was spent feeding (Fig 2A), with only slightly less time (22 %) devoted to the activity in the fall (Fig 2B).

In summer, atmospheric thermoregulation occurred after matinal and again after late afternoon feeding events (Fig 1A). Such a bimodal pattern was observed in C. p. bellii (Ernst 1972, Ernst and Ernst 1973, Schwarzkopf and Brooks 1985), C. s. troostii (Cagle 1950), and Elseya and Emydura turtles (Webb 1978), and has been associated with days with above average air and water temperatures (Schwarzkopf and Brooks 1985). Furthermore, Miller (1979) demonstrated the pattern to be displayed by Pelomedusa subrufa kept in conditions of constant temperature/light in the laboratory, suggesting the presence of an endogenous rhythm or a response for avoiding build up of a potentially lethal heat load during basking. At midday, C. p. bellii in this study returned to the water, perhaps to avoid overheating. Aquatic and atmospheric thermoregulation occupied 38 % of a diel cycle in summer (Table 7), resulting in 63 % of the daylight period devoted to this activity on average.

In autumn, as ambient temperature decreased, thermoregulation displaced feeding as the initial activity and the thermoregulatory pattern became unimodal. Such transition was also observed in Clemmys guttata (Ernst 1982). A pronounced decline in duration of thermoregulation compared to summer (Fig 2A,B), lower ambient maximum temperature reached on average, and absence of refresher

dives in late fall suggests that C. p. bellii did not approach CTM, and did not need to interrupt atmospheric thermoregulation.

Except for a few instances when turtles retired to water during periods of cloudiness or rain, submerged resting activities were restricted to nocturnal periods in summer. On the contrary, submerged resting events occupied a great proportion of the daylight period (34 %) in autumn (Fig 2A,B), proportion which would increase to > 60 % of the diel cycle if in autumn, turtles spent at least as much time submerged at night as they did during summer. Decline in daytime activity period and frequency in autumn and winter has been reported by several authors (Cagle 1950, Sexton 1959, Boyer 1965, Ernst 1972, Ernst and Ernst 1973, Obbard and Brooks 1981) and has been associated with decrease in water temperature (Sexton 1959, Boyer 1965). However, Obbard and Brooks (1981) observed C. serpentina to become less active in early fall when water temperature was still above 20 C, and Cagle (1950) reported Chrysemys and other turtles kept in a heated room to refuse food during winter. That light intensity and attainment of air temperature threshold seemed to closely regulate onset of daytime activity in the fall in this study strongly supports Obbard and Brooks (1981) who suggested that although water temperature seemed to influence activity levels in freshwater turtles in the spring, it had less effect in late summer and that perhaps other extrinsic factors limit activity at that time.

FEEDING

On the basis of laboratory observations on feeding behavior of turtles, series of deep vertical dives interspersed by brief surfacing bouts were attributed to feeding episodes. Similar patterns were observed in voluntarily diving sea snakes (Rubinoff et al. 1986), leatherback sea turtles (Eckert et al. 1986), and in foraging sea lions (Feldkamp et al. 1989), and humpback whales (Dolphin 1988). In the present study, C. p. bellii foraged in densily vegetated sections of the pond, as made evident from visual observations. Similarly, C. p. marginata, was reported by (Sexton 1959) to be closely associated with patches of vegetation during foraging activities. The latter was observed to use beds of aquatic plants floating at the surface as a platform, offering both support and plant and animal food items (Sexton 1959). In sharp contrast, C. p. bellii in this study constantly fed in areas of maximum depth (2.75-3.75 m) even though similar patches of aquatic vegetation were present in shallow waters. Although few studies have examined the feeding behavior of freshwater turtles, several authors reporting on food selection and preference of Painted turtles offer evidence of the wide variety of food types consumed by the species in nature (Gibbons 1967, Hart 1982, MacCullough and Secoy 1983). In addition, a gradual shift from carnivorous to herbivorous diet with increasing plastron length was shown in C. scripta (Clark and Gibbons 1969, Hart 1983) and C. picta (Hart 1982). This change in diet paralleled a habitat shift in feeding sites from shallow to deep water in

C. scripta (Hart 1983). Also, a seasonal shift from animal matter in summer to plant matter in fall or winter was reported for C. p. bellii (Pearse 1923) and in kinosternid turtles (Mahmoud 1968). A vertical migration of preferred food or a seasonal shift in diet could explain the observed tendency of C. p. bellii to increasingly restrict feeding dives to the upper 1.5 m of the water column in the fall during the present study. Although a restriction of activity to the upper part of the water column might reveal avoidance of cooler water temperature in some cases (Sexton 1959), it is unlikely to be a plausible explanation here since depth-related stratification of aquatic temperature was not found. Stability of feeding patterns exhibited by C. p. bellii during the present study further support suggestions that this species as well as other fresh-water turtles can exploit various habitats by modifying diet and foraging patterns to optimize energy gain:cost ratio in each specific situations (Sexton 1959, Gibbons 1967, Mahmoud 1968, Clark and Gibbons 1969, Parmenter 1980, Hart 1982, 1983, MacCullough and Secoy 1983).

By early October, feeding events were restricted to late afternoon and only occurred after lengthy basking sessions. Similar autumnal declines in foraging activity were observed in Trionyx muticus (Plummer 1977), C. serpentina (Obbard and Brooks 1981), and C. picta (Sexton 1959, MacCullough and Secoy 1983), but much earlier in the fall despite similar or lower latitudes. Clement weather conditions throughout summer and fall may explain the delay in cessation of

feeding activity in the present study. Sexton (1959) and MacCullough and Secoy (1983) reported that cessation of feeding occurred at water temperatures of 14-15 C and preceded the end of other activities such as basking and traveling. In this study, feeding events were recorded for one month after this temperature threshold was reached in the pond. It appeared that air temperature was the limiting factor in late fall during this study since air temperatures of 18-21 C were required to start thermoregulation, which in turn initiated food gathering. Aquatic temperature of 8 C during the last recorded feeding on October 14 is much lower than in previous reports. Since Crawshaw et al. (1980) reported that half the excess heat is lost about 3.5 min after a 0.8 kg turtle enters the water and air temperature at time of entry was 29C at onset of last feeding event, the turtle would have experienced a drastic decline in body temperature in a very short time. A period of activity -travel and foraging- exceeding 3 h suggests that the turtle could increase body temperature above that of water to facilitate maintenance of activity level, or could function adequately at such low temperature. Frair et al. (1972) observed body temperature as great as 18 C over ambient water temperature in Dermochelys coriacea.

Although Jackson and Ultsch (1982) demonstrated that turtles possessed physiological responses to slow rate of heat loss, and C. picta was shown capable of maintaining body temperature 1 to 10 C above low ambient temperatures in laboratory conditions (Baldwin 1925, Ernst 1972, Peterson 1987), the turtle would have a body temperature far

lower than the optimal temperature for food intake (25 C in this species; Kepenis and McManus 1974). Riddle (1909) demonstrated that digestion in turtles was decreased to half its optimal rate at 18 C and showed that among "cold-blooded" vertebrates, turtles possessed the highest minimum temperature at which pepsin will act. Kepenis and McManus (1974) found assimilation efficiency and net caloric intake to be highest at 35 C in C. picta. Both values were greatly diminished at temperatures < 20 C. Digestive turnover rate was ~ 60 h for C. picta at 25 C, and increased to 81^{+} h at temperature < 15 C (Parmenter 1981). This suggests that a turtle feeding at low temperature would not only incur the cost of activity performed at body temperature lower than optimal but would also reduce the gain associated with food intake due to low caloric absorption. Despite the apparent lack of benefits, readily available food sources may justify foraging in this case.

Feeding dive duration varied greatly, from a few seconds to a maximum > 58 min (Fig 4). The mean frequency distribution showed > 70 % of dives to be < 3 min in duration. Since turtles in this study did perform dives greatly exceeding 3 min duration, long dives must yield some benefits. Perhaps turtles dive repeatedly for short spans of time to locate areas of high food abundance and increase dive duration once such area has been found. The tendency for short dives (< 3 min) to occur in sequence and be interspersed by groups of long dives offers evidence for this foraging strategy. Furthermore, observations of feeding events in the laboratory revealed turtles to consume all food

available during a single dive (Pers. obs.). Since C. picta is known to select a wide variety of food items, variation in dive duration may also be due to the different handling time of various prey types. However, MacCullough and Secoy (1983) showed that C. p. bellii selected preferred food items regardless of availability. In view of the wide array of potential prey items available in the pond, and the competition-free environment, searching for preferred foods would be the expected strategy since it would offer a greater return of energy. As opposed to leatherback sea turtles, sea lions, and humpback whales in which dive duration was found to be positively correlated to dive depth (Eckert et al. 1986, Feldkamp et al. 1989, Dolphin 1988, respectively), dive duration in this case may be a measure of feeding success rate.

Although frequency distributions of feeding dives were deemed similar between sexes, cumulative percentages of dives < 3 min was greater for females (x=73.1 %) than for males (x=65.4 %), suggesting that males spent less time searching for food than females. Also, of all feeding dives > 10 min (n=31), males accomplished twice as many as females (20:11). This suggests that males might be more efficient foragers than females, consume more food, or might simply possess a greater ability to dive for longer periods of time.

Examination of dives < 60 s revealed the majority to be between 10-29 s duration (Table 4). Observations of diving behaviour in the

laboratory (chapter 2) showed that turtles dove repeatedly when first placed in the experimental tank and did so until able to settle at the bottom at neutral or negative buoyancy. Adjustment of lung volume at start of a dive to attain a particular buoyancy at a given depth promotes buoyancy control, and minimizes energy required to reach and maintain desired depth. Laboratory observations showed that short dives (< 60 s) were performed by turtles attempting to adjust lung volume for negative buoyancy at depth prior to long dives. That over 40 % of dives lasted < 60 s suggests that turtles used such a strategy in the field. Mean duration of dives < 60 s was similar between sexes but averaged 35 % of total number of feeding dives in males and over 48 % in females. Such an increased frequency indicates that females spent more time adjusting buoyancy, perhaps due to the altered body tissue density resulting from developing follicles and eggs prior to oviposition.

The majority of feeding dives were brief, with 68.6 % of all dives lasting less than the average dive duration (x=153 s; n=472) (Fig 4). As discussed above, several possibilities exist to justify the investment of energy in frequent short dives. Although frequency distribution of feeding dives was strongly skewed towards short dives, a closer examination of time distribution at 60 s intervals showed more uniformity amongst intervals (Fig 4). Only 27.8 % of total time is spent on feeding dives < 3 min, compared to 72.1 % of total number of feeding dives. In contrast, 21.7 % of total time is devoted to dives >

10 min whereas 3.5 % of total number of feeding dives are in that category (Fig 4). That more time is invested in the long feeding dives (> 3 min) overall, despite the high frequency of short dives further justifies energy investment towards buoyancy adjustment at initiation of feeding event since such measures would optimize both foraging time and energy gain.

Surfacing bouts prior to and following a feeding dive were brief, with over 90 % of them < 3 min in duration (Fig 5). Relatively short surfacing intervals also were observed in freely diving leatherback sea turtles (Eckert et al. 1986), sea snakes (Rubinoff et al. 1986), sea lions (Feldkamp et al. 1989), Northern elephant seals (Le Boeuf et al. 1986), and humpback whales (Dolphin 1987) in nature, and in Chelys fimbriata (Lenfant et al. 1970) and C. p. bellii (chapter 2) under laboratory conditions. Close examination failed to reveal correlations between duration of pre- and post-dive surfacing bouts and dive time in summer and only identified a weak positive correlation between pre-dive surfacing time and dive duration in one turtle in the fall (Appendix 3). Such lack of correlation also was established in leatherback sea turtles (Eckert et al. 1986), sea snakes (Rubinoff et al. 1986), and California sea lions (Feldkamp et al. 1989) and suggest that longer dives in these animals do not require longer surfacing bouts (Eckert et al. 1986). If lactate debt incurred during submergence is prevented by acomplishing routine dives aerobically, longer surfacing bouts will not be required (Eckert et al. 1986, Seymour 1979). In addition, if aerobic dive limits

(ADL), defined by Kooyman (1985) to be the maximum breathhold that is possible without any increase in blood lactic acid concentration during or after the dive, are respected, serial dives with short surfacings between them will be possible. In fact, ADL has been established and shown to be respected by divers such as C. scripta (Ackerman and White 1979, sea snakes (Seymour 1979), and Weddell seals (Kooyman et al. 1980, Kooyman et al. 1983, Castellini et al. 1988). That numerous reptilian and mammalian divers display such brief surfacing bouts regardless of dive duration supports the utilization of such strategy and it is likely that in the present study C. p. bellii adhered to such pattern. With regard to reptiles however, this conclusion must be drawn with caution. Several authors have demonstrated crocodiles (Glass and Johansen 1979) and turtles (Jackson et al. 1974, Glass et al. 1978, Milson and Jones 1980) to respond to increase in end-tidal PCO2 by increasing tidal volumes, time occupied by inspiratory and expiratory movements, ventilation, and by decreasing length of breathhold between ventilatory periods. All these factors would serve to increase pulmonary gas exchange and oxygen replenishment and would not necessarily require an increase in surface duration. Castellini et al. (1988) have also demonstrated dive length to periodically exceed ADL, resulting in increased blood lactate and hematocrit values. Such long dives were always followed by several short dives, during which blood lactate concentration steadily declined, but hematocrit remained elevated. As a result of exceptionally long dives, it is possible that turtles incur elevation in blood lactate

concentration, which could be cleared during subsequent aerobic dives or periods of rest following cessation of foraging activities. Furthermore, the ability to expel CO_2 aquatically (Jackson 1976, Jackson et al. 1976, Ackerman and White 1979, Feder and Burggren 1985, chapter 2) could facilitate longer dives in turtles. Ackerman and White (1979) estimated the critical lung gas tension (PO2=22 torr) to be reached in 45 min at 22 C in submerged resting C. scripta. This limit would be attained much more rapidly in an active animal, but since only 3 % of feeding dives exceeded 10 min (Fig 4) and the maximum observed dive duration was 59 min in the present study, the majority dives performed by C. p. bellii were most likely aerobic. Kooyman et al. (1980) proposed that such a strategy, resulting in minimum time required at the surface, would insure a greater proportion of time spent underwater and increase time invested in foraging per se. Northern elephant seals, observed to utilize such strategy, were found to spend 89 % of time submerged (Le Boeuf et al. 1986). During feeding events in the present study, C. p. bellii spent 71 % of total time underwater.

Mass-specific lung volume was shown to increase with increasing body weight in C. s. elegans (Perry 1978). Since adult females are generally much larger than adult males in C. p. bellii, females would be expected to have a greater pulmonary oxygen storage when diving. Blood volume on the other hand, revealed to be inversely related to body weight in C. s. elegans (Hutton 1961), but the high lung volume/body mass ratio and the relatively low hemoglobin concentration

in turtles compared to mammals result in lungs being the major storage site for O2 in turtles (Caligiuri et al. 1981). In addition, Hutton et al. (1960) demonstrated the lack of relationship between oxygen consumption with body size or volume in C. s. elegans. Eckert et al. (1986) reported the larger of two leatherback sea turtles to exhibit a greater proportion of longer dives. Kooyman et al. (1983) calculated ADL to be greater in larger Weddell seals due to increased blood and pulmonary O_2 stores. Based on this information, females in the present study should be capable of greater O_2 stores, faster replenishment of O_2 following a dive, and less exertion for similar dive duration than males. On the contrary, females not only stayed longer at the surface between dives (Table 5A,B), but had shorter individual feeding dives on average and had a lower frequency distribution for longer dives than males. Again, developing follicles and eggs in females might explain the differential foraging characteristics between sexes. The internal volume taken up by follicles and eggs might cause the space normally available for lungs to be reduced prior to oviposition. As shown by Jackson (1971), resting lung volume varies in inverse proportion to the fluid volume of the bladder and cloacal sacs. In fact, Crawford et al. (1976) observed significant increase in lung volume in a turtle after expulsion of fluid and feces from the cloaca. Prior to oviposition, follicles and eggs are likely to add to the cost of foraging in females by further limiting availability of O_2 store in the lungs. If the proportion of total time underwater is taken as a measure of foraging efficiency, the fact that females spent 66 % of time submerged during

feeding events compared to 75 % in males is an indication that the former is a much less efficient forager than the latter, probably due in part to differential reproductive burden.

THERMOREGULATING

That atmospheric thermoregulating was invariably initiated after cessation of feeding activities on sunny days during summer conflicts with reports from several authors stating that basking started immediately after sunrise and preceded all other daytime activities in diurnal fresh-water turtles (Boyer 1965, Ernst 1972, Ernst and Ernst 1973). However, gradual increase in number of turtles basking throughout the morning in the present study agrees with observations made by Auth (1975), Miller (1979), and Schwarzkopf and Brooks (1985) that frequency of basking turtles will peak at certain operative environmental temperatures. Auth (1975) and Obbard and Brooks (1979) also established a positive relationship between frequency of basking and light availability, which in turn was deemed important in promoting heat gain in C. s. elegans (Boyer 1965). That thermoregulation succeeded morning feeding events in the present study and that turtles, alligators, and crocodiles were observed to select higher ambient temperature after a meal (Gatten 1974A, Lang 1979, Parmenter 1981) supports Cagle's (1950) suggestion that increased body temperature favors digestion. As mentioned previously, enzyme action, ingestion, food turnover rate, and caloric intake are favorably influenced by increased body temperature and serve to justify the sequence of events observed in this study. At onset of atmospheric thermoregulation average air temperature was 23.4 $\pm$ 3.1 C with the

greatest proportion of turtles emerging between 22 and 24C (Fig 6). A greater than expected percentage of emergence occurred between 28 and 30 C, and closer examination of weather patterns compiled on dates of occurrence revealed two trends which explain the phenomenon. In some cases, early morning cloud cover dissipated, letting the sun shine through at the precise moment turtles emerged to bask. In all other instances, temperatures rose drastically very early in the morning, or suddenly within a short period of time (3-4C in <30 min) immediately prior to onset of atmospheric thermoregulation. These observations support the importance of light intensity and air temperature as factors influencing onset of basking. Crawford et al. (1983) proposed that turtles could minimize time spent basking if emergence occurred well above preferred body temperature, resulting in rapid heat increase. As mentioned above, basking is shown to favor digestion and it is therefore unlikely that the incurred digestive benefits would reach their full effects if basking time was kept at a minimum. The fact that onset of atmospheric thermoregulation in this study occurred at air temperatures considerably lower than observed daily maxima indicates that turtles did not attempt to minimize basking time by brief exposure to high air temperature but that emergence probably occurred at air temperature favoring progressive and stable heat gain and maintenance for periods of time lengthy enough to optimize digestion. During atmospheric thermoregulation episodes, turtles often entered the water for brief periods of time, and soon resumed basking, usually at the same site. Boyer (1965) estimated total water loss in C. s. elegans

(150-450 g) to be between 0.23 and 0.43 $g \cdot h^{-1}$ at ambient temperature of 18-27 C and relative humidity of 50-80%. Ernst (1972) obtained similar results from C. picta under similar conditions. Boyer (1965) concluded that at average environmental temperature and humidity, heat loss from evaporation in turtle was negligeable and that animals that had the ability to return to water would have little use for evaporative cooling. However, Baldwin (1925) demonstrated that restrained turtles exposed to extreme heat will respond by salivating and urinating on the legs decreasing body temperature. In an increasing ambient temperature, it is probable that turtles in the present study used refresher dives to fine tune thermoregulation, allowing them to decrease body temperature by contact with a cooler medium, to hydrate the integument, which could favor some evaporative cooling upon subsequent emergence. This would allow turtles to continue basking to optimize benefits obtained from increased body heat. During summer, atmospheric thermoregulation occurred in a bimodal pattern and periods of extreme heat at midday were spent under patches of dead vegetation near shore. Such behavior has been frequently observed in turtles (Cagle 1950, Boyer 1965, Auth 1975, Webb 1978, Miller 1979, Spotila et al. 1984) and implies that a temperature at or near the maximum voluntarily tolerated has been attained (Boyer 1965). Occurences of aquatic thermoregulation in turtles have been reported (Sexton 1959, Spray and May 1972, Spotila et al. 1984) and Spotila et al. (1984) showed that atmospheric thermoregulation will be bypassed if water temperature is high enough for turtles to maintain a preferred body

temperature. Since surface water temperature in the pond remained between 23 and 27 C during summer, it is probable that withdrawal to water allowed turtles to maintain body heat at a preferred level, but it is more likely that the primary goal of immersion was avoidance of extreme atmospheric heat since turtles sought cover under vegetation and only emersed the head intermittently. Aquatic basking per se was not observed in the present study. In mid to late afternoon, turtles emerged from the vegetated shore area and often foraged for variable periods of time. Turtles that initiated feeding in mid afternoon frequently resumed atmospheric thermoregulatory activities after cessation of foraging and usually did so until the selected site shaded over. Turtles that started feeding later, bypassed atmospheric thermoregulation. Closer examination of information revealed a lack of pattern within and among turtles, and among sexes. Initiation of feeding probably depended on turtles reaching a body temperature conducive to activity or may have been regulated by food availability, both of which would depend on ambient temperature and other extrinsic factors which would in turn show seasonal variation. Since increased body temperature was shown to favor digestion, feeding early enough to allow subsequent thermoregulating activities would be an advantageous strategy for turtles. In view of extremely high temperatures during summer 1988, it is possible that high body temperature in mid afternoon limited foraging. In addition, digestion in the absence of thermoregulatory activity may not have been too taxing since water temperatures in mid summer were quite high and would allow

maintenance of preferred body temperature after submergence. If true, turtles in early and late summer would have fed in mid afternoon and subsequently basked, when ambient temperatures were not yet extreme, when cool water temperature favored basking and daylight extended late enough to allow it. Turtles would have fed in late afternoon and bypassed atmospheric thermoregulation in mid summer, when ambient temperature reached extremes, and when warm water temperature did not hinder digestion. This was the case in the present study.

In autumn, onset of atmospheric thermoregulation was generally markedly delayed and seemed dependent on air temperature since the majority of onsets occurred within a very narrow range of temperatures (18-21 C) (Fig 6), the latter being significantly lower than average air temperature at onset during summer. The delay of onset to midday and earlier nightfall in autumn decreased daily basking duration which undoubtedly limited heat gain. Several reports show that activity in turtles become limited at water temperature neighboring 15 C (Sexton 1959, MacCullough and Secoy 1983, Ernst and Ernst 1973) and cessation of feeding ensues. Low water temperature also was reported to limit basking activity (Boyer 1965). Despite a reduction in atmospheric thermoregulation time and a probable limited heat gain, benefits must have ensued since it was observed until mid October at water temperature of 8 C. Similarly, Boyer (1965) and Auth (1975) found that basking stopped at water temperature of 7 C for two species of

Chrysemys. Gordon and MacCullough (1980) also reports Graptemys turtles to bask on warm sunny days during September and October. Increase in body heat to level high enough to continue activities such as feeding would be one such benefit. Indeed, occurrence of atmospheric thermoregulation in the fall appeared to be the determining factor controlling initiation of feeding. From early September on, although atmospheric thermoregulation took place without subsequent feeding, the reverse pattern never occurred. Similar observations were reported by Ernst (1982). The ability to obtain food, even in limited amount, would have some benefits as it would augment caloric storage prior to hibernation. Thermoregulation behavior would also result in elevated body temperature that is more nearly optimal for physiological processes than those in cold water (Boyer 1965). Because of the high cost associated with hibernation, it is probably advantageous for turtles to delay torpor and to maintain body functions, at a reasonable cost, for as long as possible. Since predators were absent from the site in the present study, the danger and ensuing cost associated with emergence on land with reduced muscular agility caused by low water temperature would not have been a detriment in this case.

Boyer (1965) and Auth (1975) observed that although turtles did not emerge to bask in shaded areas, shading of the site did not result in cessation of atmospheric thermoregulation or shifting of position. Although turtles returned to the water soon after clouding over and prior to shading at night during summer, they frequently remained in

shaded areas in late afternoon for extended periods of time in the fall. In autumn, a return to cold water would result in a fairly rapid loss of heat gained through atmospheric thermoregulation. By remaining in air, the elevated body temperature is probably maintained for a longer period of time (Auth 1975). During summer, seeking refuge in the water most likely favored conservation of gained heat since clouding or shading over would have resulted in a quick decline from extremely warm ambient temperature. That refresher dives were never observed in the fall suggests that overheating did not occur during that period.

TRAVELING

Turtles usually traveled short distances between various activities. Contrary to Sexton (1959), who observed Chrysemys to swim well beneath the surface of open water when moving from one patch of vegetation to another, turtles in the present study generally swam immediately below the surface, in a porpoising manner. Sexton (1959) described all activities performed by turtles to be closely associated with patches of aquatic vegetation. That even basking did not occur on land suggests that predators may have been a contributing factor in that study in limiting turtles to the aquatic environment and perhaps caused wariness even in the water. That turtles in this study thermoregulated and traveled on land, and swam close to surface in open water suggests a lack of similar danger.

A travel event averaged 41 min in duration and varied greatly between sexes. The fact that males regularly traveled to the south side of the pond, sometimes partly over land, and occasionally to an adjacent pond explains the greater proportion of time invested in the activity. Gibbons (1970) also found a large number of males to move among ponds on a regular basis and suggested that they were more active and utilized a larger area than females. Females usually restricted their daily activities to a specific area of the pond. Nesting activities or travel on land were never observed in females in the present study.

In a seasonal migration study between two bodies of water, Sexton (1959) reported a tendency for more females to emigrate than males. However, Gordon and MacCullough (1980), Morreale et al. (1984), and Pluto and Bellis (1988) reported that with the exception of nesting females, males traversed the greatest distances and traveled more frequently than females. Morreale et al. (1984) and Ernst and Barbour (1972) suggested that observed differences in activity and movement patterns between sexes can be explained in terms of maximizing individual reproductive success. Morreale et al. (1984) hypothesized that males move to increase their chance for multiple matings and reported his findings to support the hypothesis. The differential patterns observed in males in this study would have increased chances to locate potential mates, to increase the number of eggs fertilized by copulation with more females, which would in turn contribute to their reproductive success.

SUBMERGED RESTING

Modifications in rate of activity (Auth 1975) and diving patterns (Eckert et al.1986) were reported in turtles at the onset of nightfall. Similarly, C. p. bellii in the present study retired to shallow water (0.30-0.60 m) at dusk and descended to rest on the substrate.

Although some freshwater turtles are believed to be nocturnal or at least to display some level of activity during the night (Boyer 1965, Ernst and Barbour 1972), Obbard and Brooks (1981) indicated the majority of C. serpentina to be inactive after 1800 h. Furthermore, Brett (1971) and Graham and Hutchison (1978) found a decrease in locomotor activity associated with the onset of night conditions in C. scripta and C. picta respectively and concluded the latter to be under endogenous control but responding to stimuli from the external environment. This is supported by information from the present study in that activity was not absent during nocturnal periods, but was restricted to brief intermittent surfacing bouts between relatively long periods of immobility at the bottom.

Dive duration varied greatly among turtles (Table 6), and although this might be due to individual variations alone, single submergences were much longer in males than in the female. The reason for this is unclear, especially when larger turtles have greater O_2 storage capacity

and should therefore be capable of longer dives (Tenney and Tenney 1970, Perry 1978), which is supported by observations of Eckert et al.(1986).

The female spent 15 to 24 % of time at the surface on night 1 and 2, and the male on night 4 emersed only 2 % of the total time. In addition, buoyancy adjustment dives (<60 s) composed 15.4 to 40.0 % of total dives in the female and were absent in males. Similar sexual variations also occurred during feeding events, and further support previous suggestions that submergence ability at this stage is lessened in females, possibly due to limitations imposed by reproductive events.

Duration of individual surfacing bouts resembled that of feeding events, with over 95 % of bouts lasting < 3 min. The positive correlations established between duration of preceding and subsequent surfacing bouts and submergence time for turtle A on nights 1 and 2 suggests that ADL was frequently exceeded, resulting in increased surfacing time required to replenish and store oxygen. That duration of subsequent surfacing bouts was negatively correlated with submergence time in the male supports Caligiuri et al. (1981)'s demonstration of a depression of energy requirements during prolonged diving in turtles. Ackerman and White (1979) found O_2 stores in C. scripta to be sufficient to support O_2 requirements for 36 min at 24 C, assuming no decrease in O_2 utilization following complete cessation of O_2 supply. That average dive time for turtle C on night 4 exceeded 1

h and 45 min under similar conditions supports Caligiuri et al. (1981)'s conclusion. Jackson and Schmidt-Nielsen (1966) and Jackson (1968) measured a reduction of heat loss with decreasing blood and lung O_2 content. A dive of 2-4 h reduced heat production to 20 % of initial submergence and metabolism became primarily anaerobic (Jackson and Schmidt-Nielsen 1966). It is interesting that turtle C concluded the average dive just short of the 2 h limit. It is probable that abolishment of breathing, a decrease in cardiac work (Andersen 1961, White and Ross 1966, Jackson 1968, Kooyman 1985), and a reduction in brain, neuromuscular, and skeletal muscle activity (Jackson 1968, Robin et al.1981) contribute to lower energy requirement. In addition, diving sea snakes were found to use pulmonary shunts to conserve lung oxygen (Seymour 1982).

Aquatic O_2 uptake in turtles has been widely documented (Root 1949, Dunson 1960, Girgis 1961, Belkin 1968, Gatten 1980, Feder and Burggren 1985) and although it has been deemed insufficient in meeting the needs of submerged turtles (Belkin 1968), it is possible that when metabolism is lessened, it becomes a significant O_2 supply (Jackson and Schmidt-Nielsen 1966). Although documented contribution of aquatic O_2 uptake in species similar to C. p. bellii range from 4 to 6 % of total O_2 uptake (Feder and Burggren 1985), it would undoutedly contribute to prolong nocturnal submergence.

More important than aquatic O_2 uptake in favoring longer resting

dives may be the ability for turtles to excrete CO_2 aquatically. Although the rate of CO_2 loss does not increase to the extent that the arterial PCO_2 does (Jackson 1976), the ability of C. scripta to rid the body of up to 20 % of CO_2 produced while submerged (Feder and Burggren 1985) certainly delays severe hypercapnia during long periods of submergence (Jackson 1976). Aquatic respiration therefore, can be considered as a factor favorably promoting long nocturnal dives in C. p. bellii.

Individual resting dives in autumn greatly exceeded duration of nocturnal resting dives in summer. Although depression of energy requirements described above are known to occur independently of sharp decreases in body temperature (Caligiuri et al. 1981), decline in ambient and body temperatures have been demonstrated to modify metabolic rate. At 10 C, in C. p. bellii, apneic bouts increased in duration during breathing episodes, ventilation decreased, and pulmonary O_2 uptake was 6.8 times greater at 30 C than at 10 C (Glass et al.1983). Heart rate slowed with decreasing temperature in Pseudemys, and O_2 consumption was also dramatically lowered in a resting state at 10 C (Hutton et al. 1960, Gatten 1974B). Ultsch (1985) also found C. p. bellii, the most northerly subspecies, to have survival times well in excess of 25 days when submerged in normoxic water at 10 C. Furthermore, when compared to 7 other freshwater species submerged in normoxic water at 3 C, C. p. bellii survived the longest, with over 80 % of animals still in good health after 189 days. This

length of time closely corresponds to the extent of hibernation period in the northern range of this subspecies. In the fall, hibernating turtles probably undergo physiological adjustments in response to lower ambient temperature, which surely explains the ability of C. p. bellii to submerge for extended duration during the later part of the study.

Hibernation was initiated during the last week in October 1988. Although aggregation behavior is often observed during basking, turtles are usually not considered social animals. That turtles retaining active transmitters hibernated within 0.3 m of one another is interesting and strengthens Carpenter (1957)'s observation of three-toed box turtles hibernating in group in very restricted areas. The hibernaculum selected in this study was also located in the area most frequented during nocturnal resting. That turtles were found so close together may suggest the presence of favorable conditions in the area and may not necessarily represent true gregariousness. More information obtained from radio-tracking hibernating turtles is needed to elucidate this question.

Appendix 1. Frequency distribution (%) per 60 s intervals for all feeding dives for individual turtles during summer 1988. Includes CHI SQUARE among turtles for each time interval.

Interval (s)	Turtle				X^2
	A	B	C	D	
0 - 59	48.0	52.1	43.9	35.0	0.60
60 -119	17.8	15.3	16.7	20.8	0.93
120 - 179	10.5	7.0	9.9	10.9	0.91
180 - 239	5.3	5.4	6.8	12.0	0.62
240 - 299	5.9	4.1	6.8	7.1	0.92
300 - 359	3.3	2.1	6.8	4.4	0.69
360 - 419	1.3	3.3	3.0	1.6	0.88
420 - 479	2.0	3.7	0.8	2.7	0.76
480 - 539	2.0	2.1	0.0	1.1	0.65
540 - 599	0.7	1.7	0.0	1.6	0.71
600+	3.3	3.3	5.3	2.7	0.93
n (dives)	152	242	132	183	

Appendix 2. Time allocation (%) per 60 s intervals for all feeding dives for individual turtles during summer 1988. Includes CHI SQUARE among turtles for each time interval.

Interval (s)	Turtle				X^2
	A	B	C	D	
0 - 59	15.4	10.7	6.0	6.1	0.40
60 -119	10.7	6.1	8.0	12.3	0.74
120 - 179	11.2	7.4	8.0	10.6	0.90
180 - 239	3.9	11.2	8.7	15.2	0.29
240 - 299	11.4	8.9	10.0	9.2	0.98
300 - 359	8.0	6.8	12.5	9.9	0.81
360 - 419	3.7	9.2	6.5	4.3	0.68
420 - 479	6.4	11.8	2.0	8.0	0.24
480 - 539	7.2	6.1	0.0	3.7	0.14
540 - 599	2.5	3.4	0.0	6.3	0.24
600+	19.4	18.4	38.4	14.5	0.09
n (min)	359	554	388	446	

Appendix 3. Regressions of duration of preceding and subsequent surfacing bouts on feeding dive durations per individual turtles during fall 1988.

Surfacing Event	Turtle					
	C		E		F	
Prior to Dive	p=0.4612	r=0.0969	p=0.3838	r=0.1042	p=0.8620	r=0.0300
Subsequent To dive	p=0.7628	r=0.0405	p=0.0390*	r=0.2474	p=0.7118	r=0.0638

* significant positive correlation

Appendix 4. Regression of duration of preceding and subsequent surfacing bouts on night dive durations per night in summer 1988.

Surfacing Event	Night 1		Night 2		Night 3	
Prior to Dive	p=0.6356	r=0.0805	p=0.0013*	r=0.4096	p=0.5394	r=0.3178
Subsequent To dive	p=0.0579*	r=0.3146	p=0.0001*	r=0.6713	p=0.7118**	r=0.9198

* significant positive correlation
** significant negative correlation

CHAPTER 2.

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CHAPTER 2 - DIVING BEHAVIOR

INTRODUCTION

Buoyancy regulation occurs in aquatic reptiles such as crocodiles (Kirshner 1985, Wright and Kirshner 1987), sea snakes (Rubinoff et al. 1986, Graham et al. 1987), and turtles (Jackson 1969, Milson 1974, Milson 1975, Milsom and Johansen 1975). For such divers, the ability to attain desired depth at optimal buoyancy reduces energy costs associated with locomotion and maintenance of position in the water column. However, the reduction in lung volume during the last ventilatory cycle prior to submergence documented in turtles (Milson 1974) and crocodiles (Kirshner 1985) will decrease pulmonary O2 supply during a dive. Although aquatic reptiles usually dive for brief duration (Kirshner 1985, Eckert et al. 1986, Rubinoff et al. 1986), they also freely submerge for extended periods of time (Belkin 1964, Rubinoff et al. 1986, chapter 2). A low metabolic rate, which occurs in submerged C. picta during both active periods and rest (Stockard and Gatten 1983), favors long dives, despite the reduction in lung volume resulting from buoyancy control at depth. However, non-pulmonary gas loss, which occurs in reptiles during submergence (Jackson 1976, Jackson et al. 1976, Glass and Johansen 1979, present study), results in a reduction in lung volume causing buoyancy to progressively decrease during a dive.

The present study was initiated to evaluate the need for C. p. bellii to control buoyancy, and its ability to do so. Parameters such as frequency and duration of dives and surfacing bouts will be examined to determine diving characteristics in normoxic and hypoxic water. Lung volume, tissue density, and buoyancy states in various stages of a dive will be measured to assess the capacity of turtles to regulate buoyancy and to establish the mechanisms involved. Finally, dissolved O2 uptake and CO2 output will be measured in normoxia to assess the role of aquatic respiration during submergence.

MATERIALS AND METHODS

For experimental purposes, twelve Western Painted turtles Chrysemys picta bellii were collected from Crater Lake, near Pinawa, Manitoba, in July and August 1986. Turtles were kept in a 1970 L fiberglass lined tank equipped with a flow-through water system at 26 C, a wooden basking stand, and a heating lamp on a 8L:16D photoperiod. They were fed frozen fish on a weekly basis. Letters painted on the carapace allowed individual identification. For the same purpose, width and length of carapaces were measured once at the beginning of the experimental period. Dry body weights (± 0.01 g) were obtained prior to each set of experiments (Table 1). For 10 consecutive days, turtles were left to dry for 1 h, then weighed on a Mettler PM2000 with animal weighing mode option. This procedure provided minimal and maximal weights which were used to estimate gastro-intestinal and urinary/cloacal content volume and to calculate body volume, required to assess buoyancy state.

LABORATORY OBSERVATIONS ON AQUATIC LOCOMOTION

In November and December 1986, and between June and August 1987, visual observations obtained during 69 1 h periods provided information on diving, swimming, surfacing, and submerged resting

Table 1. Identification and characteristics of turtles used during laboratory study, 1986-1989.

Turtle	Sex	Carapace Dimensions (cm)		Body weight, dry (g)		
		Lenght	Width	September 1986	July 1987	December 1988
A	♀	18.0	13.5	708.1-731.3	700.47-724.80	701.74-722.26
B	♂	18.7	14.2	723.0-770.0	730.80-758.25	689.57-742.00
C	♀	18.6	15.0	962.2-1002.6	963.85-1003.11	952.82-988.05
D	♀	20.8	15.0	1067.4-1116.0	1059.44-1112.88	1106.81-1150.31
E	♂	16.9	11.6	523.3-539.7	526.73-545.77	530.08-568.95
F	♀	21.0	15.8	1319.4-1379.7	1309.53-1330.33	1303.88-1350.13
G	♀	17.0	12.5	626.9-640.5	614.85-634.96	609.43-631.82
H	♂	18.0	13.1	684.3-721.8	654.52-700.64	-
I	♀	19.4	13.7	891.7-902.1	887.40-909.79	874.38-896.46
J	♀	19.8	14.7	976.2-995.2	990.84-1014.35	977.49-1010.04
K	♀	20.0	14.0	923.9-995.2	940.09-981.59	980.52-1017.40
L	♀	21.9	15.1	1299.1-1328.5	1291.27-1331.46	1272.83-1311.53

behavior of C. p. bellii. A 1970 L tank equipped with 4 side windows was used for observation. Water (26 C, 54 cm deep) flowed in the tank but basking stand and heating lamp were not provided. Randomly selected groups of 4 turtles were placed in the tank 1 h prior to observations. Twenty-three hours of observations were gathered for each of 12 turtles.

DIVING CHARACTERISTICS IN NORMOXIC AND HYPOXIC LABORATORY CONDITIONS

To determine the importance of aquatic O_2 uptake, the proportion of submergence time, the frequency of surfacing, and the duration of surfacing bouts were compared in normoxic and hypoxic laboratory conditions. The experimental tank previously described was modified by placing perforated Tygon tubing anchored with lead weights on the periphery of the bottom. During hypoxia, dissolved O_2 was reduced to < 1.0 ppm by gently bubbling N_2 through the tubing. During normoxia, air was circulated in the system to provide similar conditions. Dissolved O_2 level fluctuated between 8.6 and 9.5 ppm in normoxia. A 30 cm wide styrofoam ring was placed on the surface of the water, against the wall of the tank, to reduce surface area and minimize oxygen exchange between air and water. The ring also increased circulation of N_2 bubbles in the water in hypoxia. Dissolved O_2 was recorded continously with a YSI 54 O_2 meter, 24 h/day throughout the experiment. Randomly selected groups of 4 turtle were placed in the

tank 1h prior to experiment. During 1 h sessions, surfacing frequencies were recorded for each turtle, using a digital counter, and the time of surfacing was recorded for each of 2 turtles with a stopwatch. In December 1987, twenty-four episodes in hypoxic conditions provided information on surfacing frequency and duration of surfacing bouts, for each of 12 turtles. A similar series of experiments was completed in normoxic conditions in January 1988. Data on duration of surfacing bouts and their frequency were used to calculate total submergence duration per hour and average lengths of surfacing bouts for individual turtles. Analysis of total proportion of time submerged and frequency of surfacing bouts revealed heterogeneity among individual turtles (Tukey's multiple range test). For group comparison between normoxic and hypoxic conditions, homogeneity among turtles was attained by deleting data on turtle K for total submergence duration and for turtles A, B, D, I, J for frequency of surfacing bouts.

Comparisons between normoxia and hypoxia was done for each individual turtle, but sample sizes (n=4 or 8) weakened statistical interpretation. Therefore, comparisons of individuals were based on common tendencies observed among turtles, and were reported as such despite the lack of statistical significance. Support from statistical analyses is included where appropriate. Data from all turtles were included in the group comparison for duration of surfacing bouts since homogeneity among turtles was established in both normoxic and

hypoxic water.

Body weight (W_b) was used to compare size-specific diving characteristics between turtles since it was shown to be directly proportional to lung volume in the buoyancy studies.

BUOYANCY

To assess buoyancy state of turtles at various stages of a dive, individual body weight and body volume were measured using the procedure of Gee (1988). Body volumes were estimated using a combination of submerged weight (Ws) measurements during voluntary dives and whole-body plethysmography. Turtles were individually released in the experimental tank described above, filled to a depth of 54 cm with freshwater and equipped with a metal mesh weighing pan suspended 2.5 cm off the bottom from a balance (Mettler PM2000). When a voluntary dive was initiated, a timer was started. The turtle was allowed to settle at the bottom, and then carried gently onto the weighing pan with modified tongs. Submerged weight ($\pm$ 0.01g) was recorded once a minute for a portion of the dive (9 to 72 min). Before the dive ended, the turtle was slowly transferred from the pan to an immersed plethysmograph next to the pan, to determine lung volume.

A variation of the method of whole-body plethysmography described in Andersen (1961) was used to assess lung volume (V_l). The plethysmograph chamber (22 x 30 x 18 cm in internal dimensions), was build from 1.1 cm thick clear acrylic. One end of the box was permanently sealed with an acrylic plate fitted with two 3-way valves, each situated 4 cm off the bottom to correspond to the approximate lung position of turtles. The opposite end was equipped with 2 hinges

on one side. The door was tightly closed against a rubber O-ring inserted around the edges of the box, and was held in place by toggle clips placed in 4 positions around the free edges of the door. A perforated acrylic panel slid in a 3-way position groove to keep the turtle in place once in the box.

Care was taken to remove all air bubbles from the inside walls and valves of the plethysmograph when it was immersed in the experimental tank. Once a turtle was in place, the door was tightly shut and the plethysmograph was lifted out of the water and transported to an adjacent room for lung volume measurement. A pressure-transducer (Stratham model P23BB) was connected to one of the 3-way valve on the end plate of the plethysmograph with a short piece of thin tubing. A glass syringe was used to inject 2 ml of water into the plethysmograph through the second 3-way valve. Pressure changes in the plethysmograph were registered on a Beckman R511A Dynograph recorder. The procedure was completed in 5-10 min.

Since the animal's lungs contain the only compressible volume in this system, Andersen (1961) used Boyle's law to estimate lung volumes, as follows:

$$P_1 V_1 = P_2 V_2$$

$$= (P_1 + \Delta P)(V_1 - \Delta V)$$

where P_1 = pressure acting on the lungs of the turtle before water was injected in the plethysmograph.

V_1 = the initial lung volume of the turtle (ml).

P_2 = pressure acting on the lungs of the turtle after water was injected in the plethysmograph.

V_2 = the lung volume (ml) of the turtle after injection of water.

ΔP = change in pressure resulting from injection of 2 ml of H_2O in system.

ΔV = change in lung volume (= volume of water injected).

Use of these formulae involved the assumption that aside from compression of the animal's lungs, the system remained static when water was injected in the plethysmograph. Expansion of the plethysmograph and tubing connecting it to the pressure-transducer rendered the assumption invalid and resulted in abnormally high lung

volume measurements. To correct for this error, known volumes (50 ml, 100 ml, 150 ml) of air approximating the expected lung volumes of turtles were injected in the immersed, tightly closed plethysmograph and the above procedure was used to measure pressure changes for each volume resulting from injection of 2 ml of water in the system. Calibration was obtained on a daily basis and turtles' lung volumes were estimated using the calibration curves.

Three submerged resting lung volumes were obtained from each of turtles C and H, and 2 measurements were obtained from B. Two to four injections (2 ml H_2O) were made for each lung volume measurement and the resulting average was subsequently used. The submerged weight of the turtle corresponding to the time of lung volume measurement was then extrapolated from a curve of data obtained prior to plethysmograph experiment in the tank. Knowing body weight, it was then possible to estimate body volume using:

$$W_s = W_b - (V_b + V_l)$$

where W_s = submerged weight (g)

W_b = body weight, dry (g)

V_b = gas-free body volume (ml)

V_l = lung volume (ml)

then: $V_b = (W_b - W_s) - V_l$

Since lung volumes were measured at atmospheric pressure, the results were adjusted to account for hydrostatic pressure on the turtle's lungs at a depth of 51.5 cm, level at which submerged weights were recorded. The adjustments were as follows:

Boyle's law : $P_1 V_1 = P_2 V_2$

$= (P_1 + 51.5) V_2$

$$V_2 = \frac{P_1 V_1}{P_1 + 51.5}$$

where P_1 = atmospheric pressure (cm H_2O)

V_1 = lung volume at P_1

P_2 = pressure at 51.5 cm depth (= P_1 + 51.5 cm H_2O)

V_2 = lung volume at 51.5 cm depth

P_1 was recorded daily, from a digital barometer placed in the laboratory.

Body volumes were estimated separately for each lung volume measurement and were regressed against body weight. Resulting equations were used to determine a body volume for each turtle, which

was selected for subsequent calculations.

Tissue density (D) was calculated for each turtle using:

$$D = \frac{W_b}{V_b}$$

where D = tissue density ($g \cdot ml^{-1}$)

W_b = body weight, dry (g)

V_b = gas-free body volume (ml)

To assess tissue density and body volume, minimal body weight obtained as previously mentioned was used. It was assumed to be the most exact measure of body weight, with minimum gastrointestinal, urinary, or cloacal content.

Estimation of gastro-intestinal, urinary/cloacal content volume and the ratio of this volume on body volume were used to assess influence of the presence of water/food in turtles on buoyancy state. The difference between minimum and maximum values obtained during 3 series of dry body weight measurements was assumed to result from the presence of food, urine, and/or water in the digestive tract and/or urinary/cloacal sacs of turtles. It was converted to volume using:

$$D_c = \frac{W_c}{V_c}$$

$$V_c = \frac{W_c}{D_c}$$

where D_c : density of content ($g \cdot ml^{-1}$)

W_c : dry weight of content (g)

V_c : volume of content (ml)

with the density of food (1.0570 $g \cdot ml^{-1}$) having been measured previously and the density of water being 1.0000 $g \cdot ml^{-1}$. Any combination of food, urine, and water will have densities and volumes ranging between the lower and upper limits estimated here.

To estimate lung volume required for positive buoyancy during surfacing bouts, the volume of the emersed portion of the body was assessed by photographing surfacing turtles from above and laterally. Then, turtles' carapace and head areas corresponding to emersed body parts were imprinted in plasticine and water was poured in the depressions to estimate volumes. The procedure was repeated 5 times for each of two turtles. Since turtles tended to retract their head,

imprints of head parts were obtained from preserved turtles of similar size (Chrysemys scripta). Minimum (head, partial) and maximum (head and carapace, partial) emersed volumes for each turtle were converted to corresponding mass using previously estimated individual tissue density, as follows :

$$W_e = V_e \times D_t$$

where W_e = weight of emersed portion of the body (g)

V_e = emersed volume (ml)

D_t = tissue density ($g \cdot ml^{-1}$)

Since 1 ml of respiratory gases will support 1 g of tissue in water (Gee 1970), the increase in lung volume ($V_{l(e)}$) required to lift V_e will be equivalent to W_e (g).

then,

$$V_{l(t)} = V_{l(n)} + V_{l(e)}$$

where $V_{l(t)}$ = total lung volume at surface (ml).

$V_{l(n)}$ = lung volume required to make turtle neutrally buoyant ($=W_b-V_b$) (ml).

$V_{l(e)}$ = extra lung volume required to support body tissue above surface (ml).

Repeating the procedure used in lung volume measurement, buoyancy state during various parts of a dive was assessed by recording the submerged weight of a freely diving turtle resting on the weighing pan, once every minute for the duration of a dive. Lung volumes can be estimated at any particular time of a dive using :

$$W_s = W_b - (V_b + V_l)$$

$$V_l = (W_b - W_s) - V_b$$

Buoyancy was calculated at each minute of a dive by dividing the lung volume by the weight of the gas-free turtle (Wb - V_b) (1.0 $ml \cdot g^{-1}$ = neutral buoyancy; < 1.0 $ml \cdot g^{-1}$ = negative buoyancy; > 1.0 $ml \cdot g^{-1}$ = positive buoyancy) (Gee 1970). Lung volume at time 0 was extrapolated from the information obtained during the dive and buoyancy was determined for turtles at beginning and end of a dive using :

$$Vl_{(s)} = \frac{Vl_{(b)} \times P_2}{P_1}$$

$$Vl_{(s)} = \frac{Vl_{(b)} (P_1 + 51.5)}{P_1}$$

where $Vl_{(s)}$ = lung volume at start of dive (ml)

$Vl_{(b)}$ = lung volume at bottom at corresponding time (ml).

P_1 = atmospheric pressure (cm H_2O)

P_2 = pressure at 51.5 cm depth (P_1 + 51.5 cm H_2O)

NON-PULMONARY EXCHANGE OF O_2 AND CO_2 IN H_2O.

To determine the role played by non-pulmonary gas exchange in density changes during the course of a dive, and consequently in buoyancy control, dissolved O_2 uptake and CO_2 output were measured in free-diving turtles. Turtles were placed individually in a large glass aquarium (122 x 62 x 63 cm) with a flow-through water system at 25 C, and allowed to rest for 1 h before start of experiment. Upon reaching the bottom after a voluntary dive, the turtle was placed in the immersed plethysmograph, which was equipped with an O_2 meter probe (YSI 54 O_2 meter) wired through 1 opening previously containing a 3-way valve. The perforated panel was put in place to prevent erratic movement of the turtle and the door was tightly closed. Experimental

procedure lasted 60 min. Dissolved O_2 level was recorded once at the start of the rest period, at the start of the experiment, and again at the end. Temperature was maintained at 25 C inside the plethysmograph. Dissolved CO_2 level was measured by the titrimetric method (A.P.H.A. 1965) using samples of water obtained from the aquarium 1 h prior to the start of experiment and again at initiation of experiment. It was assumed that these samples had CO_2 level similar to water inside the plethysmograph since it was immersed with door open during the rest period and surrounding water could circulate freely in it. At completion, the plethysmograph was lifted from the aquarium, the turtle carefully removed and a sample of water was extracted for analysis. Dissolved CO_2 level was measured from 2 samples in all cases. Prior to each run, the inside of the plethysmograph was washed with detergent and thoroughly rinsed to avoid bacterial contamination. In December 1988, experiments were repeated 5 times for each of 4 turtles ($2♀$, $2♂$). In addition, 4 control runs using water left in the plethysmograph after an experiment, were done to measure dissolved gas (O_2, CO_2) exchange resulting from bacterial contaminants present in excrements and on the body of the turtle. The control runs showed that all results were negligeable.

In statistical analysis (ANOVA), differences were considered significant if $p \leq 0.05$. Significant differences have been indicated by an asterisk (*) in tables and figures.

RESULTS

OBSERVATIONS ON AQUATIC LOCOMOTION AND RESTING BEHAVIOUR

At the surface, the turtle's emersed body volume varied during the breathing cycle. During inspiratory phases (Fig 1A), the body was parallel to the surface and the superior portion of the carapace and head were partially emersed. During the expiratory phases (Fig 1B), the posterior portion of the body tilted down to ~45^{o} angle to the surface and only the anterior tip of the head was emersed. Expansion and contraction of the flank area around the hindlimbs and to a lesser degree around the forelimbs, correlated with the upward and downward tilting of the turtle's body during a breathing cycle, respectively. During apneic periods, turtles remained stationary as illustrated in Fig 1A and 1B, or in a position intermediate to them. Turtles rarely moved about at the surface; if movement occurred, it was slow and propulsion was accomplished by the front limbs.

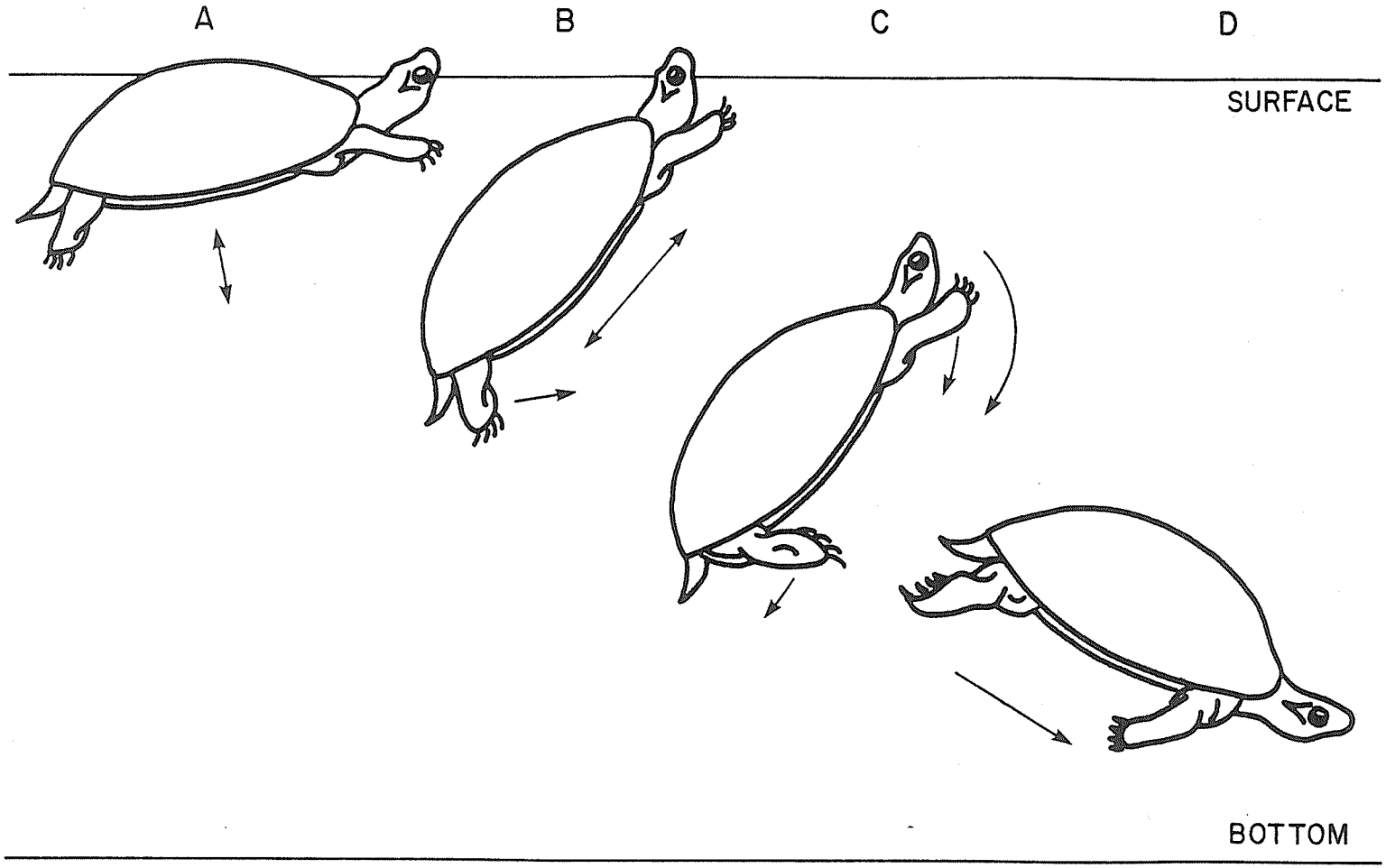
Immediately prior to a successful descent, a turtle's body was positioned downward as in the expiratory phase (Fig 1B). Fully extended hindlimbs swang forward, ventro-laterally to body, initiating a caudad descent in the water column (Fig 1C). At approximately 3 body lengths down from the surface, the turtle became momentarily statio-

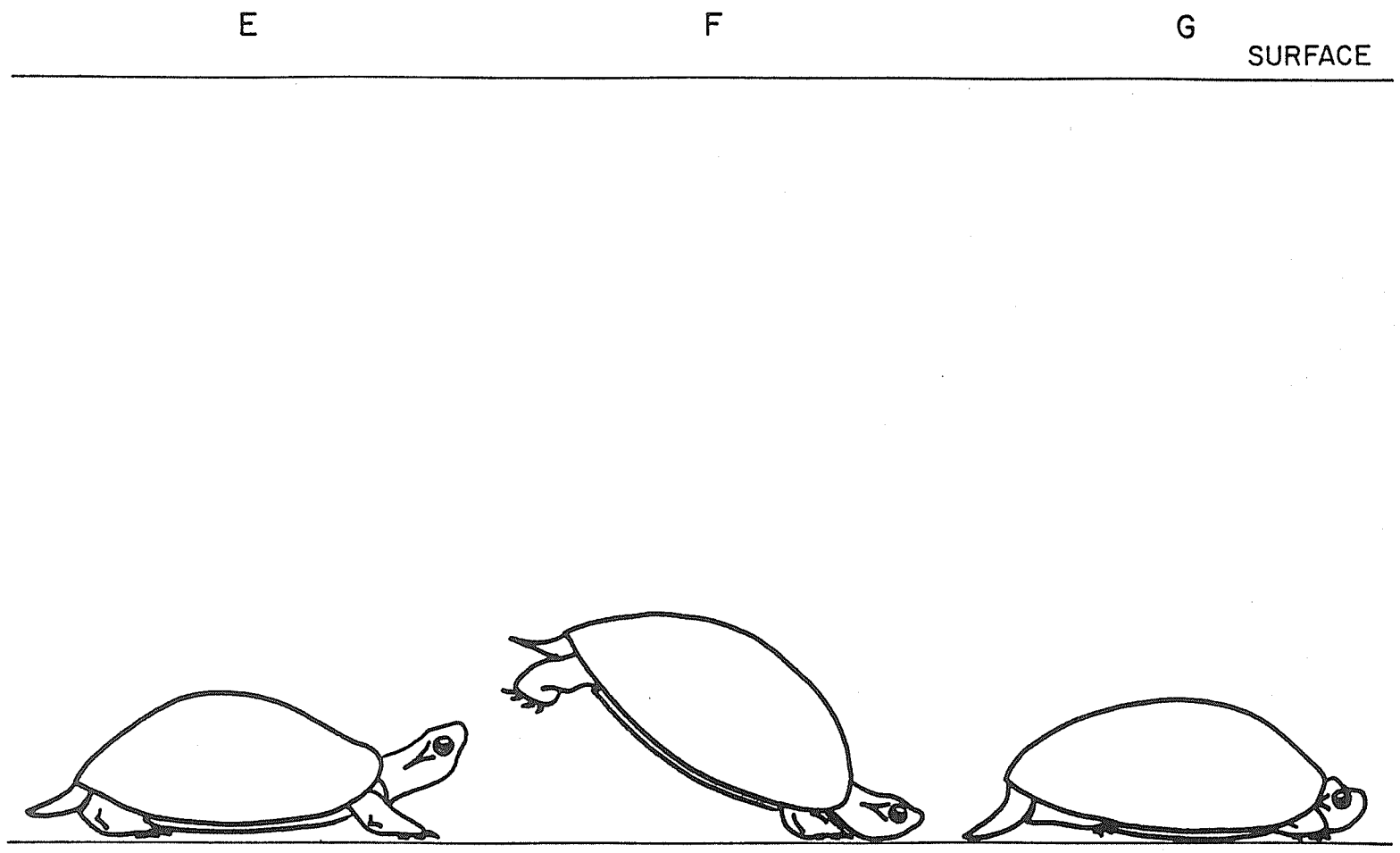
ary, upon which the body pivoted down around a tranversal axis near the posterior end of the carapace (Fig 1D). At that point, synchronized protraction of the limbs helped to complete the descent, which was usually passive.

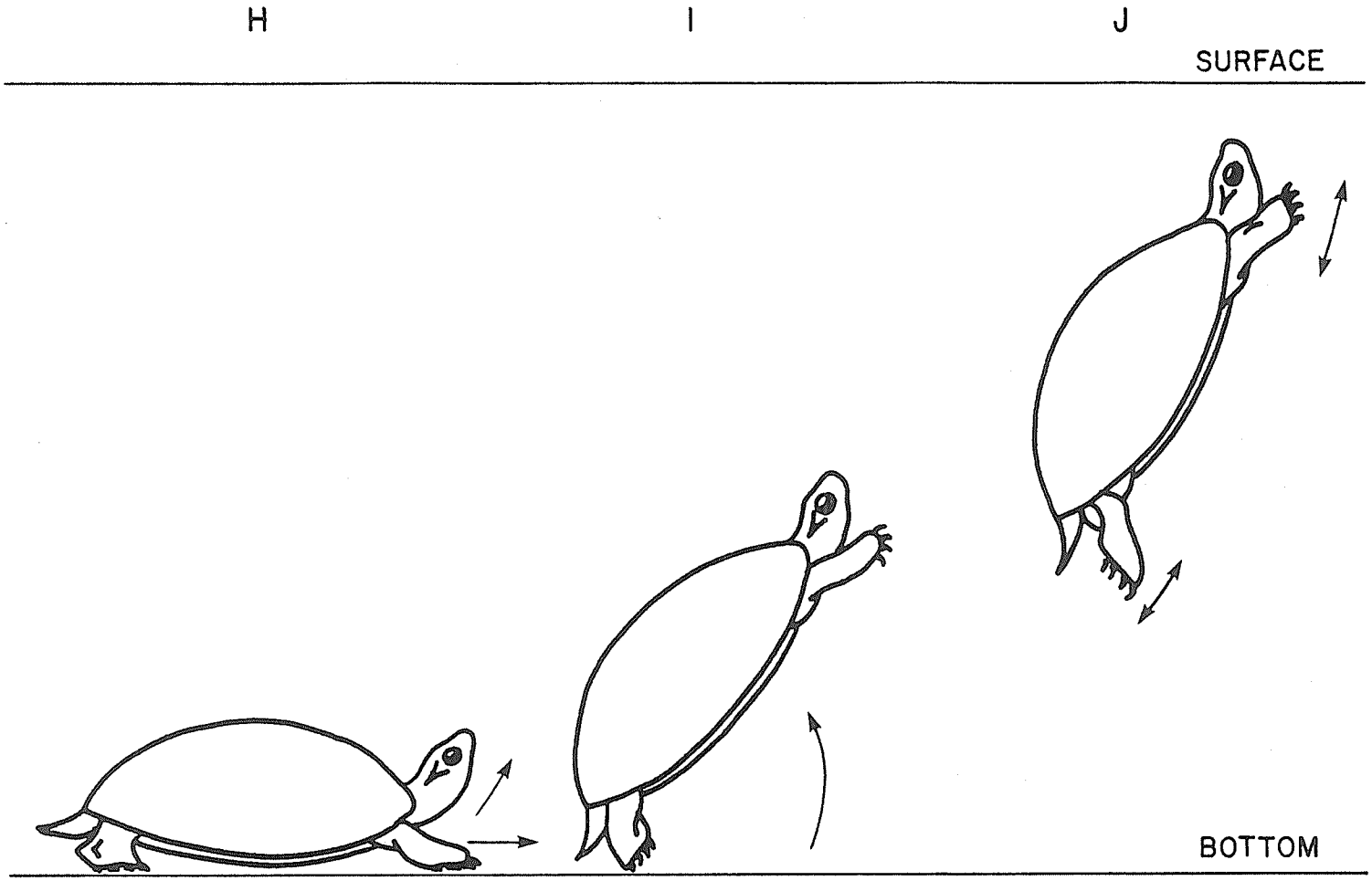
Occasionally, turtles initiated a descent from an inspiratory phase position (Fig 1A). In such cases, a positively buoyant state forced turtles to actively swim down, alternating protraction of diagonally opposing limbs. Attempts to reach the bottom in such a manner was frequently unsuccessful and resulted in the turtle bobbing back within a few seconds. Such attempts usually occurred in series, with a turtle resurfacing momentarily between each submergence. If a successful descent was not achieved, the turtle eventually remained at the surface. If a turtle was startled by loud noises or sudden movements while at the surface, it went down in a forward dive, tilting its head down and actively descending, and released gas bubbles through the mouth. Release of gas bubbles was not observed during undisturbed voluntary dives but was common when handling submerged turtles. Gas bubbles also tended to lodge under the front edge of the carapace during inspiratory phases at the surface. During a descent, they were released from the latero-posterior areas of the carapace when turtles pivoted forward.

After reaching bottom, turtles often moved around for various

Figure 1A-J. Body position of a turtle in the water column at various steps of a dive.


A
B
C
D
SURFACE
BOTTOM


E
F
G
SURFACE


H
I
J
SURFACE
BOTTOM

lengths of time, by swimming close to the substrate or by bottom-walking (Zug 1971). Diagonally opposing limbs are used alternatively when walking, even if the turtle is only "skimming" over the substrate. Subsequently, turtles settled in one area for the remainder of the dive. Body positions at rest varied and progressed in a predictable manner. Early on in a dive, turtles remained parallel to the bottom with the body supported and slightly elevated by the limbs. Head and tail were extended outward at rest (Fig 1E) and frequently, either the caudad or craniad end slowly rose (Fig 1F). This position was usually temporary, and the body resumed a parallel position to the substrate after a few minutes. As a dive progressed, hindlimbs slowly retracted under the carapace against the posterior flanks, and support was then provided by the forelimbs and the posterior tip of the tail resting on the bottom (Fig 1G). The forelimbs slowly retracted against the anterior flanks, leaving the plastron to rest on the bottom and the tail slightly elevating the posterior area. During submergence, the gular region constantly contracted and expanded. Resting turtles often "yawned" under water. If these two events occurred when turtles were positioned at an angle (Fig 1F), a rhythmic movement of the body ensued.

Prior to ascent, limbs extended forward, and head tilted up (Fig 1H). Passively, turtles regained a ~45^{o} angle position, with only the distal claws of the hindlimbs remaining in contact with the substrate (Fig 1I). Ascent was initiated by a push from hindlimbs synchronized

with protraction of the forelimbs, sending the turtle up in a vertical position. Ascent was active, with turtles frequently having to swim vigorously to reach the surface (Fig 1J). Turtles often completed all steps involved in an ascent without surfacing. They skimmed the surface, slowly swimming in an horizontal position, and then proceeded down shortly after. Resting at the bottom resumed.

In a group, turtles seemed to synchronize their activities with those of others. Surfacing by an individual prompted surfacing of others even when positioned at opposite end of the tank. Joining a common resting area, arriving turtles frequently climbed on top of others to rest.

DIVING CHARACTERISTICS IN NORMOXIC AND HYPOXIC AQUATIC CONDITIONS

In normoxia and hypoxia, total submergence time averaged 51 $min \cdot h^{-1}$. Despite wide variation between individuals, comparison between the two treatments revealed that 75 % of turtles stayed submerged longer on average in normoxic water (Table 2). On average, turtles spent an additional 90 $s \cdot h^{-1}$ underwater in normoxia (Table 3) and were more active during submergence than turtles in hypoxia. In both treatments, submergence time in males exceeded that of females by 90 to 120 $s \cdot h^{-1}$ (Table 4). Frequency distribution of submergence time among individuals showed that in 73 % of cases, turtles remained submerged > 50 min in normoxia, compared to 60 % in hypoxia. Frequency rapidly decreased for submergence time > 55 and 58 min, but the trend remained similar between both treatments (Table 5). The frequency of surfacing bouts averaged $25.1 \cdot h^{-1}$ (n=48; range:0-115; S.D.= $\pm$ 25.2) in normoxic water and $16.6 \cdot h^{-1}$ (n=48; range:0-51; S.D.= $\pm$ 12.9) in hypoxic water, with individual average frequencies varying greatly in both treatments (Table 6). Frequency of surfacing was greater in normoxia than in hypoxia (ANOVA: $F_{1,110}=5.19; p < 0.025$) (Table 3). Comparison between sexes suggested that females surfaced more frequently than males per hour in hypoxic water but both sexes had similar frequency of surfacing bouts in normoxic conditions (Table 4). Negative correlations were established between frequency of surfacing

Table 2. Average submergence time ($s \cdot h^{-1}$) for individual turtles in normoxia and hypoxia, during four 1 h events.

Turtle	Average Submerged Time		p
	Normoxia	Hypoxia	
A	2900.0	2821.5	n.s.
B	3401.0	3515.5	n.s.
C	3299.3	3321.0	n.s.
D	3482.5	3258.8	n.s.
E	3027.3	2699.5	n.s.
F	2716.0	2952.5	n.s.
G	3123.5	3033.5	n.s.
H	3460.3	3348.3	n.s.
I	3421.5	3170.3	n.s.
J	3094.0	3011.0	n.s.
K	2127.5	2059.3	n.s.
L	3451.0	3203.5	n.s.
$\bar{X}$	3125.3	3032.9	

Table 3. Comparison of average submergence time, frequency of surfacing, and surfacing duration between turtles in normoxia and hypoxia. Number of event (n) in parentheses.

Parameter	Normoxia	Hypoxia	p
Submergence[1] Time (s) (44)	3215.2	3125.1	> 0.10
Frequency[2] of Surfacing (56)	19.6	14.6	> 0.025
Surfacing[3] Duration (s) (48)	28.4	39.7	> 0.05

[1] not including K

[2] not including A B D I J

[3] including all turtles

Table 4. Comparison of average submergence time, frequency of surfacing, and surfacing duration between sexes in both normoxia and hypoxia. Number of event (n) in parentheses.

Parameter	Normoxia		Hypoxia	
	♀	♂	♀	♂
Submergence Time (s)	3184.8 (32)	3296.2 (12)	3096.5 (32)	3187.8 (12)
Frequency of Surfacing	19.4 (40)	20.2 (16)	15.7 (40)	12.0 (16)
Surfacing Duration (s)	32.0 (33)	16.8 (10)	38.9 (36)	42.7 (10)

Table 5. Cumulative frequency distribution (%) of submergence time in 1 h periods in normoxia and hypoxia.

Submergence Time (min)	Normoxia	Hypoxia
> 50	72.9	60.4
> 55	45.8	37.5
> 58	20.8	14.6

Table 6. Average frequency of surfacing for individual turtles in normoxia and hypoxia during eight 1 h events.

Turtle	Frequency of Surfacing		p
	Normoxia	Hypoxia	
A	42.25	31.63	n.s.
B	11.13	2.75	n.s.
C	16.00	11.88	n.s.
D	3.13	6.50	n.s.
E	20.88	9.25	< 0.03
F	30.13	18.63	n.s.
G	15.50	14.25	n.s.
H	19.50	14.75	n.s.
I	7.63	9.88	n.s.
J	45.88	25.88	n.s.
K	24.63	20.13	n.s.
L	10.75	13.38	n.s.
$\bar{X}$	20.62	14.91	

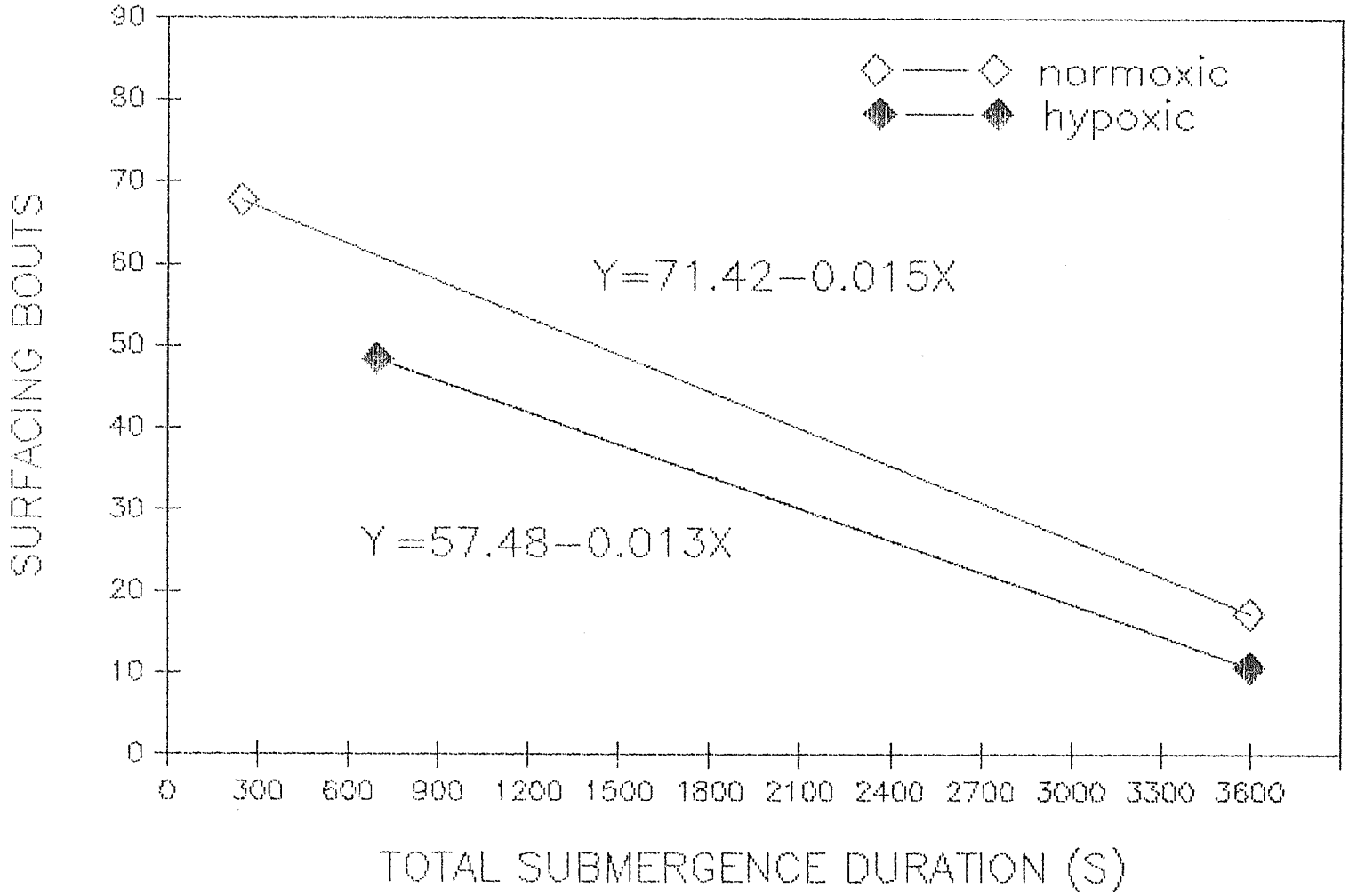
bouts and total submergence duration in both normoxia ($p < 0.01$; $r=0.4060$) and hypoxia ($p=0.0001$; $r=0.5854$) and although both were deemed similar, the regression line for hypoxic water showed consistantly lower frequency of surfacing bouts than in normoxic water for corresponding total submergence times (Fig 2).

Although duration of surfacing was not significantly different between treatments (ANOVA: $F_{1,88}=2.95$, $p > 0.05$), individual averages tended to be greater in hypoxia than in normoxia (Table 7), with surfacing bouts in hypoxia averaging 39.7 s (n=47; S.D.= $\pm$ 25.0 s; range:12.6-128.6) and 28.4 s (n=43; S.D.= $\pm$ 36.8 s; range:6.2-239.5 s) in normoxia (Table 3). Comparative analysis revealed females and males to surface for similar duration in both normoxic (ANOVA: $F_{1,45}=1.32$; $p > 0.10$) and hypoxic water (ANOVA: $F_{1,45}=0.19$; $p > 0.10$) although average duration of surfacing bouts for females was twice as long as for males in normoxia (Table 4).

Table 7. Average surfacing duration (s) for individual turtles in normoxia and hypoxia during four 1 h events.

Turtle	Duration of Surfacing		p
	Normoxia	Hypoxia	
A	20.3	19.6	n.s.
B	21.0	45.7	n.s.
C	17.3	24.7	n.s.
D	43.3	59.5	n.s.
E	20.6	59.7	< 0.05
F	23.5	29.6	n.s.
G	38.0	40.9	n.s.
H	7.5	23.3	n.s.
I	30.4	42.6	n.s.
J	12.7	22.5	< 0.03
K	80.2	80.3	n.s.
L	17.6	30.1	n.s.
$\bar{X}$	27.7	39.9	

Figure 2. Regression of the frequency of surfacing bouts on submergence duration in a 1h period, in normoxia and hypoxia. n=48.


normoxic
hypoxic
Y=71.42−0.015X
Y =57.48−0.013X
SURFACING BOUTS
TOTAL SUBMERGENCE DURATION (S)
0
10
20
30
40
50
60
70
80
90
0
300
600
900
1200
1500
1800
2100
2400
2700
3000
3300
3600

ASSESSMENT OF BUOYANCY

MEASUREMENT OF LUNG VOLUME AND ASSESSMENT OF TISSUE DENSITY

Lung volume (V_l) at neutral buoyancy averaged 16.83 $ml \cdot 100g^{-1}$ (Table 8) (n=8; SD= ± 1.43; range: 13.83-18.77 %) and was similar among turtles (ANOVA: F2,5= 0.88; $p > 0.10$). Estimated body volume averaged 83.17 $ml \cdot 100g^{-1}$ of body weight. Analysis of calculated body volume against previously obtained minimum body weight yielded a strong positive correlation ($p < 0.0001$; r=0.9964) (Fig 3). Estimated tissue density averaged 1.2027 $g \cdot ml^{-1}$ (n=8; SD= ± 0.0204) (Table 8) and was deemed similar among turtles (ANOVA: $F_{2,5}=0.89$; $p > 0.10$). Assessment of tissue density (D_t) from two turtles found dead in the field yielded values of 1.1755 and 1.1951 $g \cdot ml^{-1}$ (Table 8).

ASSESSMENT OF GASTRO-INTESTINAL, URINARY, AND CLOACAL CONTENT VOLUME

Volumes taken up by food and fluids ranged from 1.3 to 9.2 % of minimum body volume (Table 9). Average content volume represented 4.70 % (n=35; SD= ± 2.03) of body volume for water ($D=1.0000\ g \cdot ml^{-1}$) and 4.47 % (n=35; SD= ± 1.94) of body volume for food ($D=1.0570\ g \cdot ml^{-}$

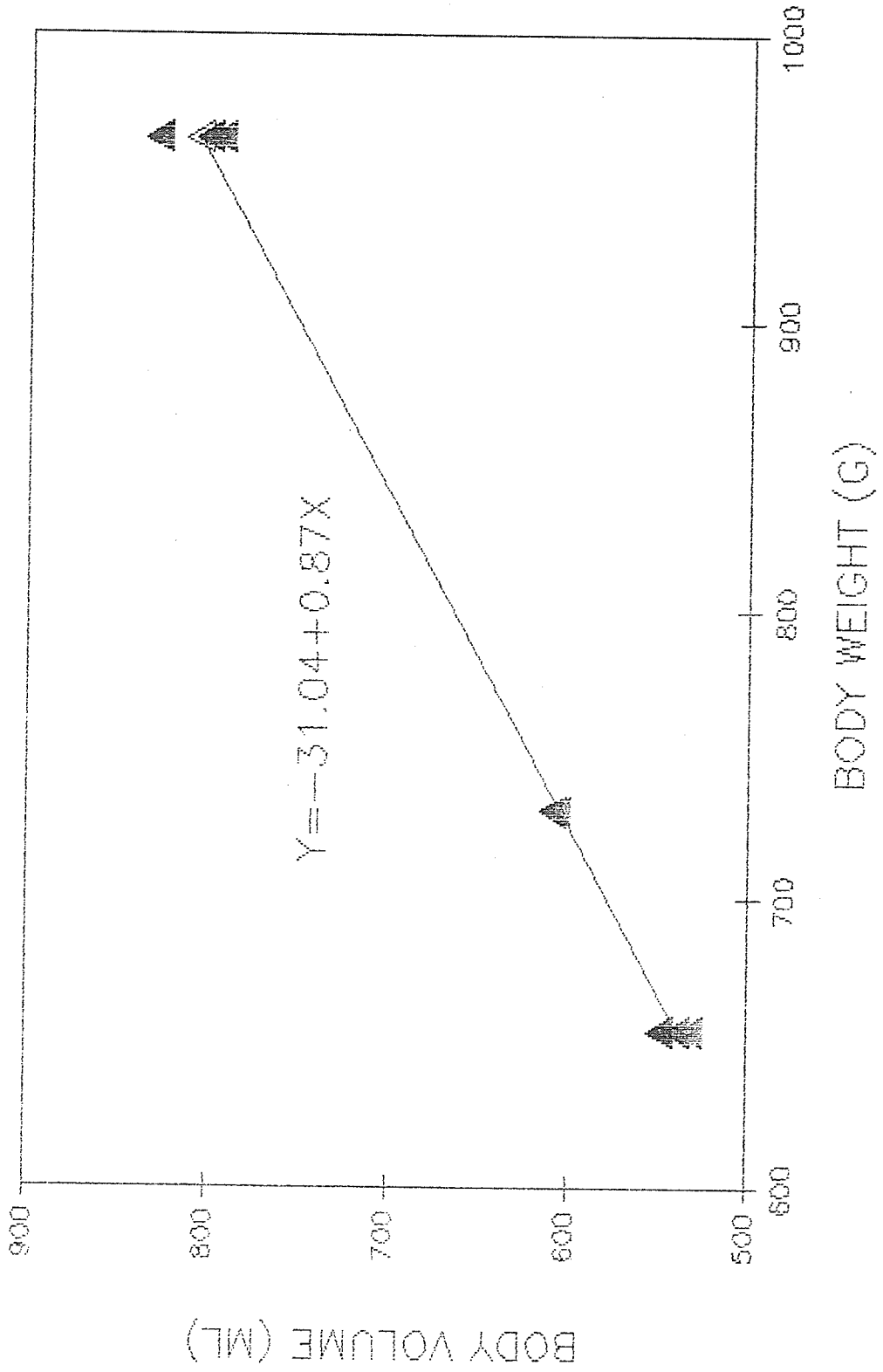
Table 8. Lung volumes (ml) obtained by plethysmography, and estimated tissue density ($g \cdot ml^{-1}$) for 3 live and 2 dead turtles.

Parameter	Turtle B	C	H	Dead	Dead	$\bar{X}$
Body Weight Dry (g) (W_b)	730.80	963.85	654.52	976.93	845.20	
Lung Volume (ml) (V_l)	124.61 122.49	133.31 161.53 168.57	122.84 106.55 116.12	145.84	137.96	
$\frac{V_l}{W_b}$ ($ml \cdot 100g^{-1}$)	17.05 16.76	13.83 16.76 17.47	18.77 16.28 17.74	14.93	16.32	16.83 (live) 15.63 (dead)
Body Volume (ml) (V_b)	606.19 608.31	830.54 802.32 795.48	531.68 547.97 538.40	831.09	707.24	
Tissue Density D_t ($g \cdot ml^{-1}$)	1.2056 1.2014	1.1605 1.2013 1.2117	1.2310 1.1944 1.2157	1.1755	1.1951	1.2027 (live) 1.1853 (dead)

Table 9. Average food/fluid volume (% body volume) for individual turtles, and by sex, as estimated from differences between minimum and maximum body weights. Standard deviation in parentheses.

Turtle	H_2O	Food
A	3.90 (0.36)	3.73 (0.31)
B	7.20 (2.43)	6.87 (2.32)
C	4.77 (0.32)	4.53 (0.31)
D	5.37 (0.65)	5.10 (0.66)
E	5.80 (2.79)	5.50 (2.70)
F	3.83 (1.78)	3.63 (1.68)
G	3.73 (1.00)	3.57 (0.95)
H	7.60 (1.41)	7.25 (1.34)
I	2.47 (0.92)	2.33 (0.90)
J	3.03 (0.87)	2.90 (0.82)
K	6.33 (2.51)	6.03 (2.42)
L	3.33 (0.55)	3.13 (0.55)
♀	4.09 (1.53)	3.89 (1.47)
♂	6.78 (2.21)	6.45 (2.12)

Figure 3. Regression of body volumes (Vb) indirectly obtained by plethysmography, on minimum dry body weights (Wb) for 3 turtles.


BODY VOLUME (ML)
900
800
700
600
500
600
700
800
900
1000
BODY WEIGHT (G)
Y=-31.04+0.87X

1). Food and fluid volume in females averaged 3.9-4.1 % body volume, and 6.5-6.8 % in males. Although one female stored a % volume exceeding that of males in one instance, differences were significant between sexes (ANOVA: $F_{1,33}=15.47$; $p < 0.0005$). If the difference between minimum and maximum body weights was assumed to be food and/or water, the average body density (D_b) for turtles B,C and H was reduced from $1.2027 g \cdot ml^{-1}$ (Table 8) to $1.1956 g \cdot ml^{-1}$ (n=8;SD= $\pm$ 0.0184) and $1.1928 g \cdot ml^{-1}$ (n=8;SD= $\pm$ 0.0184), respectively (Table 10).

BUOYANCY STATE AT SURFACE

Emersed body volume (V_e) as % of total body volume (V_b) during a surfacing bout ranged from 0.5 % when only the anterior tip of a turtle's head was out of water and the submerged body was at ~ 45^o angle to the surface of the water, to 5.4-6.1 % when most of the head and the superior part of the carapace were emersed with the body parallel to the surface. To emerse such a body volume, lung volume must be increased by 2.8-35.1 % of that necessary to provide neutral buoyancy (Table 11) which in turn, represented an increase of 0.5 to 7.0 % over the body volume (V_b) at neutral buoyancy (Table 11). The difference in additional lung volume between minimum and maximum emersed body volume varied from 5.9-6.8 % of body volume among turtles.

The lift provided by the increased lung volume during the state of positive buoyancy supported 103-135 % of the body mass in water (Table 12).

Table 10. Body density (Db) of turtles containing average food/fluid content.

Parameter	Turtle B	Turtle C	Turtle H
Body Weight (min) ----- % (max)	96.38	96.09	93.42
Tissue Density ($g \cdot ml^{-1}$)	1.2035	1.1912	1.2137
Weight Food/Fluid W_b (max) %	3.62	3.91	6.58
Body Density with H_2O ($g \cdot ml^{-1}$)	1.1962	1.1837	1.1996
Body Density with food ($g \cdot ml^{-1}$)	1.1983	1.1858	1.2034

Table 11. Estimated buoyancy ($ml \cdot g^{-1}$) at surface. Emersed body volume was measured on turtles A and C, and extrapolated to turtles B and H.

Turtle	Weight of Emersed Body (g)		Buoyancy at Surface ($ml \cdot g^{-2}$)		Emersed Body Volume / Total Body Volume	
	min	max	min	max	min	max
A	3.6	42.9	1.0295	1.3514	0.62	7.42
C	4.4	51.7	1.0282	1.3308	0.54	6.40
B	3.6	42.1	1.0285	1.3339	0.60	6.96
H	3.3	37.7	1.0284	1.3247	0.61	7.00

Table 12. Average buoyancy ($ml \cdot g^{-1}$) at various steps during a dive, estimated from lung volume and submerged weight during dives, and emersed body volume at surface for 4 turtles.

Buoyancy ($ml \cdot g^{-1}$)	Turtle A	B	C	H
At Surface	1.0295-1.3514	1.0285-1.3339	1.0282-1.3308	1.0284-1.3247
At Onset of Dive at Surface	-	1.0155	0.9820	0.9945
At Onset of Dive at Bottom	-	0.9672	0.9355	0.9450
At End of Dive at Bottom	-	0.9317	0.8860	0.8985
During Final Phase of Ascent	-	0.9782	0.9302	0.9456

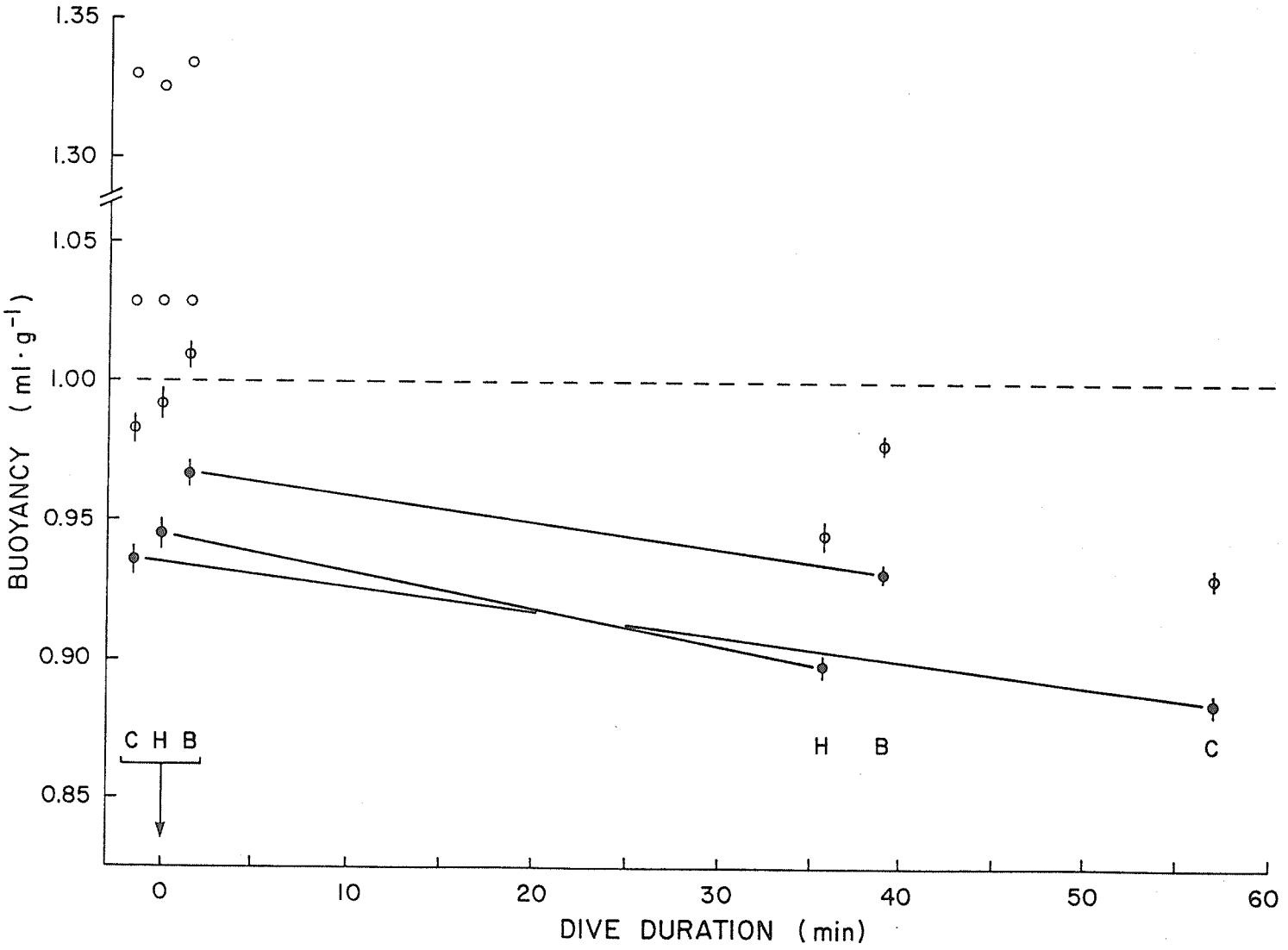
BUOYANCY STATE DURING DIVES

At the start of a dive, immediately after complete submergence, buoyancy averaged 0.9982 ml · g^{-1} (n=25; SD= ± 0.0325; range:0.9137-1.0370) for 3 turtles, creating a near neutral buoyancy. Buoyancy was similar among turtles (ANOVA: $F_{2,22}$=2.14; p > 0.10) and between sexes (ANOVA: $F_{1,23}$=2.05; p > 0.10) with averages for both males (1.0033) slightly greater than that of the female (0.9820) (Fig 4). During descent, hydrostatic pressure resulted in negative buoyancy. Upon reaching bottom (51.5 cm deep), buoyancy was reduced to a mean of 0.9500 ml · g^{-1} (n=25; SD= ± 0.0310; range:0.8680-0.9850) for three turtles (Table 12, Fig 4). There was no relationship between buoyancy at start of the dive and dive duration (p > 0.80; r=0.0316). Increase in submerged weight (W_S) presumably due to gas loss from lungs, averaged 0.18 ml·kg^{-1}·min^{-1} (n=25; SD= ± 0.10; range: 0.07-0.44) and was deemed similar among turtles (ANOVA: $F_{2,22}$=2.53; p > 0.10) and between sexes (ANOVA: $F_{1,23}$=1.44; p > 0.10) (Table 13). There was no correlation between rate of gas loss and number of days since last meal (p > 0.10;r=0.2119). Total gas loss at end of dive averaged 7.46 ml·kg^{-1} (n=18), ranging from 1.19 to 16.16 ml·kg^{-1} for dives lasting 11 to 75 min. At completion of a dive, buoyancy at depth averaged 0.9061 ml·g^{-1} (n=25;SD= ± 0.0335; range=0.8282-0.9751) (Table 12, Fig 4). Total gas loss increased with length of submergence, causing buoyancy to decrease gradually with dive duration. Buoyancy at surface just before a breath averaged 0.9523 ml·g^{-1} (n=25; SD= ± 0.0350; range: 0.8716-

Table 13. Average rate of gas loss ($ml \cdot kg^{-1} \cdot min^{-1}$) for individual turtles, by sex, for the group, estimated from submerged weight during dives.

	Gas Loss ($ml \cdot kg^{-1} \cdot min^{-1}$)		
	B ♂	H ♂	C ♀
Per Individual	0.15 (8)	0.23 (11)	0.14 (6)
By Sex	0.20 (19)		0.14 (6)
$\tilde{X}$	0.18 (25)		

Figure 4. Profile of average buoyancy state ($ml \cdot g^{-1}$) at various stages of a dive for turtles C, H, B. Average dive range was B: 28.5-49.5 min (n=8) ; C: 42.0-72.0 min (n=6) ; H: 20.0-51.5 min (n=11).


1.35
1.30
1.05
1.00
0.95
0.90
0.85
BUOYANCY (ml · g⁻¹)
C H B
H B
C
0
10
20
30
40
50
60
DIVE DURATION (min)

1.0239) (Table 12, Fig 4). Significant differences in buoyancy at the surface prior to onset of ventilatory cycle were found between turtles B and C (ANOVA: $F_{2,22}=4.91$; $p < 0.025$).

NON-PULMONARY O_2 and CO_2 EXCHANGE IN WATER

Uptake of dissolved O_2 from the water averaged 2.86 $ml \cdot kg^{-1} \cdot h^{-1}$ (n=20; SD= ± 1.71; range:0.00-6.72) (Table 14A). Dissolved O_2 uptake was similar among turtles (ANOVA: $F_{3,16}=0.48$; $p > 0.70$) and between sexes (ANOVA: $F_{1,18}=0.02$; $p > 0.80$). Mass-specific O_2 uptake did not vary with body weight ($p > 0.70$; $r=0.0728$).

Dissolved CO_2 output to the water by means of non-pulmonary gas exchange averaged 12.75 $ml \cdot kg^{-1} \cdot h^{-1}$ (n=19; SD= ± 3.39; range:5.20-18.10) (Table 14B). Dissolved CO_2 output was similar among turtles (ANOVA: $F_{3,15}=3.23$; $p > 0.05$) and between sexes (ANOVA: $F_{1,17}=0.37$; $p > 0.50$). As in dissolved O_2 uptake, mass-specific dissolved CO_2 output did not vary with turtles' body weight ($p > 0.90$; $r=0.0089$).

Comparison between CO_2 output to water in this experiment and gas loss during assessment of buoyancy during submergence revealed no significant differences (ANOVA: $F_{1,42}=1.19$; $p > 0.20$). Output of CO_2 to water averaged 12.75 $ml \cdot kg^{-1} \cdot h^{-1}$ and gas loss during a voluntary dive averaged 11.04 $ml \cdot kg^{-1} \cdot h^{-1}$ (n=25; SD= ± 6.15; range:4.00-27.00).

Table 14. Average rate of dissolved O_2 uptake ($ml \cdot kg^{-1} \cdot h^{-1}$) for 4 individual turtles (n=5), by sex, and for the group (A), and average rate of dissolved CO_2 output ($ml \cdot kg^{-1} \cdot h^{-1}$) for 4 individual turtles (n=5), by sex and for the group (B).

A

O_2 Uptake ($ml \cdot kg^{-1} \cdot h^{-1}$)	Turtle B ♂	E ♂	C ♀	I ♀
Per Individual	3.57	2.26	2.94	2.66
By Sex	2.92		2.80	
$\bar{X}$	2.86			

B

CO_2 Output ($ml \cdot kg^{-1} \cdot h^{-1}$)	Turtle B ♂	E ♂	C ♀	I ♀
Per Individual	16.50	10.66	12.60	11.98
By Sex	13.26		12.29	
$\bar{X}$	12.75			

DISCUSSION

OBSERVATIONS ON AQUATIC LOCOMOTION AND RESTING BEHAVIOR

Aquatic reptiles such as turtles and crocodilians all need to come out on land at some point of their diel or seasonal cycle to nest, bask, and travel. Upon entering the aquatic milieu, they are required to maneuver in the vertical water column to feed, rest, travel, bask, and copulate. To species such as D. coriacea, which is known to dive to depth of 475 m in a matter of minutes (Eckert et al. 1986), exposure to abrupt changes in environmental conditions add to the physical cost of accomplishing such a dive. Although D. coriacea probably represents an extreme case in reptilian terms, it demonstrates the need for those animals which exploit the vertical water column to lessen the cost of diving through buoyancy control. Although this need has been readily and frequently acknowledged (Zug 1971, Seymour 1982) and buoyancy control mechanisms have been studied in several reptiles (Jackson 1969,1971, Milson 1974, Kirshner 1985, Graham et al. 1987), few investigations have associated buoyancy control to the specific needs of reptiles in the field (Rubinoff et al. 1986, Graham et al. 1987, chapter 1). A handful of studies on the topic have attested to the ability of several reptiles to regulate buoyancy in a laboratory setting (Jackson 1969, Milson 1974, Milson and Johansen 1975, Kirshner 1985, Graham et

al. 1975,1987) or to the gradual attainment of its control during development (Davenport and Clough 1986). Observations of aquatic locomotion and activities in this study have revealed C. p. bellii to surface, rest at the bottom, and navigate about in the water column with minimal effort, suggesting that buoyancy control is an important aspect of their aquatic life. This has been further substantiated by evidence of their ability to dive repeatedly in relatively deep water, to emerse for various periods of time and to submerge and rest on the substrate for hours at a time in a semi-natural environment (chapter 1).

Despite peculiar respiratory characteristics and the role of lungs in both respiration and buoyancy control in aquatic reptiles, few studies have centered on this topic and only basic respiratory control mechanisms have been described. Upon returning to the surface after a dive, all turtles, and crocodiles initiate a ventilatory cycle with an expiration (Gaunt and Gans 1969, Tenney et al. 1974, Glass et al. 1978, Milson and Jones 1980, Kirshner 1985). Although ventilation is termed triphasic in these animals (Gaunt and Gans 1969, Milsom 1974), the cycle ends at the inspiratory phase prior to apnea (Tenney et al. 1974, Glass et al. 1978, Milson and Jones 1980, Kirshner 1985) and terminates with an expiration only immediately prior to submergence (Kirshner 1985). Such ventilatory sequences interspersed by apneic periods of varied duration translate into "bobbing" body movements and stationary phases observable in surfacing animals (Belkin 1964, Gaunt and Gans 1969, present study). Also noticeable is the expansion-contraction of

the flank area, mainly around the hindlimbs. Such movements are caused by changes in internal pressure associated with breathing phases (Gaunt and Gans 1969). On land, all phases of the breathing cycle are active in turtles (Gaunt and Gans 1969, Milson 1974, Tenney et al. 1974), being regulated by groups of muscles associated with the viscera and the pectoral and pelvic girdles, capable of varying the volume of the visceral cavity, and in turn causing lung volume changes (Gaunt and Gans 1969). In water, turtles take advantage of the hydrostatic pressure to exhale passively at surface (Gaunt and Gans 1969, Tenney et al. 1974).

A dive was initiated from an expiratory position (Fig 1B), the turtle engaging in specific steps to perform a successful descent. Despite the particular process involved, the phenomena has not been described previously in turtles. Interestingly, an account of diving behavior in Crocodylus porosus by Kirshner (1985) revealed sequences of events strikingly similar to those observed in C. p. bellii. Kirshner (1985) noted that extending the webbing and swinging both hindlimbs anteriorly allowed C. porosus to submerge with little effort. In shallow water, the animal reached the bottom tail first but in deeper water, it often changed direction mid-water and descended head first. Chrysemys picta bellii consistently completed a dive head first, after pivoting forward in mid-water. The advantages resulting from such sequence of events are unclear, but it could allow a turtle to leave the surface with a minimum of disturbance reducing both attention by predators and

disturbances to prey. The initial caudal propulsion and the need for directionality later during the dive favor this progression and failure to follow such pattern implied a requirement for active swimming to reach the bottom of the tank, with turtles obviously struggling against a positively buoyant state. Return to the surface to release lung gas (Milson 1974) ensued and attempts to descend were repeated until the proper steps were accomplished. In the field (chapter 1), onset of submergence was markedly different, with a dive being initiated from an inspiratory position, the turtle propelling forward and down. This pattern was observed during feeding events and might be justified by the active state of the animal once submerged. Precise buoyancy control at depth observed in the laboratory would be more important during submerged resting than feeding dives in nature. If frightened, a turtle propelled itself forward and down, swimming vigorously. Gas bubbles, which were never released during normal descents, possibly due to reflex closure of the glottis upon submergence (Milson 1974), were expelled on the way down as also observed by Milson (1974) and Kirshner (1985). This helped decrease buoyancy since frightened turtles successfully remained at the bottom upon descent. In addition, severe bradycardia (Belkin 1964, Seymour 1982), increased peripheral resistance, muscle ischemia, anaerobic metabolism (Seymour 1982) and decreased gular movements (Girgis 1961) known to occur during forced or fright dives facilitated lengthy submergence.

The ease with which they maneuvered over the substrate attest to

the ability of turtles to regulate buoyancy prior to submergence. Such control allowed turtles to bottom-walk faster and much more efficiently than they could in a terrestrial situation (Zug 1971). As turtles settled on the substrate, the cranial or caudal end of their body frequently tilted upwards and usually remained in that position for a few minutes. The mechanisms involved in this event, or its role, if any, have not been documented, but several hypotheses can be examined. First, muscles involved in respiration also contribute to locomotion, but their action during respiratory pauses have no effect on lung volume (Milson 1974). Instead, the striatum pulmonale surrounding lungs of aquatic and semi-aquatic turtles is believed to (1), control lung volume during apnea (Carlson and Luckhardt 1920, Milson 1974), (2), to regulate buoyancy (Milson and Johansen 1975, Perry 1978), and (3), control the orientation of a reptile in water by shifting gas between pulmonary compartments (Seymour 1982) and changing the centre of lift. In fact, lung contractions are known to be powered by smooth muscles under the control of the vagus nerve (Carlson and Luckhardt 1920). Since smooth muscles regulate lung volume at onset of dive (Milson 1974), and the posterior region of the lungs contain a significant portion of the gas volume (Spragg et al. 1980, Kirshner 1985), relaxation of smooth muscles to fine tune buoyancy at depth might act to expand the posterior areas of the lungs, resulting in a tilting up of the caudal end of the body. Contractions of smooth muscles in the posterior regions of the lungs and/or relaxation of the latter in the anterior regions would shift gas from posterior areas to more highly alveolized and vas-

cularized anterior areas (Spragg et al. 1980), causing the cranial end of the body to rise momentarily. Secondly, Jackson (1969) suggested that freshwater turtles compensate for lung volume changes by altering stored water volume in cloacal or urinary bladders. Such compensation is required because of the restriction imposed by the shell on body volume. Such compensation promotes internal pressure stability (Jackson 1971). Although some turtles are known to exchange gas by ventilating cloacal sacs when swimming (Seymour 1982), it is unlikely that short-term volume compensation using this method is necessary for internal pressure stability since sea turtles, which do not possess cloacal sacs (Milson 1974), undergo dramatic lung volume changes when diving and breathing (Tenney et al. 1974, Jackson 1985). Urine production, which has been proposed as an alternate volume compensating method (Jackson 1971), is not known to increase during artificial lung volume disturbance in sea turtles (Milson 1974). Chrysemys scripta, which ventilates cloacal sacs when breathing air, is found to stop such ventilation when confined under water (Belkin 1968). Furthermore, mechanical increase in lung volume by as much as 1000 ml in Caretta caretta caretta (b.w. 1000 g) did not significantly alter position of limbs or girdles but was all accomodated for by expansion of flank areas (Milson 1974). Thus, it is unlikely that adjustment of buoyancy by alteration of stored water volume upon descent caused observed shifts in body positions.

In aquatic reptiles, reduction in lung volume is demonstrated to

occur during submergence (Kirshner 1985, Graham et al. 1987, present study). Although both thoracic and abdominal volumes show a decline during submergence in C. porosus (Kirshner 1985), intrapulmonary and visceral pressure were stable throughout quiet dives in C. porosus (Kirshner 1985) and C. picta (Milson 1974). Striatum pulmonale muscle is believed to maintain intrapulmonary pressure constant during a dive (Milson 1974). Observations of progressive limb retraction under the carapace during submerged rest in this study suggests that turtles passively maintain internal body pressure by slow and constant reduction in body volume.

After greatly varying dive periods, turtles prepared to surface, in as an established pattern as that involved during descent. Again, the procedure is very similar to that described for C. porosus (Kirshner 1985). In C. porosus, the tracheal pressure showed a tendency to increase prior to ascent, denoting a slight compression of the lungs. On the contrary, tracheal pressure decreased in both C. c. caretta and C. picta prior to ascent, perhaps representing an attempt to increase lung volume to assist in ascent (Milson 1974). Belkin (1964), Burggren (1975), and Shelton and Burggren (1976) also demonstrated the movements of the body and head prior to ventilation to cause heart rate and stroke volume to increase in C. scripta. It is likely that extension of the limbs observed in C. p. bellii expanded the lungs, decreasing specific gravity facilitating ascent. Despite this possibility, increased specific gravity caused by a reduced lung volume necessitated

vigorous swimming for the turtle to reach the surface, especially after lengthy dives. After exhaling at the surface, turtles became positively buoyant during the first inspiration. In the laboratory, ascent after a long period of submergence was the only aquatic locomotory activity observed to necessitate great energy output.

Although there are no other known reports of gregarious behavior in submerged trutles in natural or laboratory situations, large groups of turtles have been observed to bask in proximity to one another. Carpenter (1957) found groups of Terrapene ornata ornata and Kinosternon flavescens flavescens to mutually occupy hibernacula, and an aggregation of up to 300 hibernating C. p. picta was found in a small river in southern Quebec (R. Bider, pers. comm.). During the field study (chapter 1), gregariousness was not observed during feeding or traveling activities but was recorded during submerged resting, basking, and hibernation. The apparent synchronization of surfacing activity in the laboratory is most likely a response to disturbance caused by moving turtles.

DIVING CHARACTERISTICS IN NORMOXIC AND HYPOXIC AQUATIC CONDITIONS

In the experimental tank, undisturbed turtles usually settled at the bottom, motionless, and regularly surfaced to ventilate. Such behavior was reported for C. fimbriata (Lenfant et al. 1970) and Chrysemys concinna (Belkin 1964) under similar conditions. Activities while submerged were accomplished early in the dive and were slow-paced and brief. Since freshwater turtles surface prior to exhaustion of pulmonary and blood O_2 reserves, (Burggren and Shelton 1979), the voluntary dives performed during this experiment were assumed to be aerobic for the purpose of this discussion.

Chrysemys picta bellii in this experiment stayed submerged 85 % of the time, with dives ranging from a few seconds to periods sometimes > 1 h, with average dive estimated to be short (2-3 min). This agrees with voluntary dive durations reported for aquatic reptiles such as crocodilians (Andersen 1961, Kirshner 1985), water snakes (Irvine and Prange 1976, Rubinoff et al. 1986, Graham et al. 1987), sea turtles (Lutz and Bentley 1985, Eckert et al. 1986) and other freshwater species (Belkin 1964, Lenfant et al. 1970, Milson 1974, Burggren 1975, Glass et al. 1978, Ackerman and White 1979). The proportion of total time spent on inter-dive surface intervals by C. p. bellii in this study (15 %) is similar to that documented for the same subspecies elsewhere (Glass

et al. 1983) and for C. scripta and Testudo graeco (Burggren 1975), but is far less than that found for C. p. bellii feeding in the field (29 %) (chapter 1). Lower metabolic rate at rest or triggered by stress (fright dives), in voluntary dives or restrained animals during experimental procedures may explain the lower values (15 %) reported above. This is not to say that animals in the field necessarily have a higher overall cost attributed to respiratory activity. The proportion of time devoted to respiratory events during nocturnal submerged resting activities in the field, which dropped to as low as 2.1 % (chapter 1), would greatly reduce the overall daily average value. Feeding, which is probably the most costly activity routinely performed by turtles is then expected to have a high respiratory cost.

The inability to obtain aquatic O_2 caused voluntarily diving C. p. bellii to modify its diving strategy under hypoxic conditions in the present study. This was made evident by the tendency of turtles to submerge longer on average in normoxic than hypoxic conditions during 1 h periods (Table 2) and by the frequency distribution of total submergence time > 50 min to be consistently higher in normoxia (Table 5). It is possible that C. picta, which has lower metabolic demands in water than in air, both at rest and during activity (Stockard and Gatten 1983) can take advantage of available aquatic O_2 when submerged. The sea snake Lapemis hardwickii uses aquatic O2 and consistently shows partial right-to-left shunts, even with considerable O_2 in the lungs (Seymour and Webster 1975). The reduction in arterial

PO_2 would increase effective surface area for diffusive exchange and the partial pressure gradient across the skin would favor inward O_2 diffusion (Seymour and Webster 1975). Complete right-to-left shunt in freshwater turtles occurs only after lengthy dives (Millen et al. 1964), but blood is shunted away from pulmonary circulation as soon as 5 min after initiation of a dive (Shelton and Burggren 1976). Such partial shunt, as in L. hardwickii, would favor aquatic O_2 uptake in freshwater turtles. This is substantiated by the fact that although C. p. bellii survived for over 26 days when forcibly submerged in anoxic conditions at 10 C (Ultsch et al. 1984), temperature at which this species is still active and feeds in the field (chapter 1), its survival time was almost doubled in normoxia at similar water temperature (Ultsch et al. 1984, Ultsch 1985). Increased cutaneous O_2 uptake under favorable conditions may also explain the presence of high O_2 level remaining in lungs of aquatic reptiles at cessation of voluntary dives (Burggren and Shelton 1979). Aquatic O_2 uptake would also relieve the lungs of some of its respiratory functions, which would favor its role in buoyancy control. The reduction in lung volume, caused by buffering and/or cutaneous loss of CO_2 during submergence, would be slowed and the work required to swim to the surface, resulting from increased negative buoyancy, could be lessened.

Turtles in anoxia, which reduced total submergence time over 1 h periods, tended to be less active underwater, showed decreased frequency of surfacings and emersed for longer periods of time during

each surfacing bout, perhaps in an effort to lower the cost of aquatic locomotory activities. A greater proportion of submergence time and a higher frequency of total submergence time > 50 min, greater activity level, and more frequent surfacings for shorter duration displayed by turtles in normoxia suggests greater aquatic O2 uptake. The resulting increase in locomotory activity in normoxic water may have in turn indirectly promoted aquatic respiration. Seymour (1987) suggested that motion of submerged P. platurus favors cutaneous respiration by maintaining a maximum oxygen diffusion gradient. In both normoxia and hypoxia, males remained submerged for a greater proportion of a 1 h period than females. In normoxia, this trend resulted in males surfacing as often as females but the duration of surfacings was shorter. In hypoxia, males decreased the number of surfacing bouts but stayed longer at the surface on average, than females.

In general, mass-specific metabolic rate in reptiles is believed to decrease with body size, promoting increased duration in aerobic dives in larger divers (Seymour 1987). This was demonstrated in Weddell seals, Leptonychotes weddelli (Kooyman et al. 1983) and suggested for D. coriacea (Eckert et al. 1986) but is not supported by results obtained for C. p. bellii (chapter 1). In the field, males consistently performed longer dives, whether feeding or resting, than females. Mass-specific metabolism was shown to vary inversely to body size in C. porosus (Wright 1986 in Wright and Kirshner 1987), Chrysemys floridana (Kinney et al. 1977), resting Chelonia mydas (Prange and Jackson 1976),

and several squamates and chelonians (Gatten 1978) but was found not to vary in C. scripta between 10-30 C (Hutton et al. 1960), and resting juvenile (Davenport et al. 1982) and active adult C. mydas (Prange and Jackson 1976). In addition, since oxygen uptake varies with activity level (Prange and Jackson 1976), body temperature (Gatten 1974B, Prange and Jackson 1976), nutritional state (Davenport et al. 1982), and possibly photoperiod (Belkin 1964, Gatten 1974A), it is difficult to establish a general relationship between metabolic rate and body size in aquatic reptiles.

Mass-specific lung volume was reported to increase with size in both juvenile C. c. caretta (Milson 1975) and C. porosus (Kirshner 1985). However, it was shown to decrease in C. m. agassizii (Berkson 1966), C. s. elegans (Perry 1978), C. fimbriata (Lenfant et al. 1970), and C. porosus (Wright and Kirshner 1987) and not to vary with body size in C. p. bellii (present study). Only if mass-specific lung volume remained similar and metabolic rate decreased with increasing body size could larger turtles (females) dive for longer periods than smaller ones (males). In all other possible relationships between mass-specific metabolic rate, lung volume and body size, larger turtles would be expected to do worse than males, or at best to withstand similar diving duration on the basis of these two parameters alone. In addition, other physiological characteristics favor longer submergence time in smaller turtles. First, heart rate was found to slow down in larger C. floridana (Hutton et al. 1960, Kinney et al. 1977) and a correlation could not be

established between it and size or sex in C. concinna during breathing and diving (Belkin 1964). Secondly, Hutton (1961) found mass-specific blood volume to decrease in larger C. scripta but a correlation between blood volume and sex was not established for that species. Since mean blood pressure in pulmonary and systemic arteries was not related to body mass (Kinney et al. 1977), this suggests that blood, which is used to transport and not to store oxygen in turtles (Burggren and Shelton 1979), would deliver less O_2 to tissues per unit time in larger turtles. Lastly, since surface area to volume ratio decreases and skin thickness increases in larger reptiles, cutaneous gas exchange would be expected to decrease in larger reptiles (Seymour 1987). Accordingly, mass-specific aquatic O2 uptake was reduced in larger Trionyx spinifer asper (Dunson 1960) but did not vary with size or sex in C. p. bellii (present study). Considering all other factors discussed above, an equal or greater mass-specific aquatic O_2 uptake again suggests males to be capable of submerging for greater proportion of time than females. Results obtained in normoxic water in the present study support this hypothesis. That physiological differences other than aquatic oxygen uptake favor greater proportion of submergence time in males is further supported by similar observations in hypoxic conditions. In the field (chapter 1), it was suggested that development of follicles and eggs prior to oviposition could be partially responsible for shorter dive time and longer surfacing bout duration observed in females during both feeding and submerged resting activities. Reproductive activities were not observed in the laboratory and it is likely that confinement under

these conditions for such an extended period of time repressed development of follicles and eggs in females C. p. bellii. That mass-specific tissue density and lung volume in this species were not related to size or sex in the present study suggest that diving characteristics were not affected by abovementioned factors in the laboratory. On the other hand, physiological features believed to influence laboratory results may help explain sex-related differences observed in the field. That males were observed to surface for shorter periods of time in normoxia and less frequently in hypoxia suggest that physiological factors favoring greater proportion of time spent underwater in males may in turn contribute to further economy of energy by decreasing overall cost of ventilatory activity.

ASSESSMENT OF BUOYANCY

Lung volume and tissue density

Lung volume obtained by whole-body plethysmography at depth and adjusted to neutral buoyancy was 16.83 $ml \cdot 100g^{-1}$ in three live C.p.bellii (Table 8). Lung volume measured by plethysmography for the same species was 13.0 (Milson 1974) and 11.8 $ml \cdot 100g^{-1}$ (Milsom and Chan 1986) of body weight for animals "resting at the surface". In C.s.elegans, lung volume was reported to be 10-12 $ml \cdot 100g^{-1}$ for animals resting at depth (Jackson 1971). Measurement by gas dilution yielded a value of 16.0 $ml \cdot 100g^{-1}$ in the latter species resting in air (Crawford et al. 1976). Several explanations can be given for discrepancies between results obtained in the present study and those reported elsewhere for similar species. First, lung volumes in the present experiment were measured from animals resting at depth but were reported as adjusted for neutral buoyancy for standardization. Depending on the animal and its initial diving lung volume, and time elapsed since start of dive, the submerged weight at time of measurement can vary dramatically (from 5.38 to 28.93 g in this case). Since 1 ml of lung gas will support 1 g of tissue under water, adjustment for neutral buoyancy (W_s=0g) according to $W_s=W_b-(V_b+V_l)$, will result in a lung volume greater than that obtained at time of measurement. Jackson (1971), who reported resting lung volumes at depth did not account for submerged weight of the turtle at moment of measurement. This omission necessarily resul-

ted in size-specific lung volume smaller than those presented here. For example, turtle C in which a lung volume 17.47 $ml \cdot 100g^{-1}$ of body weight was reported in one instance (Table 8), had a true V_l of 139.44 ml at depth, and a submerged weight of 28.93 g. With a body weight of 963.85 g, lung volume would have been 14.47 $ml \cdot 100\ g^{-1}$ of body weight, a full 3 $ml \cdot 100g^{-1}$ less than that reported after correction. Overall, lung volume averaged 14.90 $ml \cdot 100g^{-1}$ before correction. Secondly, results reported by Milsom (1974) for C.picta were taken for animals between 700-1500 g floating at surface. In the present study, 89 % (8/9) of females weighed over 700 g (Table 1). It is likely then that the majority of turtles described by Milson (1974) were females and if lung volume at surface were made during follicle and/or egg development, their lung volume at surface could have been reduced by (1), space for lung volume being restricted by follicles/eggs, and (2), the reduced requirement for large lung volume to achieve neutral or positive buoyancy due to decreased tissue density. Similarly, turtles used by Jackson (1969), which were all females, would have been required to reduce lung volume further to rest at depth. In the present study, lung volume measurement obtained from one female did not noticeably differ from that of males but was nevertheless smaller in the former. Measurements must be done on larger sample size before conclusions can be drawn. Thirdly, behavior at time of capture may have affected results. In this experiment, turtles were placed in the plethysmograph following relatively long dives. Manipulation of the animals may have triggered lung expansion as in preparation for ascent

(Milson 1974). This is supported by the fact that once in the chamber, turtles tended to rise upwards and their movements had to be restricted during measurements. Expansion of lungs would have resulted in volume measurement that was greater than that at the moment prior to capture and extrapolated submerged weight corresponding to time of capture would have been greater than that at time of lung measurement, both of which would act to increase the obtained values. Lastly, but perhaps most importantly, the proportion of lung volume was estimated over minimum body weight obtained from individual animals over 10 consecutive days. The difference between minimum and maximum body weight measured over a short period of time would represent stored water or waste. If the latter was incorporated, it would falsify estimation of tissue density which was needed for buoyancy measurements, since water and waste have a much lower density than the tissues of turtles. To standardize calculations, minimum body weight was used throughout. If stored water was present during lung measurements, it would have increased its dry body weight but not affected its submerged weight and since minimum body weight was used, resulted again in an overestimation of lung volume. Standardization of experimental procedures and calculations should allow comparison of lung volume among and between species in the future.

Despite noticeable discrepancies in lung volume measurements reported by various authors, it is obvious that C. picta and C. s. elegans possess large lung volume in comparison to other species of

aquatic reptiles. For example, Kirshner (1985) reported lung volumes ranging from 5.0 to 9.2 $ml \cdot 100g^{-1}$ body weight in juvenile C. c. caretta and Berkson (1966), an average of 10.1 $ml \cdot 100g^{-1}$ in C. m. agassizii. Kirshner (1985) showed adult C. porosus to have lung volumes of 4.57 $ml \cdot 100g^{-1}$ at depth and Andersen (1961) determined them to be between 7.6 and 10.2 $ml \cdot 100g^{-1}$ in 2 Alligator mississippiensis. Even C. fimbriata, a sluggish bottom-dwelling freshwater turtle was shown to have a lung volume of only 6.82 $ml \cdot 100g^{-1}$ of body weight (Lenfant et al. 1970). It is clear that the capacity for a large lung volume represents great advantages for diving freshwater turtles. Coupled with a high tissue density, not only does it permit a greater O_2 storage, which favors long submergence time, but it allows them to do so without negative consequences to buoyancy control. In fact, freshwater turtles are reported to have the greatest tissue density of all aquatic reptiles, with values ranging from 1.1494 $g \cdot ml^{-1}$ for C. picta (Milson 1974) to 1.1628 $g \cdot ml^{-1}$ in C. s. elegans (Jackson 1971). Tissue density (D_t) in the present study averaged 1.2027 $g \cdot ml^{-1}$ for three live C. p. bellii (Table 8) and 1.1853 $g \cdot ml^{-1}$ for 2 dead females found in the field (Table 8). Overestimation of tissue density in live turtles could result from abovementioned procedures which likely caused increase lung volume measurement in the present study. However, these factors could not have influenced results obtained from dead animals since (1), these turtles could not vary lung volume in response to manipulation, (2), dry body weight, which was measured prior to and after lung volume measurememts, did not change, (3), submerged weight in this case coin-

cided with value at time of lung measurement. The effect of possible partial decomposition and freezing, added to the fact that the two animals were large females, which were both at an advance stage of follicle development, as shown upon dissection, could explain the lower tissue density of the dead turtles. In addition, the latter fact offers evidence to justify and support reasons given above for smaller lung volumes and lower tissue density obtained by Milson (1974) and Jackson (1971).

As for Kirshner (1985), with C. porosus, estimation of body volume from direct measurement of body weight both dry and submerged, and lung volume yielded values strongly correlated to dry body weight (Fig 3). Such method will prove indispensable when body volume is required since the latter is difficult to measure in animals, such as aquatic reptiles, which can vary lung volume to such great extent in response to stress, experimental manipulation or buoyancy control.

Assessment of food and fluid volume in gastrointestinal tract and cloacal bladders

Food and/or fluids occupied 1.3 to 9.2 % of minimum body volume in C. p. bellii. These values were very similar to those obtained for C. s. elegans by Perry (1978)), who also used minimum body weight for standardization. Ingestion or expulsion of food or fluids resulted in

individual lung measurements varying by 1.5 $ml \cdot 100g^{-1}$ body weight in C. s. elegans with one specimen showing an increase in value from 15.6 to 20.0 $ml \cdot 100g^{-1}$ after emptying its cloaca (Crawford et al. 1976). Jackson (1971) estimated stored fluid volume to vary inversely with resting lung volume in C. s. elegans, with a total combined volume approximating 20 $ml \cdot 100g^{-1}$. Since turtles with lung volume < 6 $ml \cdot 100g^{-1}$ did not compensate any further, 14 $ml \cdot 100g^{-1}$ was deemed the upper limit of stored fluid in that species (Jackson 1971). This value is greater than those obtained in the present study, suggesting that turtles probably expel fluid or feces before reaching such limit since not doing so could limit space for lung volume expansion, impeding O_2 storage and buoyancy control. Jackson (1971) concluded that maintenance of total body volume by adjusting stored fluid volume compensation was probably necessary to control pulmonary pressure with no muscular effort.

That males displayed a greater proportion of stored food/fluid volume may suggest an increased capacity to do so, perhaps due to a greater size-specific intestinal length in smaller turtles, as shown in Parmenter (1981), or larger size-specific urinary or cloacal bladders. Storage volume restriction is also likely imposed by the presence of larger reproductive organs in females. Since it is unlikely that females in the laboratory developed follicles and eggs, it can be assumed that the volume taken up by reproductive organ would correspond to the difference in food/fluid volume between sexes (2.4-

2.9%). In such case, compensation in body volume was probably accommodated for by expansion in flank areas (Milson 1974), and lung volume was probably not affected.

The density of water (1.00 $g \cdot ml^{-1}$) and food (1.06 $g \cdot ml^{-1}$) was lower than tissue (1.2027 $g \cdot ml^{-1}$) in turtles, and the inclusion of food/fluid resulted in a decrease in overall body density. Buoyancy state at depth would decrease significantly only if an increase in stored food/fluid volume was compensated for by a reduction in lung volume, but since turtles seem capable of accommodating large changes in internal volume (Milson 1974), this is unlikely. If stored food/fluid volume alone does not affect buoyancy, it could do so in cooperation with respiratory muscles. Ingestion or expulsion of fluids would result in lung volume compression or expansion if assisted by muscles to maintain overall internal pressure. Expulsion of cloacal content prior to ascent would result in lung volume expansion which would facilitate surfacing, especially after long quiet dives such as in submerged resting activities in the field. Lung volume was observed to decrease over time underwater and retraction of the limbs under the carapace is proposed as a means of maintaining intrapulmonary pressure. During long dives, stored fluids would provide hydrostatic support against which respiratory muscles and/or limbs could press on. It may also explain "yawning" observed in turtles resting at a ~45 angle at depth. Ingestion of water could be used in the manner described above to contract lung volume and allow turtle to rest parallel to substrate. The

role of stored fluids in maintenance of intrapulmonary pressure was demonstrated by Jackson (1971) in C. s. elegans, but more work is needed to explain the function of fluid storage, if any, in buoyancy control.

Buoyancy state at surface

Upon surfacing, turtles rapidly became positively buoyant, as made evident by their ability to emerse body parts and remain completely motionless. As described previously, the angle at which they floated varied with ventilatory phases, causing the body to bob up and down during breathing periods. Shifts in centre of buoyancy caused by alteration of lung volume during ventilation was found to be responsible for variation in floating angle in C. porosus (Kirshner 1985). The ability to control lung volume at the end of a ventilatory cycle is thought to be adaptive in the field for it would allow the animal to breath with a minimal portion of its body emersed, and to avoid predator detection. Such positioning was observed in C. concinna (Belkin 1964), and C. porosus (Kirshner 1985). At surface, the observed emersed body volume in C. p. bellii in the present study ranged from 0.5 to 6.1 % of total body volume with turtles usually floating at an angle during apneic periods, and being fully horizontal only during the first few inspiratory phases. The 35 % increase in lung volume necessary to accomplish full horizontal position is not unparallelled in

aquatic reptiles. Crocodylus porosus was shown to inflate its lung volume to 121.7 $ml \cdot kg^{-1}$ in horizontal position, representing an increase of 68 % over lung volume at neutral buoyancy for a 1 kg animal (Kirshner 1985). In C. c. caretta, a 2.4 % increase in body weight prompted the turtle to compensate by inflating its lung volume by 34.9 % (Milson 1974), and C. s. elegans increased its lung volume by over 20 % (Jackson 1969) and 57 % (Jackson 1971) that of neutral buoyancy when specific gravity was experimentally altered. The high compliance of lungs in turtles (Jackson 1971, Milson 1974) and a maximum volume estimated at over 26 $ml \cdot 100g^{-1}$ body weight in a 1 kg animal of a similar species (Perry 1978), certainly grants C. p. bellii the physical ability to undergo such expansion in lung volume. It is obvious that despite a rigid outershell, large changes in internal body volume can be accommodated by the laxity of the flank area. Interestingly, the change in body volume between minimum and maximum lung inflation during ventilation (5.9-6.8 %) closely corresponded to the previously calculated variability in body volume between minimum and maximum gastrointestinal/urinary/cloacal content (7.5-7.8 %). This supports the hypothesis brought forward by Jackson (1971) that maintenance of intrapulmonary pressure be accomplished by a change in stored fluid volume counterbalancing lung volume alteration. In fact, cloacal ventilation during air breathing was observed in C. scripta (Belkin 1968). Although maximal lung inflation at the surface augments conspicuousness in the field, it prompts an increase in number of breaths per breathing bout (Milsom and Chan 1986), which would be an

efficient way to expel CO_2 and to replenish O_2 stores early at the onset of a ventilatory episode. It would also favor non-pulmonary O_2 uptake by maximizing volumes of water being pumped in and out of the cloaca.

Buoyancy state during dives

Prior to submergence, the posterior portion of the body was at ~45 ^{o} angle to the surface of the water (Fig 1B) with only a small portion of the head still emersed. If this corresponded to the minimum emersed body volume previously found (0.5 % of body volume), lung volume still provided enough lift to maintain positive buoyancy (1.03 $ml \cdot g^{-1}$). This value closely corresponded to that found to be the maximum buoyancy state from which a turtle would initiate a dive (1.037 $ml \cdot g^{-1}$). However, the average buoyancy value was closer to 1.00 $ml \cdot g^{-1}$, which made turtles neutrally buoyant at onset of submergence. This state was attained by turtles expelling lung air at the end of the last ventilatory phase, exhalation which was of greater magnitude than those during normal ventilation (Kirshner 1985). This mechanism was also used by sea turtles (Milson 1974) and crocodilians (Kirshner 1985). After a last exhalation, the resulting lung volume is thought to be maintained by the contraction of striatum pulmonale, and reflex closure of the glottis (Milson 1974, Kirshner 1985). On the contrary, P. platurus inhaled prior to diving and dove with lung volume large enough to support twice its weight in water. A limited ascent occurred imme-

diately after maximum depth was reached, which was thought to position the snake in the water column at a depth resulting in neutral buoyancy at that moment (Graham et al. 1987). Although descent would be accomplished against positive buoyancy state, it would provide P. platurus with a large O_2 store, favoring a long submergence time. A more precise control would be needed for a diver to attain a specific depth with minimal energy expenditure both during descent and after reaching its selected position. Ideally, divers such as aquatic reptiles would benefit most if they could regulate pre-submergence lung volume to arrive at the desired depth in a state of neutral buoyancy. Hydrostatic pressure would act to lessen energy required to descend, and at depth, the diver could maneuver horizontally with the weight of the body in water completely supported by lung air. This strategy would provide the animal with a pulmonary O_2 store larger than if it initiated a dive at neutral buoyancy. These advantages would only be conferred if divers descended to a specific known depth, since variability of the latter would involve energy expenditure which would reduce or negate the benefits. Apparently, sea turtles and crocodilians do not exploit this strategy, and neither does C. p. bellii, which reached the bottom of the tank at a buoyancy averaging 0.95 $ml \cdot g^{-1}$. Since most aquatic reptiles initiating a dive probably cannot predict the depth at destination, it is obvious that the practicality of such strategy is doubtful. This is supported by the observed variation in depth between consecutive dives for D. coriacea (Eckert et al. 1986) in the field, and the fact that C. porosus inhabits areas in which water

levels is constantly being modified by tidal action (Kirshner 1985). It would be an advantage for C. p. bellii, which showed stability in its choice of foraging areas and displayed site fidelity for nocturnal activities in the field (chapter 1), to exploit such strategy and this phenomena was expected to occur in the laboratory, where turtles were confined to a tank with a stable water level prior to onset of buoyancy experiments. That turtles initiated a dive at neutral buoyancy instead may indicate that the certainty of arriving at depth negatively buoyant is preferable to the possible cost resulting from a lack of precise control. However, turtles recently placed in the tank prior to experiments underwent adjustment periods lasting from several minutes to a few hours, during which they dove with lung volume too large to achieve neutral buoyancy at depth. Since water level was greater in the experimental than in the holding tank, the lung volume with which they initiated a dive in the holding tank would have resulted in an increase in negative buoyancy at depth, if maintained. The reason for an increase in lung volume when first introduced in the experimental tank is not clear. A larger lung volume would increase O2 storage and still result in neutral/negative buoyancy at depth in such case. Alteration in lung volume in new situation strongly suggests that turtles regulate buoyancy. This is substantiated by the occurrence of "buoyancy adjustment dives" in the field (chapter 1). Foraging turtles were previously reported to initiate a feeding dive from an inspiratory position, phenomena which resulted in failure to achieve neutral buoyancy at depth in the laboratory. Since turtles fed

on or near the substrate, usually at depth > 3 m, it is likely that the energy required to offset positive buoyancy during descent was minimal compared to the benefits offered by a greater O_2 store during periods of considerable activity level.

In addition to a reduction in pulmonary O_2 store, negative buoyancy at depth is further enhanced by a decreasing lung volume resulting from the removal of CO_2 from the lungs, which is a common process in aquatic reptiles (Andersen 1961, Graham et al.1975, Jackson 1976, Jackson et al. 1976, Ackerman and White 1979, Glass and Johansen 1979, Feder and Burggren 1985, Kirshner 1985, present study). The rate of increase in submerged weight resulting from such a phenomena averaged 0.18 $ml \cdot kg^{-1} \cdot min^{-1}$ in C. p. bellii, a value which is lower than that calculated for C. porosus (0.32 $ml \cdot kg^{-1} \cdot min^{-1}$) (Kirshner 1985), but within ranges of gas loss estimated for P. platurus (0.07-0.43 $ml \cdot kg^{-1} \cdot min^{-1}$) (Graham et al. 1987). Contrary to C. porosus, in which rate of gas loss increased with body weight, and mass-specific rate decreased with weight, there was no relationship between these parameters in C. p. bellii, the largest and smallest turtles having a similar average rate of gas loss. There was also no correlation between rate of gas loss and time elapsed since last feeding in the present study. This would be expected since metabolic rate which was shown to dramatically increase after a meal in C. mydas, required 5 days to decline to pre-meal values (Davenport et al. 1982). However, individual C. p. bellii displayed similar rates of gas loss between dives performed on a same

day. Total gas loss was directly related to apneic duration in C. scripta (Ackerman and White 1979) and C. porosus (Kirshner 1985). This was also true in the present study, although the largest gas loss did not necessarily correspond to the longest dive. This is explained by the great variability in rate of gas loss between turtles and between dives. That the largest turtle (C) had the longest average dive and the smallest (H) performed the shortest average dive, and that both had a similarly high rate of gas loss (Fig 4) suggest that perhaps gas loss (CO_2 removal) gradually increased with increased total pulmonary O_2 uptake or that the largest turtle suffered the greatest decline in pulmonary O_2 as a consequence of longer dives. The latter is a more likely situation since metabolic rate is known to slow down during a dive (Andersen 1961) and rate of gas loss is observed to do the same (Kirshner 1985), suggesting that the rate of gas loss is directly related to the metabolic rate. Assuming O_2 level in the lungs to be 17 % at the start of a dive (Andersen 1961, Stockard and Gatten 1983), and a resting metabolic rate at 25 C between 0.15 $ml \cdot kg^{-1} \cdot min^{-1}$ (Stockard and Gatten 1983) and 0.33 $ml \cdot kg^{-1} \cdot min^{-1}$ (Gatten 1974B), turtle C would have 27-67 % O_2 left in the lungs after a 57 min dive. Since Belkin (1964) concluded that 90 % of O_2 store, should be available without stress, turtle C should be able to accomplish such dives with no difficulty.

Kirshner (1985) concluded that specific gravity was not significantly affected by gas loss since C. porosus performed relatively

short dives. However, Graham et al. (1975) found a gradual reduction in lung volume to cause a 18 % reduction in buoyancy in P. platurus. In the present study, average buoyancy of 0.9061 $ml \cdot g^{-1}$ in C. p. bellii prior to ascent resulted in an average 4.40 % reduction in buoyancy during a dive. Such decrease in buoyancy was enough to require turtles to swim vigorously to the surface at the end of a dive.

Non-pulmonary O_2 and CO_2 exchange in water

Adaptation for tolerating extreme physiological conditions such as resistance to asphyxial distress (Berkson 1966), respiratory acidosis (Ultsch et al. 1984), and lactate accumulation (Shelton and Boutilier 1982), allow aquatic reptiles to submerge for extended periods of time. Non-pulmonary gas exchange is one such mechanism exploited by turtles. Generally, the extent of their ability to obtain dissolved O_2 and to expel CO_2 to the aquatic milieu seems to be directly related to their mode of life. Aquatic turtles are more efficient at non-pulmonary gas exchange than semi-aquatic ones, which are in turn more efficient than terrestrial species (Jackson et al. 1976). Non-pulmonary gas exchange in semi-aquatic turtles is usually reported to play a small role in overall respiration (Robin et al. 1964, Belkin 1968, Jackson 1976, Ackerman and White 1979, Gatten 1980). For example, aquatic O_2 uptake represented 5.1 % of total O_2 uptake in C. serpentina at 20 C (Gatten 1980), 4.0 % in C. scripta in air equilibrated water at 22 C (Belkin 1968), and 11.8 % in Sternotherus odoratus at 25 C (Root 1949), compared to 30.0 % of total O_2 respired in T. triunguis at 24 C (Girgis 1961). However, metabolic rate in water is known to drastically decrease (Stockard and Gatten 1983) and although non-pulmonary O_2 uptake may only represent a small portion of total aquatic and aerial respiration, it will make up a greater proportion of the metabolic needs during submergence. Chrysemys picta bellii, which was found to take

up an average of 2.86 $ml \cdot kg^{-1} \cdot h^{-1}$ in aerated water at 25 C, would only meet 6.7 % of its total uptake in air according to the equation for $\dot{V}_{O2}$ of Kinney et al. (1977), but could fulfill over 24 % of its requirement during submergence based on the standard aquatic $\dot{V}_{O2}$ equation from Stockard and Gatten (1983). In fact, survival time of forcibly submerged C. p. bellii was almost twice as long in normoxic (29.3 d) compared to anoxic (17.0 d) water at 10 C (Ultsch et al. 1984) and was increased by 15 % in C. scripta, a similar species, in normoxic water at 22 C (Belkin 1968). The ability of C. p. bellii to obtain O_2 aquatically also was proposed as an explanation for the longer proportion of time spent underwater in normoxic than anoxic conditions during voluntary submergence in this study. In addition, Gatten (1980) found no difference in aquatic O_2 uptake in C. serpentina between ventilatory and submerged apneic episodes. This suggests that non-pulmonary O_2 recruitment is commonly exploited and does not only occur under specific circumstances, such as hibernation, as frequently suggested (Gatten 1980, Ultsch and Jackson 1982A,1982B). Also, turtles such as C. concinna (Belkin 1964) and C. p. bellii (chapter 1) can submerge for several consecutive hours at night, which is probably accomplished by a further decrease in metabolic rate during that period (Gatten 1974B). The contribution to metabolic demands by non-pulmonary O_2 uptake would be even greater.

Gas loss during submergence was reported for aquatic reptiles such as P. platurus (Graham et al.1975), L. hardwickii (Seymour and Webster

1975), C. porosus (Kirshner 1985), A. mississippiensis (Andersen 1961), and several species of turtles (Jackson 1976, Jackson et al. 1976, Glass et al. 1978, Ackerman and White 1979, Burggren and Shelton 1979). This has been attributed to the removal of CO_2 away from the lungs (Andersen 1961, Graham 1974, Prange and Jackson 1976, Glass et al. 1978, Burggren and Shelton 1979, Kirshner 1985). Because CO_2 is very soluble in blood, it will have a tendency to build up and not to return to the lungs (Seymour 1982). A partial cardiac shunt, which is known to occur as early as 5 min after the onset of a dive (Shelton and Burggren 1976) will favor that trend, and because of its high solubility in water, CO_2 will diffuse out as a passive consequence of a rise in arterial PCO_2 (Jackson 1976). That pulmonary PCO_2 remained lower than arterial PCO_2 throughout voluntary dives in C. scripta (Burggren and Shelton 1979) supports this hypothesis. Loss of CO_2 aquatically accounted for 9.3 % of expected CO_2 production at 22-24 C in forcibly submerged C. scripta (Ackerman and White 1979), and 9.6 (Jackson 1976) and 10.5 % (Jackson et al. 1976) of total loss (at 20 and 24 C respectively) in C. scripta with access to air. However, the latter may be underestimated since total CO_2 loss was believed high (Jackson et al. 1976). In the present study, C. p. bellii lost an average of 12.75 $ml \cdot kg^{-1} \cdot h^{-1}$ of CO_2 aquatically. This is much higher than the maximum value obtained by Ackerman and White (1979) for C. scripta under similar conditions. Aeration of water prior to experiment in this study may have created a greater CO_2 gradient which could have prompted higher CO_2 loss, or mixing of water samples before measurements by Ackerman

and White (1979) may have negatively affected the results. There is likely an overestimation of aquatic CO_2 loss in the present study since the latter would account for 40 % of total CO_2 production according to a mean RQ of 0.75 (Ackerman and White 1979) and O_2 consumption equation of Kinney et al. (1977). This would represent a net output of CO_2 according to standard aquatic $\dot{V}_{O2}$ equation from Stockard and Gatten (1983) or 75 % of total and aerial CO_2 production according to the $\dot{V}_{O2}$ equation from Gatten (1974B), in a 1 kg animal. Nevertheless, the ability to rid the body of CO_2 through non-pulmonary route is an important adaptation to divers, since it would delay hypercapnia during prolonged submergence (Jackson 1976). Aquatic CO_2 output, like O_2 uptake does not only provide benefits during extreme situations, since aquatic CO_2 output was relatively significant in fresh-water turtles even during ventilatory activities (Jackson 1976, Jackson et al. 1976). That non-pulmonary gas exchange is diffusion limited (Seymour 1982) has been demonstrated by Belkin (1968) for uptake of dissolved O_2, but Jackson (1976) showed CO_2 loss to water in C. s. elegans not to differ when placed in a solution with high PCO_2.

That cutaneous CO_2 loss is the primary factor responsible for gas loss occurring during submergence is supported by the fact that CO_2 output was significantly similar to gas loss in this study. It is probable therefore, that metabolic rate during non-pulmonary exchange and buoyancy experiments was closer to that provided by $\dot{V}_{O2}$ equation by Kinney et al. (1977) (0.72 $ml \cdot kg^{-1} \cdot min^{-1}$) than either that of

Stockard and Gatten (1983) (0.15 $ml \cdot kg^{-1} \cdot min^{-1}$) or Gatten (1974b) (0.33$ml \cdot kg^{-1} \cdot min^{-1}$), since the latter two would imply that none or very little CO_2 would be sequestered in body fluids or returned to lungs during these dives. As suggested by Burggren and Shelton (1979), this is very unlikely. Metabolic rates reported by Stockard and Gatten (1983) were obtained under conditions similar to those turtles faced during nocturnal submerged activities in the field during summer (chapter 1). Minimal metabolic rate under these conditions favor long submergence periods, as was observed in the field (chapter 1) and by Belkin (1964). Although the contribution to gas exchange by non-pulmonary routes may be relatively unimportant when faced with high metabolic demands, such contribution should become quite substantial during rest periods and at low temperatures, when metabolic needs decline.

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