Papéis Avulsos de Zoologia

A BRIEF BIOMETRICAL NOTE ON THE REPRODUCTIVE BIOLOGY OF SOME SOUTH AMERICAN *PODOCNEMIS* (TESTUDINES, PELOMEDUSIDAE)

P. E. VANZOLINI

ABSTRACT

The analysis of biometric data on small samples of clutches of Podocnemis vogli, P. sextuberculata and P. unifilis, supplemented by scattered data on P. expansa, P. dumeriliana and P. lewyana, permitted the following preliminary conclusions: (i) in P. unifilis clutch size, mean egg volume, total clutch volume and egg shape are related to the size of the female, (ii) in P. sextuberculata only total clutch size is related to the size of the female, (iii) while in P. unifilis increase in egg volume (both within and between females) tends to be correlated with a diminution of oblateness, thus approaching the condition of P. expansa, this does not happen in P. sextuberculata and vogli, (iv) ranking the species of the genus by maximum carapace length, it is apparent that the larger species tend to have larger clutches and larger eggs, most probably reflecting a dependence on body weight, (v) data on P. vogli indicate that egg density can afford an estimate of pre-natal mortality, (vi) it is possible that there are differences in egg density between species, perhaps as a consequence of differences in fat content.

A short review is made of salient points of the natural history of the genus, as well as a brief consideration of desirable approaches to the problems of its reproductive strategies.

INTRODUCTION

There is at present much justified concern over the fate of the South American river turtles, and some research is being done on their conservation and rearing. Surprisingly enough, there is practically nothing in the literature on the reproductive biology of these species. I have gathered, incidental to other work, a few data on clutch size and the dimensions of the eggs of two species of *Podocnemis*, *P. unifilis* Troeschel, 1848 and *P. sextuberculata* Cornalia, 1849. These data and a few others, culled from the literature, do not really permit an analysis in depth, but give a clue to a range of

Museu de Zoologia, Universidade de São Paulo.

TABLE 1

Females autopsied

Nº	Locality	sl	pl	cl	em
P. unifilis					
2510	Lago Jacaré, R.Trombetas	332	293	17	17
2511	" "	330	307	16	16
2708	" "	370	323	23	11
2506	" "	391	357	26	12
2589	" "	386	343	26	-
2595	" "	384	349	26	-
2529	Furo Aiaiá, R.Amazonas	398	371	26	-
2532	Carvoeiro, R.Negro	400	343	22	-
2536	Marová, R.Negro	423	374	33	-
2798	"	443	409	29	-
P. sextuberculata					
2445	Lago Jacaré, R.Trombetas	317	279	18	18
2447	" "	272	232	14	10
2444	" "	273	230	18	10
2448	" "	296	258	17	9
2451	" "	271	237	16	-
2446	" "	276	246	14	-
2455	Boca do Guajará, R.Amazonas	295	252	15	-
2458	" " "	294	253	14	-
2456	" " "	284	253	16	-
2457	" " "	312	272	19	-
2900	R.Tupana, R.Madeira	305	261	18	-

sl: carapace length; pl: plastral length; cl: clutch; em: eggs measured

problems that can be easily attacked, besides indicating that the reproductive biology of these turtles is not simple.

MATERIALS

The specimens that I autopsied and for which I have at least clutch size and shell length are listed in Table 1 (localities on Map 1). Additionally I measured in the laboratory 9 eggs of *Podocnemis expansa* (Schweigger, 1812)', MZUSP 2870 (4 eggs) and MZUSP 2871 (5 eggs), from two different nests from the Rio Trombetas, Pará (see Vanzolini, 1967).

In the literature the best data are those of Alarcón Pardo (1969) who worked on *P. vogli* Mueller, 1935, in the Peralonso (upper Meta) area of Colombia. From his work I use the measurements of one female (his number 148, see Table 1) and its eggs, plus the data on 4 clutches found in nature (his Tables 10 a, b, c, d). Goeldi (1897) supplies the measurements and weights of 5 eggs of *expansa*, presumably from Pará. Finally, from Steindachner (1902) I use the measurements of one egg of one female, of known carapace length, of *P. lewyana* A. Duméril, 1851, from the Rio Lebrija, a tributary of the Madgalena.

Map 1. Localities mentioned in the text. 1, Rio Lebrija. 2, Peralonso. 3, Marová. 4, Carvoeiro. 5, Rio Tupana. 6, Lago Jacaré. 7, Furo Aiaiá. 8, Boca do Guajará.

Data relative to my specimens are shown on Table 1; the heretofore unpublished egg measurements in the appendix.

Our samples being so small, the question arises as to how representative they are. Table 2 shows what I believe are the maximum registered carapace lengths for South American *Podocnemis*.

TABLE 2

Maximum carapace length of South American *Podocnemis*

vogli	310 mm	Alarcón, 1969
sextuberculata	317	MZUSP 2445
erythrocephala	320	Mittermeier & Wilson, 1974
unifilis	443	MZUSP 2798
lewyana	446	Dahl & Medem, 1964
dumeriliana	680	Strauch, 1890
expansa	1070	Coutinho, 1868

Williams (1954) cites 680 mm for *unifilis*, but this is very probably a mistake; although he does not give his source it is certainly Siebenrock (1902:166) who, under the heading *Podocnemis unifilis*, says: "Auch die Grösse, die Strauch von den Schalen (680 mm) der letzteren Art angibt, kommt mir bedenklich vor". In reality Strauch's 680 mm specimen was not referred by him to *unifilis*, but (on the same page) to *dumeriliana*; it is in fact the largest specimen I found mentioned. Strauch's (loc. cit.) largest *unifilis* was 425 mm long, in good agreement with Medem's (434 mm) and our (443 mm) largest specimens.

Thus the parallel statement by Coutinho (1868) that *unifilis* reaches 65 cm now stands alone in the literature; he was a reliable observer and knew his turtles thoroughly, but, in face of the subsequent literature, and having seen some hundreds of Brasilian *P. unifilis* in their breeding grounds, I prefer to keep his information in abeyance.

It is thus to be seen that our small samples of *sextuberculata* and *unifilis* are representative with regard to large specimens. As to the lower end of the scale — size at first breeding — there are at present no data, and our records must stand as paradigms for the time being.

CLUTCH SIZE AND PLASTRAL LENGTH

Either carapace or plastral length may be used as a measure of the general size of the female; in the present materials the coefficient of determination between the two measurements is around .95. I have used the plastral length, as it is more frequently adopted in the literature. The method chosen was analysis of regression of the number of eggs on the female's plastral length (Graphs 1-3, Table 3). In Table 3: N, number of individuals in the sample; R,

range of the plastral length, b and s(b), regression coefficient and its standard deviation; a and s(a), regression constant and its standard deviation; r^2, coefficient of determination.
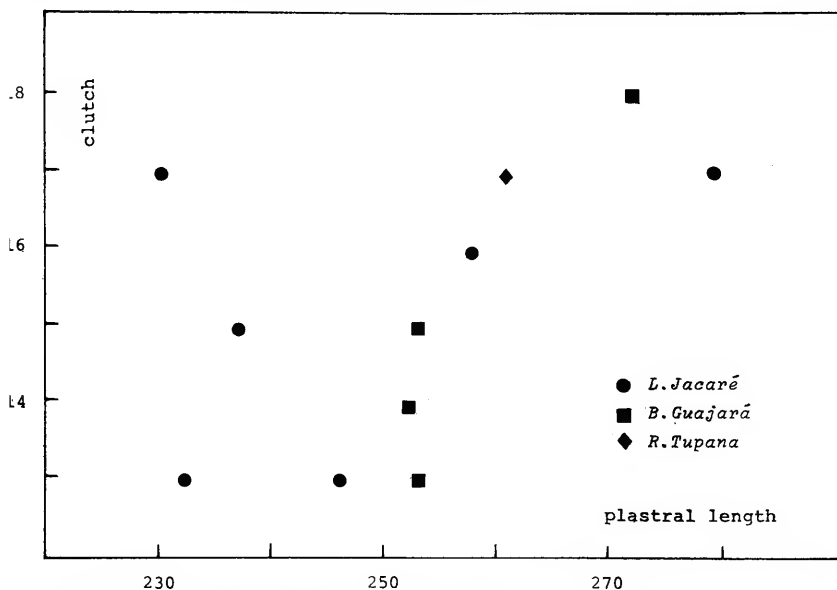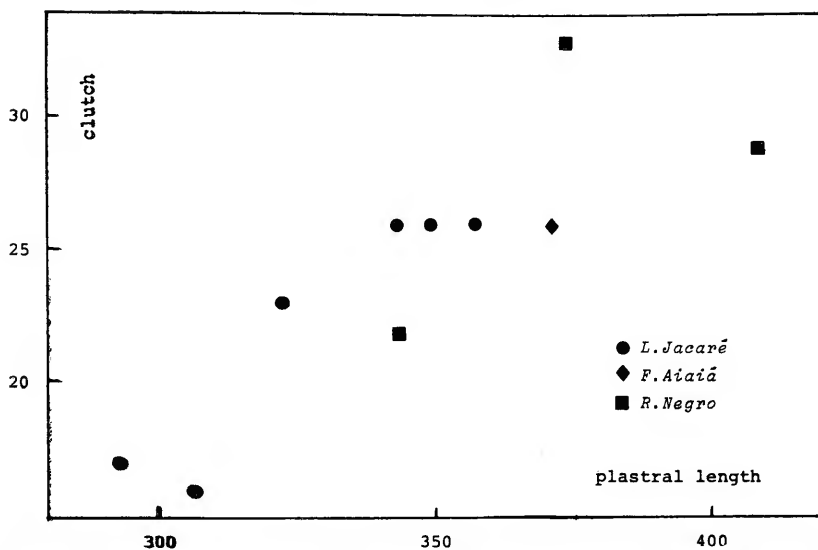

Graph 1. *Podocnemis sextuberculata.* Regression of clutch size on plastral length.

The relationship between the number of eggs and the size of the female in *P. sextuberculata* (Graph 1) was studied initially in the Lago Jacaré sample, then in the ensemble (*"sextuberculata 1"* in Table 3); no correlations were found. Inspection of Graph 1, however, indicates that the removal of one specimen (MZUSP 2444, plastral length 230 mm, 18 eggs) should result in a significantly improved regression; this is indeed the case (*"sextuberculata 2"* in Table 3). Weeding out inconvenient specimens is not a commendable practice, however, although it is true that aberrant data are frequently traceable to errors in recording, tagging or measuring. In the present case, however, my field notes are clear and explicit, and the field number, in India ink, can still be read on the shell; in spite of the nagging peculiarity, I do not feel the specimen should be rejected.

The graph for *P. unifilis* (Graph 2), on the contrary, indicates quite clear linear regressions, very good in the Jacaré sample (*unifilis* 1 in Table 3), still reasonable in the ensemble (*unifilis* 2). However, this regression, as computed, should not be used for prediction, as the variance of the larger specimens is much higher than that of the smaller ones. The graph seems to suggest that there is geographical differentiaton in this relationship, but the data are still insufficient.

Adding the data for *P. vogli* (one specimen, plastral length 221 mm, 10 eggs) and fitting a straight line to all specimens (Graph 3) one obtains a significant correlation (Table 3, "general"), although

Graph 2. **Podocnemis unifilis**. Regression of clutch size on plastral length.
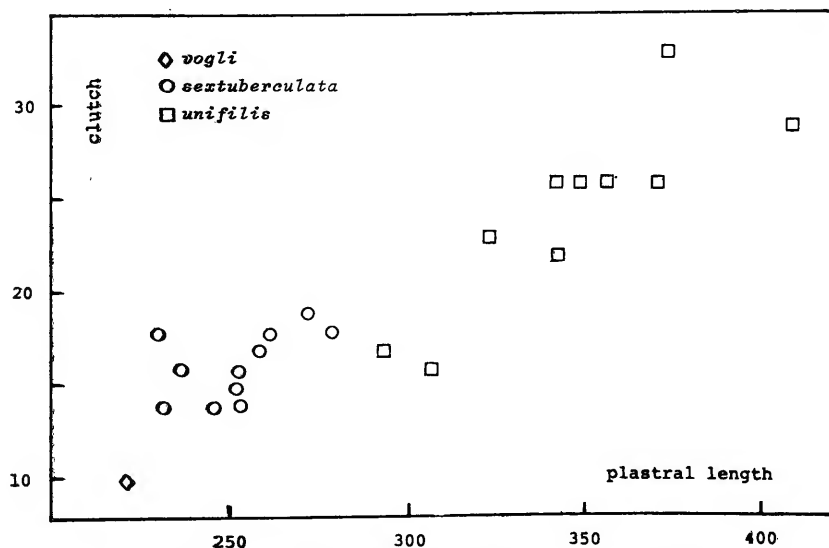
Graph 3. Regression of clutch size on plastral length.

small *unifilis* tend to have fewer eggs than *sextuberculata* of comparable size. This regression indicates that correlation of clutch size with body size at the species level is probably a property of the group.

TABLE 3

Regression of clutch size on plastral length

	N	R	b	s(b)	a	s(a)	r^2
sextuberculata 1	11	230-279	.004	.009	17.3	2.1	.03
sextuberculata 2	10	232-279	.10	.029	-9.3	7.3	.60
unifilis 1	6	293-307	.17	.032	-34.7	10.5	.88
unifilis 2	10	293-409	.13	.028	-20.6	9.6	.73
general	21	221-409	.10	.009	-8.5	2.8	.84

In fact, *vogli,* the smallest species, has clutches of 5 to 17 eggs (Alarcón, 1969); *sextuberculata,* as we see, of 14 to 19; *erythrocephala,* 5 to 14 (Mittermeier & Wilson, 1974); *unifilis* of 16 to 33; *lewyana* (very close in size to *unifilis*) of 15-30 (Dahl & Medem, 1964); *dumeriliana* of up to 100 (Medem, 1960); and *expansa,* the largest of all, of 56 to 136 (Valle, Alfinito & Silva, 1973). If we rank (Table 4) the species by maximum carapace lenth (according to Table 2) and to

TABLE 4

Rank correlation between maximum clutch

size and maximum carapace length

	sl	Rank	cl	Rank
expansa	1070	1	136	1
dumeriliana	680	2	100	2
lewyana	446	3.5	30	4
unifilis	443	3.5	33	3
erythrocephala	320	5.5	14	7
sextuberculata	317	5.5	19	5
vogli	310	7	17	6

sl: carapace length; cl: clutch

maximum clutch size, being very conservative about conceding ties, we obtain a coefficient of rank correlation (Spearman) of .93, significant at the .01 level. It will be noted that the inversions of ranks occur among the three smallest species, that are actually very similar both in clutch size and carapace legth.

Additionaly, extrapolation of the "general" equation in Table 3 would give a clutch of about 92 eggs for an *expansa* one meter long, which is a quite reasonable fit.

VOLUME OF THE EGGS

There is no parental care among turtles, and the young are born ready to fend for themselves; nevertheless the amount of protein and fat committed to the clutch is an important element in the characterization of reproductive strategies. The present data allow a preliminary inquiry on the intra- and interspecific variaton of individual egg and total clutch volume.

The eggs of *Podocnemis* are ellipsoids of revolution, of volume $v = \pi \, xy^2/6$, where x and y are, respectively, the larger and the lesser diameters of the egg.

I initially studied (Graphs 4-6, Table 5) the frequency distributions of the egg volume in the clutches at hand. In Table 5 N is the number of observations, R the range, $\bar{x}$ the mean, $s(\bar{x})$ its standard deviation, V the coefficient of variation, and $I(\bar{x})$ the interval of confidence of the mean, i.e., t standard deviations on each side.

Inspection of the table and graphs shows at once the presence of striking intra-specific and intra-locality (all *sextuberculata* and *unifilis* are from Lago Jacaré, all *vogli* from the Peralonso area) heterogeneity, both in mean egg volume and in intra-clutch variability. In Graph 4, for instance, there is no agreement among the four *sextuberculata* distributions: 2445 is markedly more variable; 2447 is extremely asymmetrical; the two more "reasonable" distributions, 2444 and 2448, have widely different means. In *unifilis* the difference in variability are not large, but no two means agree.

The differences in the distributions of *expansa* (Graph 5) are very striking, especially that between MZUSP 2870 and 2871, collected on the same sand bank at the same time by the same person (myself).

In Graph 6 (*vogli*) we see very compact distributions; d and c may be said to agree — the others differ.

In order to investigate possible causes of this intraspecific heterogeneity it is feasible, with present materials, to test the correlation between, on one side, clutch size and female size and, on the other, volume of the eggs.

Graph 7 shows that, in *P. vogli* and *sextuberculata*, clutch size and mean egg volume are not correlated; in *P. unifilis*, on the contrary, a definite regression appears.

In Graph 8 one sees again that *P. unifilis* shows correlation (albeit not very close) between mean egg volume and plastral length, but that *sextuberculata* does not (there are no data for *vogli*). It is
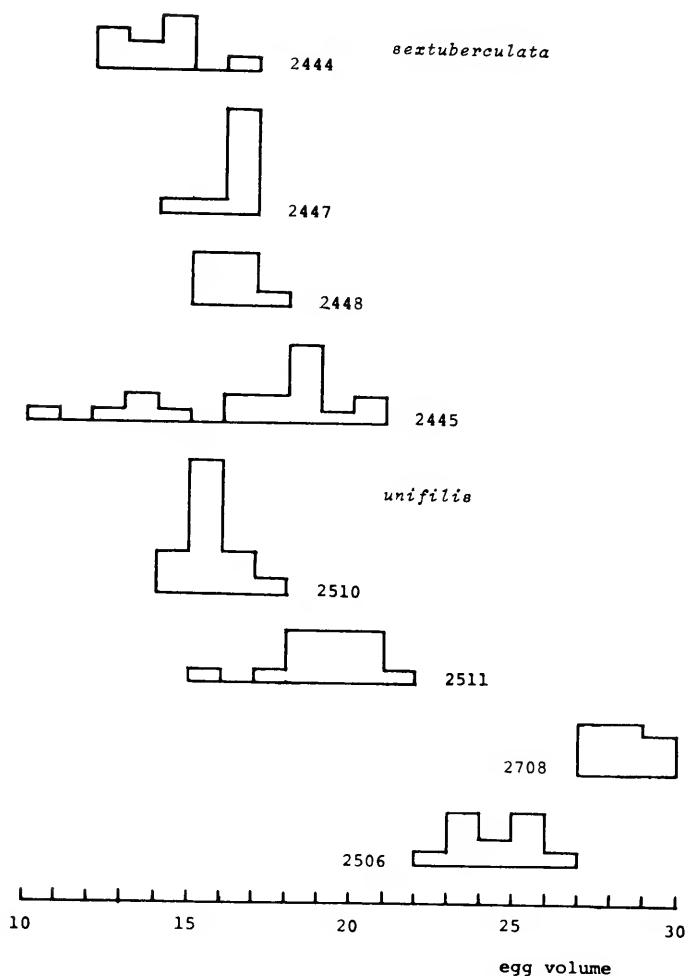
Graph 4. *Podocnemis unifilis* and *sextuberculata*. Distributions of frequencies of the egg volume.

clear that as *unifilis* females grow they tend to have more eggs and larger eggs, but that this does not happen to *sextuberculata* nor, probably, to *vogli*. There are data (Steindachner, 1902) on one *lewyana* egg, that measured 40x34 mm, from a female with a carapace length of 411 mm. Redoing Graph 8 with carapace length instead of plastral length as abscissa, this one *lewyana* may be said to agree with *unifilis* of comparable size.

If, in order to have an idea of the distributions of egg volume across the genus, one plots the observed ranges of egg volumes
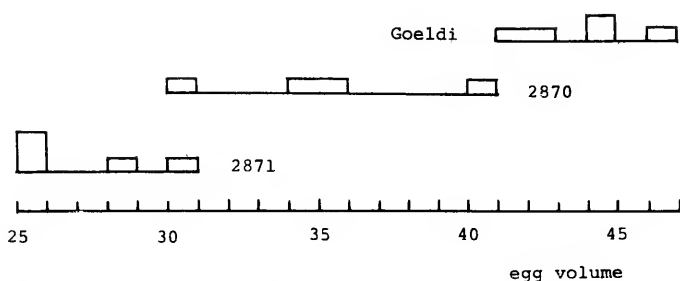
Graph 5. *Podocnemis expansa*. Distributions of frequencies of the egg volume.
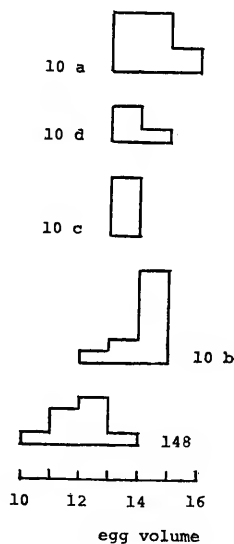

Graph 6. *Podocnemis vogli*. Distribution of frequencies of the egg volume (Alarcón's, 1969, samples).
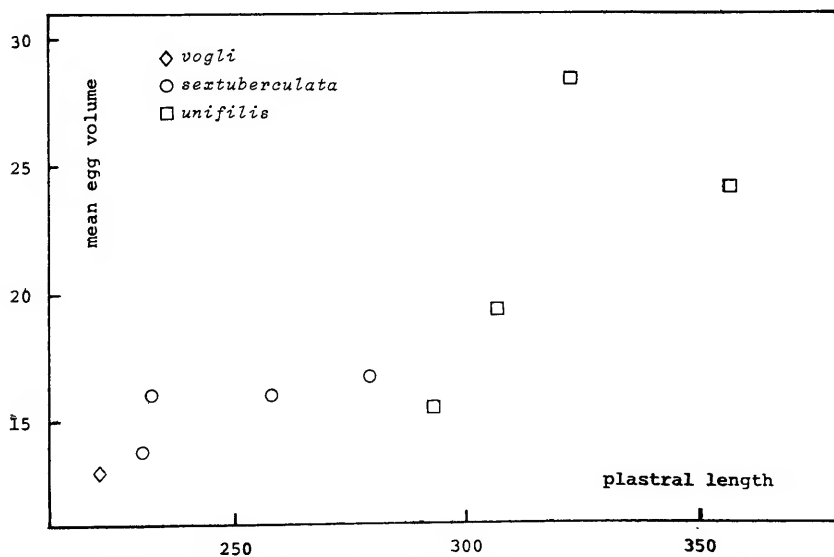
against the maximum carapace lengths of table 2 (Graph 9), a striking relationship is apparent, and the single *lewyana* specimen again falls in well with other samples.

It remains to investigate the relationship between plastral length and total clutch volume. This was obtained, of course, by simple addition in the case of the specimens of which all eggs were measured; in the others, by multiplying the total number of eggs by the mean of the sample measured.

As could be expected from preceding data, Graph 10 shows that the slope of the *unifilis* regression is very steep, since in this species

◇ *vogli*

○ *sextuberculata*

□ *unifilis*

mean egg volume

15

10

5

clutch

5   10   15   20   25
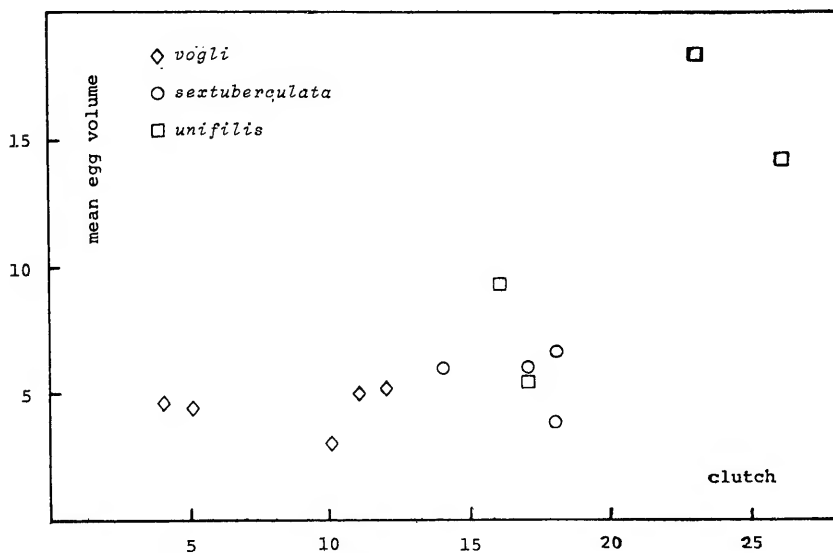
Graph 7. Regression of mean egg volume on clutch size.

◇ *vogli*

○ *sextuberculata*

□ *unifilis*

mean egg volume

30

25

20

15

plastral length

250   300   350

Graph 8. Regression of mean egg volume on plastral length.
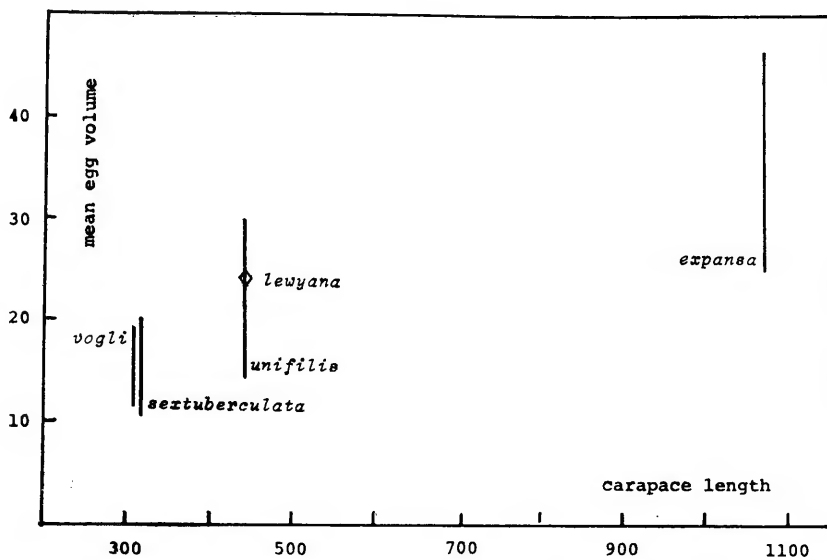
Graph 9. Range of mean egg volume against maximum carapace length recorded for the species.
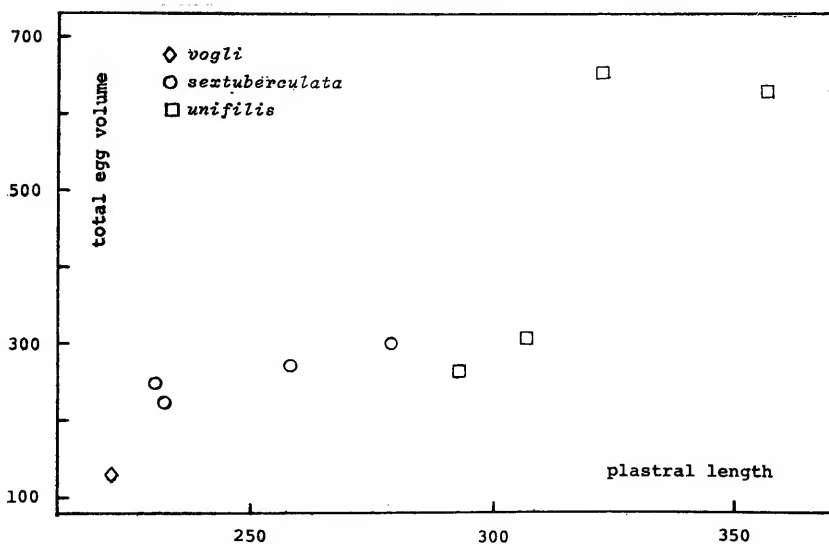
Graph 10. Regression of total clutch volume on plastral length.

TABLE 5

Distributions of frequencies of the egg volume

	N	R	$\bar{x}$	$s(\bar{x})$	V	$I(\bar{x})$
vogli 148	9	11.6–14.4	13.1	.28	6.4	12.4–13.7
10 a	12	14.6–16.6	15.3	.18	4.0	14.9–15.7
10 b	11	13.9–15.6	15.1	.14	3.2	14.8–15.4
10 c	5	14.3–14.9	14.5	.10	1.6	14.2–14.8
10 d	4	14.5–15.1	14.7			
sextuberculata 2444	10	12.4–16.4	13.9	.40	9.0	13.0–14.8
2447	10	14.9–16.8	16.1			
2448	9	15.3–17.6	16.1			
2445	18	10.6–20.3	16.8	.68	17.1	15.4–18.2
unifilis 2510	17	14.4–17.3	15.6	.18	4.8	15.2–16.0
2511	16	15.2–21.7	19.4	.38	7.8	18.6–20.2
2708	11	27.4–29.7	28.5			
2506	12	22.6–26.2	24.3	.35	4.9	23.6–25.1
expansa 2870	4	30.2–40.6	35.1			
2871	5	25.0–30.2	26.8			
Gld.	5	41.4–46.5	43.9			

both clutch size and mean egg volume increase with shell length. It is of course to be expected that, when data are available, total clutch volume will be found to be related to female weight.

Since our largest *unifilis* is the largest recorded specimen, the present data on clutch volume may be considered as a good preliminary bench mark.

In the case of *P. sextuberculata* things appear to be completely different. There is a significant regression of total egg volume on plastral length: the total amount of egg material depends on the size of the female — but how it is distributed in so many eggs of so much volume remains aleatory. There are no data for *vogli*.

DENSITY OF THE EGGS

Alarcón (1969) published a valuable table of measurements and weights of eggs of *P. vogli*. I calculated the density of all eggs; the

distribution for the individual clutches agree very closely, so Graph 11 presents only the total distribution. In the same graph are plotted the densities of 5 eggs of *P. expansa* (from Goeldi, 1897).
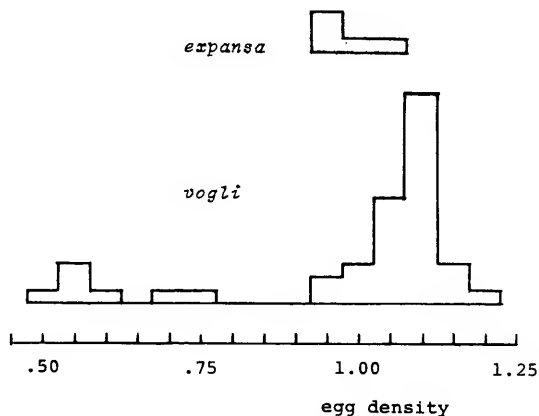
Graph 11. *Podocnemis expansa* and *vogli*. Distributions of frequencies of the density of the egg.

It is quite obvious that some of the *vogli* eggs are too light — those with a density of less than .80. This may have been due to a congenital defect or, probably, to post-mortem dehydration. It is a datum that affords a minimum estimate of pre-natal natural mortality. In Alarcón's materials 7 out of 40 eggs were obviously unviable: 1 out of 9 taken from the oviduct, 6 out of 31 found in nests.

It will be noted that the *expansa* eggs weighed by Goeldi are on the whole less dense than those of *vogli*. It is impossible to say whether this is an artifact (due, for instance, to the time lapsed between collection and weighing of the eggs) or a real difference, but it should be kept in mind that it is not impossible that inter--specific difference exist in the proportions of fat and protein in the eggs (which is the impression one gets from eating them).

EGG SHAPE

The formula $v = \pi\, xy^2/6$ indicates at once that increases in the smaller diameter of the egg (y) will be paramount in determining increases in volume, which is another way of saying that the sphere is the most economical solid. It is well known that the eggs of *expansa* are practically round, while those of the other species are more elongate. To analyze this point I calculated, for eggs measured, the eccentricity of the generating ellipse, $c = \sqrt{a^2 b^2}\,/a$, where a and b are respectively x/2 and y/2, the larger and lesser semidiameters of the egg.

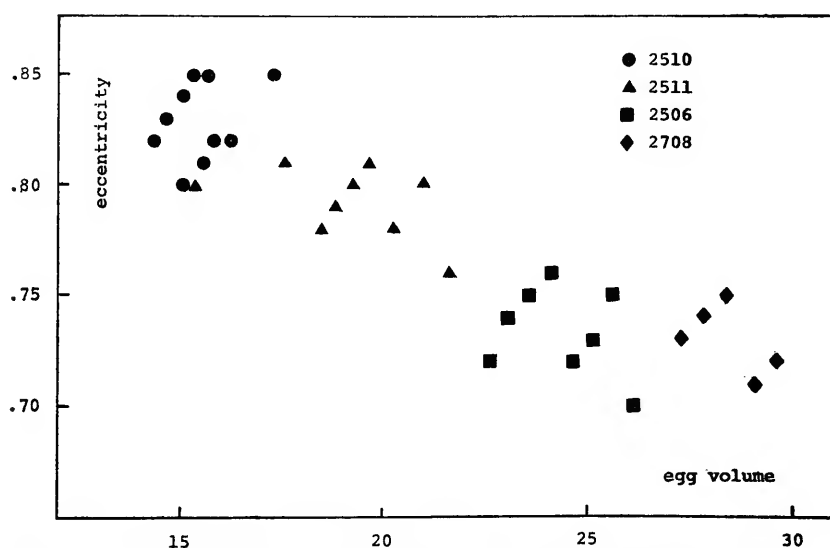Initially I plotted, for each individual clutch, the lesser against the larger diameter and the eccentricity against the egg volume. In
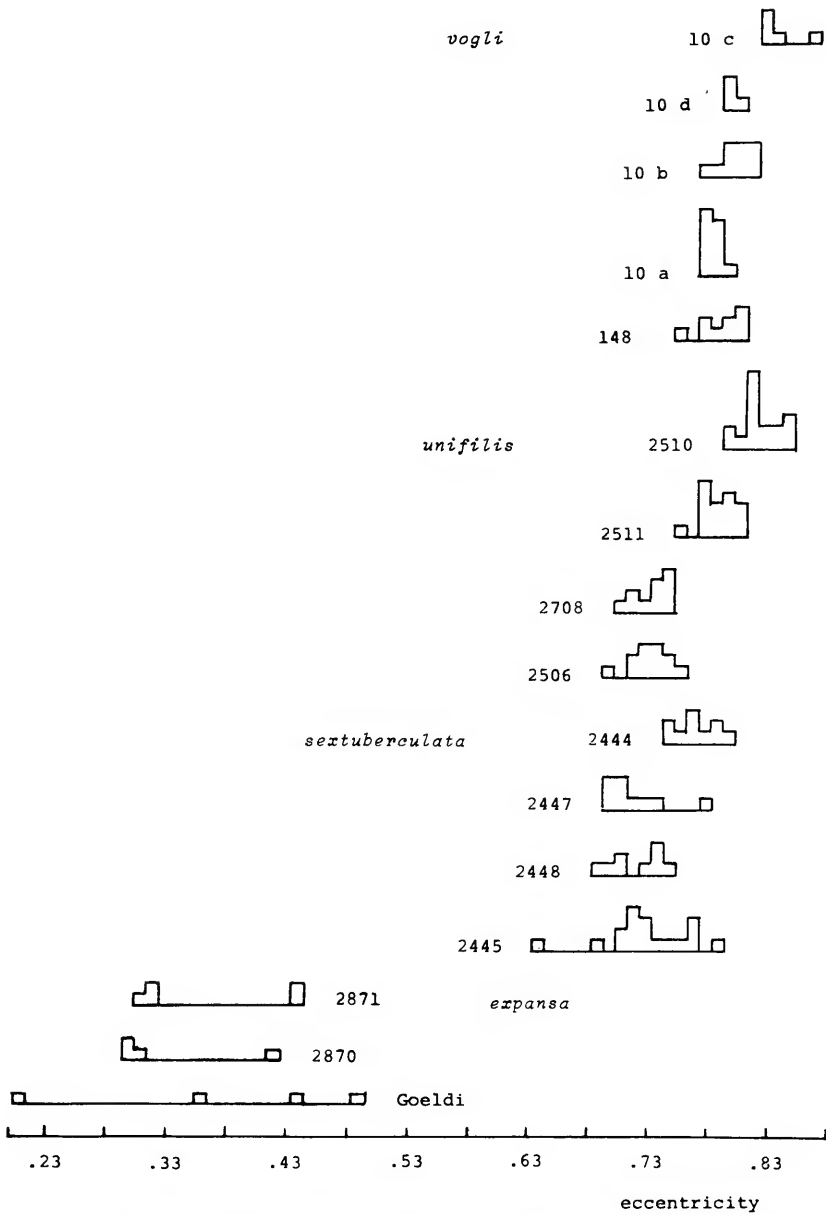
Graph 12. Distributions of frequencies of the eccentricity of the generating ellipse of the egg.
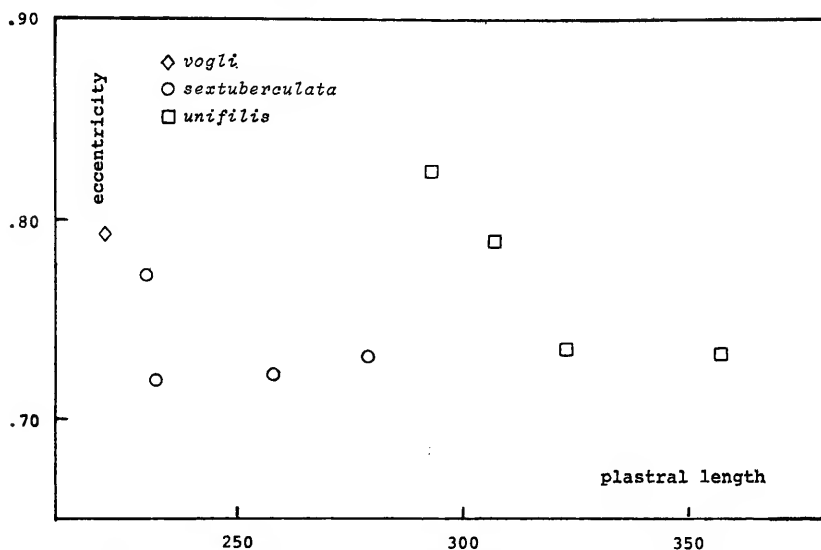
Graph 13. Regression of the mean eccentricity of the eggs on the plastral length of the female.

Graph 14. *Podocnemis unifilis*. Regression of the eccentricity of the egg on its own volume.

only two cases (*sextuberculata* 2448 and *unifilis* 2511) was there (negative) regression between egg volume and eccentricity (see graphs 13-15); in no case was a correlation found between the two diameters.

The next step was to plot on the same graph the distribution of frequencies of the eccentricity, in order to have an overview of the intra- and inter-specific relationships. It is easy to see that there is great intra-specific, but also a degree of inter-specific variability. Excluding *expansa*, obviously a special case, there are thirteen samples that can be ranked and submitted to non-parametric analysis. Scoring the lowest eccentricity as 1, one obtains (Table 6) the following picture: the three species are definitely ranked with regard to eccentricity, but there is broad overlap, and the average ranks do not correspond to the ranks in carapace length of the species within the genus (Table 2).

TABLE 6

Ranks of mean egg eccentricity

Rank	*unifilis*	*sextuberculata*	*vogli*
1		2447	
2		2448	
3		2445	
4	2506		
5	2708		
6			10 a
7		2444	
8	2511		
9			148
10			10 d
11			10 b
12	2510		
13			10 c
Sum	29	13	49
Mean	7.25	3.25	9.8

Plotting the average eccentricity against the plastral length of the specimens (Graph 13) one sees a negative relationship in *unifilis*, but no pattern in the ensemble.

The next step is to look for correlations between egg volume and eccentricity within each species (Graphs 14 to 16).

In the case of *unifilis* (Graph 14) the relationship is unmistakable — a text book case: the larger specimens have larger eggs because these eggs are more rounded. *P. sextuberculata* (Graph 15) shows no such pattern, but instead a rather disorganized one. Again, if 3 troublesome eggs (all belonging to one specimen, 2445, *not* the one that proved troublesome on the matter of clutch size) were removed,
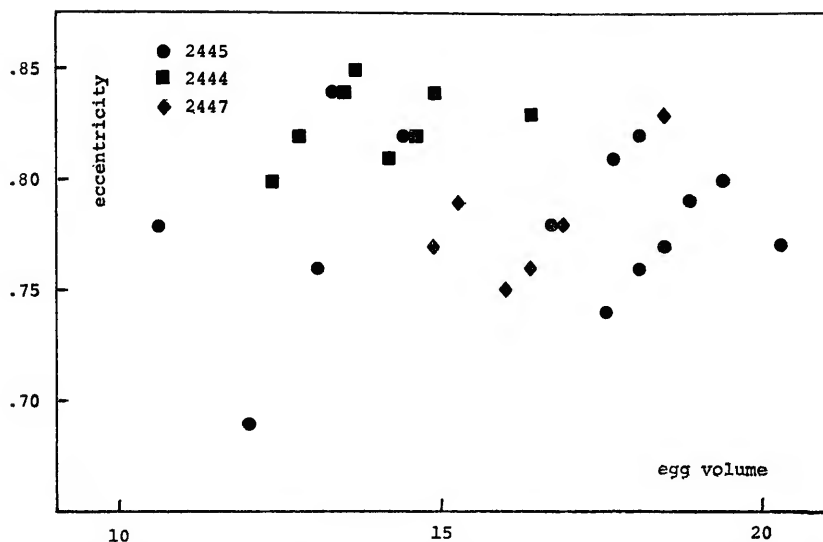
Graph 15. *Podocnemis sextuberculata*. Regression of the eccentricity of the egg on its own volume. Specimen 2448 omitted to avoid overcrowding.
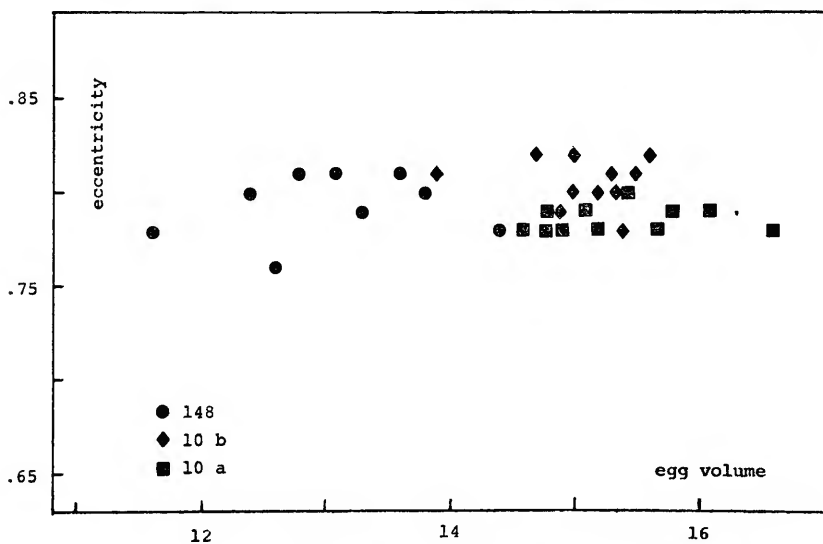
Graph 16. *Podocnemis vogli*. Regression of the eccentricity of the egg on its own volume. Clutches 10 c and 10 d omitted to avoid overcrowding.

a reasonable distribution would result; this is evidently not to be done. Finally (Graph 16), no amount of manipulation would change the lack of correlation of *vogli;* in spite of the wide range of variation of egg volume, it all happens within a moderate and unrelated span of eccentricity.

COMMENTS

It is tempting to try to place these data in the framework of current research on reproductive strategies, but, as said, the samples at hand do not justify either comparisons with other groups or theoretical conclusions. However, in order to give perspective to the results obtained, and to show what interesting materials South American *Podocnemis* are for evolutionary ecology, it is convenient to review some aspects of their natural history. Unless otherwise stated, the observations are my own, made over the years in the Amazonas, Negro, Trombetas, Xingu, Tapajós, Madeira and Purus. I have also incorporated much information from local residents. This is fully trustworthy since the natives of the Amazon know intimately the turtles that play such an important part in their lives (see, e.g., Alarcón, 1969:312).

All species live in the large river systems, under strictly tropical conditions. They have more or less sharply defined breeding seasons, geared to the regimes of the rivers. At least in the Amazon valley the fluvial regimes, while not varying much in time, vary greatly in quantity. Differences in the rise and fall of the waters are spectacular.

For instance, the Negro (and thus the Amazon) at Manaus in 1953 rose at flood to 29.7 m above sea level, but only to 21.8 m in 1926. The latter datum is close to the 21.2 m, minimum level recorded in 1913; in 1906 the minimum was 14.2m above sea level. The largest difference between maximum and minimum occurred in 1909 (14.1 m) and the smallest (5.5 m) in 1913 (data from Soares, 1959). In recent years, the rise in 1975 was almost as disastrous as that of 1953. This, despite some current notions, cannot be called a very predictable environment. In fact, traveling in Amazonia, one hears of frequent failures of the turtle crop because either the river dit not go down enough or because it rose too much too early (examples in Valle, Alfinito & Silva, 1973).

In the rivers for which I have reliable information, the species of *Podocnemis* do not lay synchronously (Table 7). *P. expansa* is always the late breeder and it seems safe to say that it lays at the lowest level of the river — and the young eclode at the beginning of the rise (e.g., data in Valle, Alfinito & Silva, 1973). *P. erythrocephala* is an early breeder in the Negro, and it is common knowledge there that females may be seen breeding at the end of the slight rise ("repiquete") that usually happens in the first week of November ("caldo de defunto"). *P. vogli* (Alarcón, 1969) apparently has a long laying season, from late October to early January. *P. unifilis* presents an interesting variation: in the Purus it lays long before *expansa*, in the Trombetas a little earlier, and in the Negro at about the same time.

The breeding behavior presents interesting variations in this context. *P. expansa* and *sextuberculata* lay their eggs in low beaches

TABLE 7

Laying season of *Podocnemis* in some Brasilian rivers

	Purus	Negro	Trombetas	Tapajós
expansa	sep-oct	dec	oct	oct
unifilis	jun-jul	dec	sep-oct	
sextuberculata	jun-jul		aug-sep	
eryhtrocephala		aug-sep		
		(nov)		
dumeriliana		aug-sep		

and bars of pure sand; they are particularly vulnerable to fluctuations of the fluvial regime. Their eggs are soft-shelled. *P. vogli* (Alarcón, 1969) and *unifilis* may wander quite far from the water to lay, and will accept a variety of substrates; I have seen a nest of the latter in a recently burnt field some tens of meters from the river and several meters above water level. *P. vogli* and *unifilis* have eggs with calcareous shells. *P. erythrocephala* is said by Mittermeier & Wilson (1974) to lay in the sandy soils of the peculiar edaphogenic formations called "campinas" (or, improperly, "caatingas") in the Negro. I have heard in the Negro that they also lay in low beaches. The shell varies from hard to flexible. These species that lay their eggs away from the water are obviously more subject to predation of females. *P. dumeriliana* nests in leaf-litter and mud. I know of no description of its eggs and have not been able to acquire any despite many attempts.

P. unifilis lays its eggs solitarily. *P. sextuberculata* may be found on the beach alone or in groups of 3-4 females; usually a number of specimens use the same area, so that there is a concentration of nests, which is not the case with *unifilis*.

P. expansa has been long known as a gregarious breeder, large numbers of females congregating on traditional beaches to copulate, to ripen the eggs by sunning and to lay. However, and probably under the pressure of human predation, in many parts it has been seen breeding solitarily or in small groups, and on beaches that would not be adequate for a herd. Several cases are also known of very small groups breeding gregariously; at Monte Cristo, Rio Tapajós, they come spontaneously every year (Valle, Alfinito & Silva, 1973); in several places in the middle Purus they come out to lay if live decoys (an adult pair of the same species) are provided. It would be surprising if these changes in behavior did not influence some aspects at least of the reproductive biology of the species. In fact, while all other known populations of *expansa* lay during the night, those that breed in Monte Cristo lay during the daytime (Valle, Alfinito & Silva, 1973).

A very important point to be studied as soon as possible is that of the number of clutches laid by each female in one season. Both

Mondolfi (1955) and Alarcón (1969) are very definite about at least some *P. vogli* laying twice in the same season. Medem (1964) found one female *P. unifilis* with 19 shelled eggs and 12 nude yolks. My *sextuberculata* 2445 had 18 shelled eggs and 18 yolks, the largest of which had a diameter of 24 mm. It has been said above that specimens of *erythrocephala* in the Negro may be seen laying two months after the regular season; whether these are late breeders or females that are laying a second clutch is not known. It is obvious that an estimate of the prevalence of two clutches is indispensable to the understanding of the reproductive biology of the group.

All species of *Podocnemis* have large geographic ranges; those of *expansa, sextuberculata* and, especially, *unifilis*, are really enormous. This in itself favors geographic differentiation, the opportunities for which are enhanced by the differences in breeding season in different rivers (Table 7) and by fidelity to traditional breeding sites, both facts leading to restriction of gene flow. It would also be surprising if reproductive strategies or, at least, some parameters, were not sensitive to geography.

Another important peculiarity of the genus is the enormous spread in size, from the small *vogli, erythrocephala* and *sextuberculata* through *unifilis* and *lewyana* to giant *expansa*, from 20 centimeters to one meter, from less than half a kilo in *vogli* (Alarcón, 1969), to more than 45 kilos in *expansa* (Valle, Alfinito & Silva, 1973). Correspondingly, in the medium and large species there is also a broad span between age at first breeding and full female size, which, coupled with large clutch sizes, gives room for much adaptive variation.

This is exactly what the present data indicate. At the intraspecific level, we find that, in *P. unifilis*, clutch size, mean egg volume and egg shape are linked to body size. That they are not in *P. sextuberculata* may be in itself due to the difference in size. The relationships between clutch size and mean egg volume found within species obtain also at the interspecific level. It seems evident that an exploration of these relationships in different parts of the range of each species, in diverse contexts of sympatry and predation, will reveal much of theoretical and practical interest.

On the reverse side, a consideration of the reproductive biology of *Podocnemis* puts into relief the fact, so obvious but so frequently forgotten, that, unless all aspects of possible relevance to the theoretical and practical study of reproductive strategies (see, e.g., for turtles, Legler, 1960; Tinkle, 1961; Moll & Legler, 1971; Moll, 1973; in general, Stearns, 1976), are taken into due consideration, and analyzed in as detailed a way as possible, field data, at times laboriously gathered, may end up by being of very little use. The citation of examples, means, extremes and other devices to summarize data afford little, if any, insight into the really important biological phenomena.

This fact, plus the tremendous geographic ranges of the species and the amount of time in the field demanded by even the simplest investigations, makes the full publication of raw data very desirable, if not mandatory.

CONCLUSION

If one takes as a standard a thorough review of current research on reproductive strategies, such as, e.g., Stearn (1976), one sees that

there is very little in the literature on *Podocnemis* of any help to an understanding of the biology of their reproduction.

It is true that many facts will be hard to obtain, especially demographic data and detailed life histories; other aspects, however, such as those briefly treated here on the strength of meager materials, or suggested on the basis of broad natural history information, can — and should — be more intensively studied without any great trouble.

APPENDIX

Egg measurements

sextuberculata

2444

38	25	42	29
38	25	42	29
39	25	43	28
40	26	43	29
41	25	43	30
41	26	43	30
41	26	44	28
42	25	44	28
42	26	44	29
43	27	**2447**	
2445		39	27
34	26	39	28
35	24	39	28
37	26	39	28
40	29	40	27
41	25	40	28
41	26	40	28
41	28	40	28
41	28	40	28
41	29	41	28

2448

39	28
40	27
40	27
40	28
40	28
40	29
41	27
41	28

unifilis

2506

45	31	45	26	46	29
46	31	45	26	46	30
46	31	46	25	47	28
46	31	46	25	47	28
46	32	46	26	48	28
46	33	46	26	48	28
47	31	46	26	48	29
47	32	47	25	**2708**	
47	32	48	25	43	33
47	32	49	26	48	34
48	31	**2511**		49	33
48	32	43	26	49	33
2510		45	28	49	33
43	26	46	27	49	34
43	26	46	28	49	34
44	25	46	28	50	33
44	26	46	28	50	33
45	25	46	29	50	33
45	25	46	29		
45	26	46	29		

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