On clutch size and hatching success of the South American turtles *Podocnemis expansa* (Schweigger, 1812) and *P. unifilis* Troschel, 1848 (Testudines, Podocnemididae)

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ABSTRACT

Data on clutch size and hatching success of *P. expansa* were gathered for seven beaches traditionally used by the species and re-analyzed statistically by means of regression analysis, of the number of eggs on the number of females (or nests) and of the number of young on the number of eggs. All regressions were linear, passed through the origin and had excellent fits. Average clutch size varied from 75 to 123, and presented geographic differentiation: (i) Rio Orinoco, (ii) Rio Trombetas + Rio Branco and (iii) Rio Juruá + Rio Purus. Average hatching success was ca. 83%. In *P. unifilis* there was also geographic variation in clutch size, the Iquitos area showing the highest values. Hatching success of *P. unifilis* was uniformly high: only one sample, from Iquitos, had less than 90% success. The outstanding fit of the clutch size regressions leads one to consider egg volume variability, which was found to be high in both species, in contradiction with current optimal egg size theory.

Key words: turtle reproduction, hatching success, clutch size, optimal egg-size theory, *Podocnemis expansa*, *Podocnemis unifilis*.

INTRODUCTION

Turtles whose reproductive cycle is geared to the alternation of river flood/low flow are particularly sensitive to the damming of large rivers for hydroelectric projects, which unavoidably involves regularization of regime, and thus obliteration of fluvial cycles. This is the case with the South American species of Podocnemis. They are important animals from multiple angles, biological, esthetical and economic; the problems concerning their conservation are both difficult and urgent. It is possible to assist their reproduction and so to mitigate environmental impacts, but assistance needs to be based on firm ecological grounds.

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P. expansa ("tartaruga", turtle par excellence) is a widely distributed (Wermuth and Mertens 1996), very large, even spectacular animal, whose females lay their eggs communally, in herds frequently very numerous, on traditional beaches. It has naturally attracted much attention since early days (e.g., Humboldt 1814). Given its vulnerability, due to gregarious egg-laying, and to irrational human predation, it has been the object of much concern, and effort is currently being spent on conservation.

P. unifilis (tracajá) is a smaller, less spectacular turtle, which does not aggregate as *P. expansa* in large herds at laying time, but is nevertheless a very important staple food. It is available at all times, and the meat and eggs are highly esteemed.

In spite of the commonness of the species, and

of a considerable amount of printed comment on them, it is remarkable how little hard information is available. The literature is uneven, often unprofessional, scattered, and at times hard to obtain. This paper is an attempt to gather and organize original data from published sources on the reproductive biology of these two forms, specifically on clutch size and hatching success.

Both parameters are important. Clutch size is indispensable to the estimation of reproductive effort, and so to the application of concepts of optimization and trade-off. Hatching success is additionally important from a more practical viewpoint, the evaluation of management techniques, such as transplantation of nests.

MATERIALS AND METHODS

The data gathered in the literature were mostly raw, not statistically analyzed. As they consist essentially of proportions (number of eggs vs number of females or nests, number of young hatched vs number of eggs laid), and as several independent samples were usually available, I used whenever possible regression analysis, followed by analysis of covariance and by the application of Tukey's test. I did not make use of all data available in the literature, but discarded sets of data that seemed incongruous to me.

All statistical methods are intentionally elementary and can be found in texts such as Dixon and Massey (1983), Zar (1999) or Vanzolini (1993).

In the text and tables the following statistical conventions are followed:

N, observations in sample

R, R(x), R(y), ranges of the variables

m, mean $\pm$ its standard deviation

s, sample standard deviation

V, coefficient of variation

b, coefficient of regression $\pm$ its standard deviation

a, regression constant $\pm$ its standard deviation

F, quotient of the variance due to regression by the
     error (significance of the regression)

df, degrees of freedom

r^2, coeffecient of determination

ns, not significant at the 5% level

*, significant at the 5% level

**, significant at the 1% level

***, significant at the 0.1% level.

Geography is extremely important in this context; in the text I do not enter in details about the localities, but there is a Gazetteer at the end.

RESULTS: *PODOCNEMIS EXPANSA*

CLUTCH SIZE

P. expansa was described by Schweigger in 1812. The first information on its breeding habits dates from Spix (1824: 2). In the description of *Emys amazonica*, a synonym, Spix mentions that it occurred in the rivers Solimões, Branco and Javarí and remarks, very much to the point: "In November it investigates, in groups, sandy islands, deposits 130 eggs in holes three feet deep, tramples down the sand with the breast; the young emerge from the sand in two weeks" (my translation). The mention of November as the month of reproduction indicates that Spix saw it at Ajaratuba, on the Rio Solimões, near the mouth of the Rio Purus (Vanzolini 1981: xv).

Since then *P. expansa* has been repeatedly and extensively mentioned in the literature. However, the needed set of data for the proper study of reproductive strategies – good samples of females from a single locality, at the same time, measured and weighed, and the respective clutches counted and weighed – does not exist. The available data are of two sorts: anecdotal, such as Spix's above, with which I shall not deal, and references to (usually aggregate) numbers of nests (alternatively of females found nesting), and of eggs, laid, hatched and failed. Of these data I try to make the best use, complementing, whenever possible, the statistical treatment.

Mosqueira-Manso (1945) is the first author to present actual data on the reproduction of *P. expansa* at the famous beach of Pararuma, on the Orinoco, cited since the days of Humboldt. He reports (Table II, this paper) 3172 eggs from 35 excavated nests, averaging 90.6 eggs/clutch.

Blohm and Fernández-Yépez (1948: 45) say, also from personal experience at Pararuma, that clutches may reach 150 eggs, but usually contain 85 to 90. Later in the same paper they state that findings of up to 125 eggs are rare, and place the average at 75.

Ramirez-E. (1956) has a very valuable paper on the same area of the Orinoco. He has data, for 7 consecutive years (1950 to 1956), for four beaches spread along some 80 km of river: Pararuma, Playa del Medio, Playa Blanca and Cabullarito. He presents for each beach and year the number ("calculo aproximado", Cuadro Nr. 3, p. 53) of "Tortugas ponedoras" (laying turtles) and of "Huevos puestos" (eggs laid). The number of samples (years), 5 to 7, available for each beach and the broad ranges of the variables make this a favourable case for regression analysis. This was performed and the results are (Table I, Fig. 1):

1. All regressions are linear.

2. The fits are unusually good. In many years of using statistical methods in zoological research I have never seen such high levels of significance ("calculo aproximado" indeed).

3. The four localities agree closely among themselves, and the joint regression is precisely as good as the individual ones.

4. In all cases the intercept (the regression constant, a) does not differ significantly from zero; consequently the regression equation y'= a + bx reduces to y' = bx, and b = y'/x – the slope, or coefficient of regression, i.e., the increase in the dependent variable consequent to an increase of one unit in the independent variable, actually estimates the average clutch size. In this case we have 75 eggs.

Roze (1964) says, about the same Orinoco beaches, that the number of eggs is variable, 150 in one nest being a record, and 82-86 the average.

Valle et al. (1973: VIII-E 75) report, for another traditional beach, Taboleiro Leonardo, on the Rio Trombetas, also well-known in the literature, a range of 56-136, and an average of 75 eggs per nest.

Brito (1978) has counts of eggs per nest, fertile and unfertile, in three beaches of the middle Rio Purus, a tributary of the Solimões on its right bank: Aramiã, Axioma and Mapiciarí. His data show a very broad spread (Table II). The three beaches are heterogeneous in clutch size: Axioma agrees with Aramiã and both differ from Mapiciarí. The approximate distance between the beaches, going downriver are: Aramiã–Axioma 145 km, Axioma–Mapiciarí 39 km.

Correa (1978) has tables of the number of laying females and of eggs laid in 6 beaches in the Rio Branco (Mandulão, Anta, Gaivota, Aricurá, Pacheco and Santa Fé) and in 8 beaches on the Rio Juruá (Joanico do Pato, Floresta, Harmonia, Santa Helena, Nova Olinda, Onça, Reforma and São Sebastião). Within each riverbasin clutch sizes may be shown graphically to be homogeneous (they stand on a straight line), so it is possible to do a regression analysis (Table I). The results are closely analogous to those of Ramirez-E. (1956).

Vecchi (1978), a newspaperman, visited Taboleiro Leonardo during a research campaign by the Brazilian federal conservation agency. He was given, and published in a magazine feature, data on clutch size for the seasons 1976-1977 and 1978 (Table II). The data differ at the 5% level, showing lack of homogeneity in time: in fact in consecutive years.

Alho and Padua (l982) have data on 393 females nesting on Taboleiro Leonardo. I do not fully understand their statistical treatment, but two kinds of data can be extracted from the paper. In their Table I it is seen that clutch size varied from 63 to 134, with average 91.50 ± 1.15 eggs (standard deviation calculated by myself). Their Table III, however, permits a regression analysis, such as performed with the data of Ramirez-E. (1956) and Correa (1978). The regression is linear, with an exceedingly good fit; the intercept does not differ significantly from zero and the slope (average clutch) is 98.9.

TABLE I

***Podocnemis expansa*, regression of the number of eggs on the number of females or nests.**

| N	R(x)	R(y)	b	a	F	r²
Ramirez-E. 1956						
Pararuma						
5	2905-10500	217875-772500	73.5 ± 0.90	6790 ± 102973 ns	6674.7***	0.9996
Playa del Medio						
7	4930-26200	69750-1965000	75.0 ± 0.03	111 ± 208456 ns	4641350***	0.99999
Playa Blanca						
6	85-7700	6375-577500	75.0 ± 0.02	−0.02 ± 82147 ns	9885063***	0.9885
Cabullarito						
6	1200-7520	90000-564000	75.0	0		1
All beaches						
24	85-26200	6375-196500	75.0 ± 0.08	479 ± 133162 ns	968685***	0.99998
Correa 1978						
Rio Branco						
5	9-157	838-15447	98.3 ± 0.98	69.2 ± 2276 ns	10123***	0.9996
Rio Juruá						
5	21-141	2136-16888	122.6 ± 7.22	−283.8 ± 2765.2 ns	288.4***	0.98979
Alho & Padua 1982						
24	15-475	1365-44664	98.9 ± 1.53	−1317.6 ± 2778.7 ns	4169.2***	0.9948
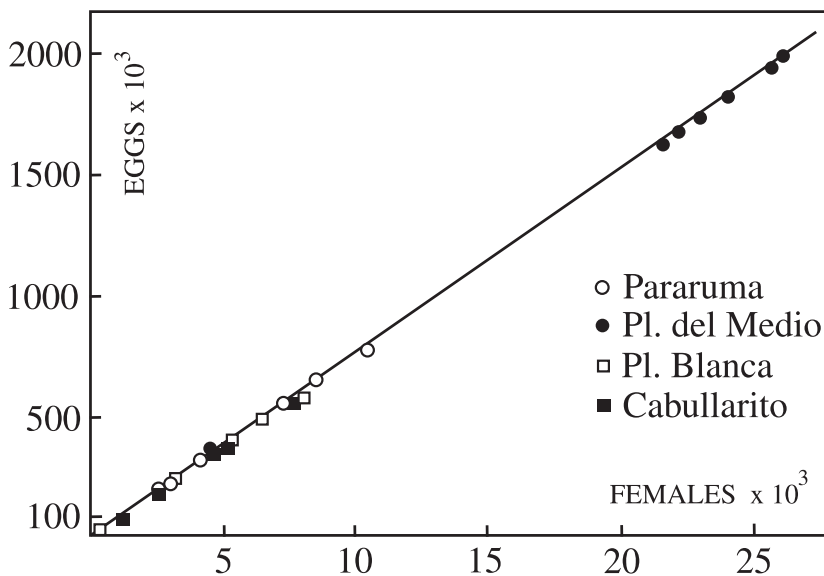
Fig. 1 – *Podocnemis expansa*. Regression of the number of eggs laid on the number of laying females, beaches on the Rio Orinoco (data from Ramirez-E. 1956).

COMMENTS

We have some scattered data that do not contain much information, but also seven excellent regression analyses from widely distributed localities.

Analysis of covariance shows that the slopes (which, it will be remembered, estimate the average clutch), are highly heterogeneous (F = 40039 for 6 and 44 degrees of freedom). Application of Tukey's test

TABLE II

Podocnemis expansa, **data on clutch size.**

Author	Beach	Nests	Eggs	Average
Mosqueira-Manso 1945	Pararuma	35	3172	90.6
Brito 1978	Aramiã	327	35897	109.9
	Axioma	110	12727	115.7
	Mapiciarí	239	37886	158.5
Vecchi 1978	Leonardo 1976-77	3167	265973	84.0
	1978	1478	133737	90.5

TABLE III

P. expansa, **clutch size, slope, Tukey's test.**

Sample	b
1. Pararuma	73.5
2. Playa del Medio	75.0
3. Playa Blanca	75.0
4. Cabullarito	75.0
5. Rio Branco	98.3
6. Leonardo	98.9
7. Juruá	122.6

(Table III) makes excellent geographic sense:

1. The four Orinoco samples cluster tightly at 75 eggs/clutch, in agreement with Blohm and Fernández-Yépez (1948), not with Mosqueira-Manso (1945).

2. The Trombetas and Rio Branco samples agree closely at nearly 100 eggs/clutch.

3. The Juruá sample stands out at 122 eggs/clutch; the geographically close Purus samples (Table II) also have high numbers.

HATCHING SUCCESS

It is safe to assume that no clutch will ever have a perfect hatching success. Mortality in the nest is unavoidable due to causes of three kinds: (i) intrinsic to the eggs (failure of fertilization or divers types of lack of viability); (ii) nest predation and (iii) drowning.

P. expansa nests during the low water season and hatches as the rivers begin to rise. Any premature rise of the river will result in a concomitant rise of the water table and flooding of the deeper layers of the nest. This has been witnessed many times. The clutches on which we have data were all protected against predators, so the causes of mortality must have been intrinsic or due to nest flooding.

The data available in the literature consist essentially of counts of excavated nests, specifying the number of young, live and dead, and of addled eggs. The quotient of the number of live young by the total sum is the hatching success.

Valle et al. (1973) have data on the hatching success of *P. expansa* at Taboleiro Leonardo for the seasons of 1965, 1966 and 1970-1972, for the beach at Monte Cristo, Rio Tapajós, for 1971 and 1972), and for the beach at Rolino, also in the Tapajós, for 1972. Table IV shows clearly that the years 1970 and 1971 were clearly anomalous, with very low survival rates; this is probably due to early rises of the Trombetas. As it was done in the case of clutch size, I tested graphically, on a scatter diagram, the presence of regression of the number of viable young against the number of eggs laid, excluding, the abnormal years. The regressions proved, as in the case of clutch size, to pass through the origin and to have extremely high coefficients of determination (Table V).

The data of Brito (l978) and Correa (1978) are amenable to the same type of analysis (Table V). Analysis of covariance showed all samples to be ho-

TABLE IV

***Podocnemis expansa*, data on hatching success.**

Author	Beach	Eggs		Success
		Laid	Hatched	
Mosqueira-Manso 1945	Pararuma	3172	2878	0.91
Valle, Alfinito & Silva 1973	Leonardo 1965	397500	300000	0.75
	1966	540000	472500	0.89
	1970	225000	45000	0.20 ←
	1971	236250	68748	0.29 ←
	1972	126308	98773	0.78
	Monte Cristo 1971	10836	8765	0.73
	1972	18293	13390	0.73
	Rolino	492	342	0.70
Brito 1978	Aramiã	35897	33522	0.93
	Axioma	12727	10030	0.79
	Mapiciarí	37886	31189	0.82
Vecchi 1978	Leonardo	251261	218338	0.87
Licata & Elguezabal 1997	Refúgio Arrau			0.82
Naturatins 2001	Lajeado	1719	400	0.56

TABLE V

***Podocnemis expansa*, regression of the number of live young on the number of eggs laid.**

N	R(x)	R(y)	b	a	F	r^2
Valle, Alfinito & Silva 1973						
Tapajós + Trombetas						
6	492-540000	342-472500	0.84 ± 0.036	-4284 ± 79667 ns	536.885***	0.9926
Correa 1978						
Rio Branco						
5	838-4440	423-3570	0.83 ± 0.044	-150 ± 688 ns	353.685***	0.9916
Rio Juruá						
5	2137-16888	1873-14538	0.86 ± 0.028	234 ± 2374 ns	922.330***	0.9968
Naturatins 2001						
6	72-216	40-105	0.37 ± 0.105	22 ± 9 ns	12.557*	0.7584

mogeneous ($F < 0.00015$); the joint regression has a coefficient of determination of 0.9926, and a coefficient of regression (average success) of 0.83. This is in agreement with the hatching success of $85.98\pm 1.066\%$ quoted by Alho and Padua (1982) for the beach at Leonardo and of 81.7% cited by Licata and Elguezabal (l997) for the Orinoco (Wildlife Refuge of the Arrau Turtle). It is less than the rate of ca. 95% cited (without further documentation) by Alho et al. (l979) for Leonardo.

Finally, Naturatins, the conservation agency of the state of Tocantins, is currently conducting a management program of *P. expansa* and *P. unifilis* in the area of influence of the hydroelectric plant at Lajeado, on the Rio Tocantins, one of the major rivers of Central Brazil. They have published (Naturatins 2001) very interesting data on the hatching success of eggs from transplanted nests of both species. It is obvious that these data cannot be directly compared with those obtained in more natural conditions, but

such a comparison is useful in estimating the success of the management policies. Tables IV and V indicate that hatching success of *P. expansa* under management is lower than in the other cases studied. When I first became aware of this I contacted the colleagues at Naturatins: they had already noticed the fact and were taking steps. This fully validates the use of these prospected data in the orientation of conservation practices.

COMMENTS

We have thus geographically variable clutch sizes and a practically fixed hatching success in the absence of predation. An extremely interesting, and to me unexpected, angle is the presence of uniformly high coefficients of determination, especially in what regards clutch size, with differences of close to 50% in number between river drainages and practically perfect correlations within any given drainage. This to me means that very severe selective pressures are at work, and explains the cases of geographical differentiation found. This can only be understood in the light of optimization theory: what is the most efficient investment a female can make in reproduction. I'll return to this.

RESULTS: *PODOCNEMIS UNIFILIS*

CLUTCH SIZE (TABLES VI AND VII)

Coutinho (1868) is the first author to mention clutches of *P. unifilis*. Based on his extensive experience in Amazonia, and without citing definite localities, he states that clutches vary from 25 to 30 eggs.

The next author is Mondolfi (1955), who studied turtles on the upper Orinoco valley (rivers Cunaviche and Capanaparo). He cites three nests, with 22, 24 and 28 eggs, and three autopsied females, with 14, 18 and 18. The difference between the two sets, small as they are, is statistically significant, and the data are better abandoned.

Medem (l960) cites four nests from the upper-Rio Caquetá, Colombian Amazonian, with 18-24 eggs (no further details). Medem (l964) had counts from 13 nests from the lower Rio Ariari, Colombian Amazonia. In 1969 Medem published on 24 nests from Isla Vieja, upper Rio Caquetá. His two sets of data are incompatible (t = 7.782***, 51 df). It is not probable that the difference be due to predation, which would have to have been very selective. These data are better not taken into consideration for the time being.

I (Vanzolini 1977 b) presented data on *P. unifilis* clutch size from the rivers Negro (Carvoeiro, Marová), Trombetas (Lago Jacaré) and Amazonas (Furo do Aiaiá). The samples (very small) do not show heterogeneity; the joint data are presented on Table VI. My archival data permit computation of the regression of clutch size on plastral length of the females; the fit is not ideal, but the presence of correlation is unmistakable.

Foote (1978) has a table on clutches from the area around Leticia and from the lower Putumayo (cited jointly), from which it is possible to compute the statistics for a sample of nests (Table VI).

Correa (l978) has data from the Rio Juruá, amenable to regression analysis (Table VII). As in the case of *P. expansa* treated above, the intercept does not differ significantly from zero and thus the slope estimates the mean clutch, in the case 25. The coefficient of determination, as in the case of *P. expansa,* is very high (0.9854), which again speaks for very strong selective pressures. Correa (*l.c.*) also mentions a total of 1469 eggs from 59 females from the Rio Purus – a mean of 24.9 ± 1.13, in close agreement with the Juruá sample.

Fachin (l982), in a thorough monograph on *P. unifilis* in the Iquitos area, presents data on 53 nests. Soini (l983) has two sets of data from the same Iquitos region. One, which I here shall call (a), consists of a distribution of frequencies of eggs in 7 nests, from which statistics can be computed straightforwards. The other, (b), is a table ("Cuadro 2") with clutch size statistics for the months of July, August and September-October of 1979 through 1982. This table affords some very interesting recalculations. It is possible to perform an analysis of variance, that shows the samples to be thoroughly homogeneous

TABLE VI

***Podocnemis expansa*, data on clutch size.**

Author	N	R	m	s	V
Mondolfi 1955 (nests)	4	22-28	24.0 ± 1.41	2.8	11.8
(females)	3	14-18	16.7 ± 1.33	2.3	13.9
Medem 1964	13	20-27	23.2 ± 0.61	2.2	9.5
1969	40	5-24	13.1 ± 0.70	4.5	34.2
Vanzolini 1977b	10	16-33	24.4 ± 1.63	5.1	21.1
Foote 1978	12	22-41	27.3 ± 1.65	5.7	20.9
Fachin 1982	53	22-43	31.1 ± 0.63	4.6	14.8
Soini 1983(a)	7	18-33	26.4 ± 2.34	6.2	23.4
1983(b): viii.1979	52		31.7 ± 0.97		
ix-x.1979	3		29.3 ± 2.67		
vii.1980	68		35.2 ± 0.81		
viii. 1980	86		33.8 ± 0.71		
ix-x.1980	7		26.3 ± 2.34		
vii.1982	33		37.0 ± 1.07		
viii.1982	70		33.9 ± 0.84		
ix-x.1982	19		33.3 ± 1.12		
Pritchard & Trebbau 1984	5	19-35	24.4		
Thorbjarnarson et al. 1993	22	14-31	23.3 ± 0.98	4.6	19.7
Souza & Vogt 1994	46		23.7 ± 0.69	4.7	19.6

TABLE VII

***Podocnemis unifilis*, regressions.**

N	R(x)	R(y)	b	a	F	r^2
Number of eggs on number of females (Correa 1978)						
5	161-1336	4772-34075	25.0 ± 1.76	1495 ± 5035 ns	202.140***	0.9854
Number of live young on number of eggs						
Medem 1969 15	9-24	8-22	0.92 ± 0.094	-1.123 ± 1.0833 ns	96.073***	0.8808
Correa 1978, Rio Juruá 5	4772-34075	4421-31842	0.93 ± 0.017	155 ± 4677 ns	2747.228***	0.9989
Fachin 1982 12	29-40	28-35	0.64 ± 0.087	11.0 ± 0.82***	53.734***	0.8431
Naturatins 2001 21	2-304	1-280	0.88 ± 0.039	-3.3 ± 15.48 ns	513.601***	0.9643
Number of eggs on plastral length (Vanzolini 1977b)						
10	293-409	17-33	0.13 ± 0.028	-20.6 ± 1.71***	22.061**	0.7739

(F = 0.757 for 8 and 337 df). They agree also, and closely, with Fachin's (1982) data. The data for the Iquitos area are very solid indeed. (Fachin (1993) used again his 1982 data, with no novelties in the analysis).

Pritchard and Trebbau (1984) have data for 5 nests in the Rio Cinaruco, Venzuelan Orinoquia, and Thorbjarnarson et al. (1993) have data on the Rio Capanaparo, another Orinoco tributary. Souza and Vogt (1994) have data on the Rio Guaporé, State of

Rondonia, Brazil (Table VI).

Looking at the geographic picture, it is seen that the coverage is ample. The Iquitos area stands out, with a large and homogeneous set of samples, with a range of at least 22-43 and a mean of 34.2 eggs per clutch. All other samples agree among themselves, with means varying from 23 to 27 eggs per clutch.

HATCHING SUCCESS

Medem (1969) has extensive data from Isla Vieja, Rio Caquetá. Plotting his number of young vs number of eggs shows that his materials can be separated in two groups: one with disastrous results (survival of 1-2 eggs), the other with better results, falling on a straight line, whose statistics are shown on Table VII.

Correa (l978) has summary data for the Rio Purus (Table VIII) and sets for 5 beaches on the Rio Juruá (Pupunha, Pato, Reforma, Joanico Central and São Sebastião), which are amenable to regression analysis (Table VII).

Fachin (l982) has a very heterogeneous set of data for the Iquitos area. I culled out the obviously divergent data, and did regression analysis on the remainder (Table VII). The regression does not pass through the origin, so it is not comparable with those so far seen. I present these data for the sake of completeness, but show also (Table VIII) the bulk rate. Finally, Soini (l983) has data for the Iquitos area (Table VIII).

TABLE VIII

Podocnemis unifilis, **hatching success.**

Author	Eggs	Young	Rate
Correa 1978, Rio Purus	1469	1430	0.973 ± 0.0042
Soini 1983	1206	944	0.783 ± 0.0119
Fachin 1982	399	377	0.970 ± 0.0061

As mentioned for *P. expansa*, Naturatins has published data on the hatching success of transplanted nests of *P. unifilis* on the Tocantins (Table VII). It is seen that the regression of young hatched alive on the number of eggs laid is excellent

($r^2 = 0.9643$), passes through the origin, and that the survival rate, 88% is normal for the species. This is a very successful management program.

COMMENTS

Looking at the ensemble of the data, it is seen that, out of five sets of data analyzed, success is above 90% in four, a little below 80% in one. The distributions of frequencies of Soini (l983) and Fachin (1982) for the Iquitos area differ statistically ($\chi^2 = 6.597$ for 1 df). The latter agrees with the ensemble of the data and of course should be preferred.

DISCUSSION

GEOGRAPHIC DIFFERENTIATION

A striking fact, noticeable for both species, is the very limited variability of clutch size, indicating strong selective control. This goes hand in hand with geographical variation in the clutch size of *P. expansa*, and, to a somewhat lesser degree, of *P. uniflis*.

Geographic variation in *P. expansa* had ben previously found by Sites et al. (1999), who studied microsatellite markers from seven beaches on the Rio Araguaia (Gaivota, Cascalho, Três Furos, Volta Grande, Rebojinho, Barreira Branca and Fazenda Montaria) and from one beach on the Rio Tapajós, near Santarém. They found homogeneity among the Araguaia samples, but sharp differences between this and the Tapajós materials.

Valenzuela (2001) also studied geographic variation in microsatellite markers of *P. expansa*, in four beaches on the Rio Caquetá (Centro, Guadual, Yarumal and Tamanco), spread along some 100 km of river; she further compared the Caquetá turtles with those from the Araguaia, using materials from the study of Sites et al. (1999). She found the expected differences between the two river basins, but also, unexpectedly, within the Caquetá. This is plausibly explainable in terms of the fidelity of the turtles to their taboleiros, where, moreover, they copulate gregariously immediately after laying.

However, I also found geographic differentia-

TABLE IX

Podocnemis. **Statistics of the distributions of frequencies of egg volume.**

Sample	Locality	N	R	m	s	V
P. unifilis						
Mondolfi 1955	Apure	5	21.9-24.2	22.80 ± 0.398	0.86	3.8
Foote 1978*	Leticia, Içá			20.09		
Fachin 1982*	Samiria			19.94		
MZUSP 2890	Fonteboa	35	09.8-19.8	14.93 ± 0.380	2.24	15.1
2880	Coarí	18	14.2-20.7	15.90 ± 0.354	1.50	9.5
2881	"	6	10.3-12.4	11.65 ± 0.317	0.78	6.7
2506	Trombetas	12	22.6-26.2	24.32 ± 0.347	1.20	4.9
2510	"	17	14.4-17.3	15.59 ± 0.177	0.73	4.7
2511	"	16	15.2-21.7	19.38 ± 0.377	1.51	7.8
2708	"	11	27.4-29.7	28.50 ± 0.221	0.71	2.6
2874	"	10	14.7-18.5	16.09 ± 0.443	1.40	8.7
2891	"	13	13.7-17.7	14.90 ± 0.295	1.06	7.1
2892	"	19	14.9-18.9	16.37 ± 0.269	1.17	7.2
4014	Araguaia	23	19.4-23.6	21.27 ± 0.246	1.18	5.6
P. expansa						
MZUSP 2870	Trombetas	4	30.2-40.6	35.05 ± 2.142	4.28	12.2
2871	"	5	25.8-30.2	26.80 ± 1.012	2.66	8.4

*calculated from averages.

tion in clutch size and hatching success in *P. unifilis*, which is not known to be faithful to particular beaches, or to have herd behavior. There have been no genetic studies of this species.

OPTIMAL EGG-SIZE THEORY

The strict control of clutch size leads us into optimal egg size theory (OES), which opposes size of offspring to size of clutch: "offspring size is usually less variable than offspring number"... "a well-founded assumption of these [OES] models" (Rowe 1994: 35). Or else: "they all agree with OES that fluctuation in resources for reproduction should affect clutch size, whereas egg size within a female should remain relatively constant" (Roosenburg and Dunham 1997: 290). Or, still: "...a major prediction from OES theory is that, within a population, the amount of variation in reproductive output among females should result primarily from variation in the number of osffspring produced and secondarily from variation in egg size" (Congdon 1989: 367).

Reliable estimates of egg volume can be indirectly obtained from measurements of egg diameters (Vanzolini 2001). We have in the Museum collection eleven samples f *P. unifilis* eggs from a variety of Brazilian localities. In the literature, Mondolfi (l955) has measurements of 5 eggs. Fachin (l982: Table V) has a table containing average diameters of eggs from the Rio Samiria. Analogous data can be read from Foote's (1978) Figure 3. (Volumes calculated from diameter averages coincide within 1% with volumes analytically determined. It goes without saying that no estimates of variance can be obtained, but the visual comparisons are nevertheless valuable). All the data available are shown on Table IX, where are also included the data for two samples of *P. expansa* eggs, collected by myself at the Taboleiro Leonardo, Rio Trombetas. They were
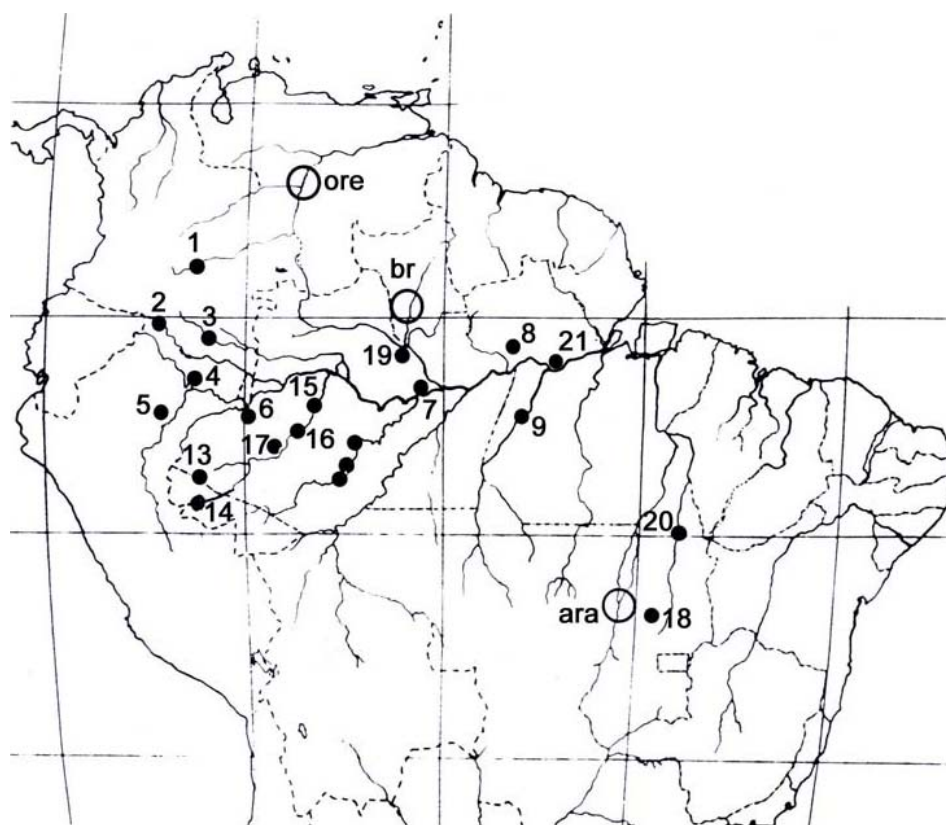
Fig. 2 – Beaches mentioned. 1, Rio Ariari. 2, Isla Vieja. 3, Rio Caquetá (Centro; Guadual; Tamanco; Yarumal). 4, Iquitos. 5, Rio Samiria. 6, Leticia. 7, Ajaratuba. 8, Rio Trombetas (Lago Jacaré; Taboleiro Leonardo). 9, Rio Tapajós (Monte Cristo; Rolino). 10, Rio Purus (Pato; Joanico Central; Joanico do Pato; Joanico Central). 11, Rio Juruá (Pupunha; Harmonia). 12, Rio Juruá (Onça; São Sebastião). 13, Rio Juruá (Floresta). 14, Rio Juruá (Reforma). 15, Rio Purus (Aramiã). 16, Rio Purus (Axioma). 17, Rio Purus (Mapiciarí). 18, Barreira Branca. 19, Rio Negro (Carvoeiro; Marová). 20. Rio Tocantins (Lajeado). ARA, Rio Araguaia (Rebojinho; Volta Grande; Ilha do Cascalho; Três Furos; Gaivota; Fazenda Montaria). BR, Rio Branco (Ilha Aicurá; Anta; Mandulão; Pacheco; Santa Fé). ORE, Rio Orinoco, Pararuma region (Cabullarito; Rio Arauca; Rio Cunaviche; Playa Blanca; Rio Capanaparo; Rio Cinaruco; Playa del Medio; Refugio de la Tortuga Arrau; Pararuma).

freshly laid eggs unearthed by subsequent females.

Simple inspection of Table IX shows much variation in egg volume. Analysis of variance for the 7 samples from the Trombetas (a compass of 120 km) afforded a value of $F = 248.517^{***}$ for 6 and 91 d.f. Analysis of variance including all available materials also affords a high value of F (130,535***, 11 and 173 d.f.), but Tukey's test reveals no regularities – it rather stresses the extreme and uneven, patternless, character of the variation.

The only two samples of *P. expansa* eggs available, already laid, collected within meters and minutes of each other, differ significantly (t = 3.744**, 7 d.f.) in volume.

The present data were prospected, not obtained from planned and orderly executed research. Even so, they permit to say that these two large species of river turtles fail to obey an important pattern predicted by optimal egg-size theory.

Criticism has been raised against the applica-

GAZETTEER

Latitudes South and longitudes West taken for granted. l.b. = left bank; r.b. = right bank.

Aiaiá, Furo, enters the Rio Amazonas (r.b.) at 0230, 5420.

Aicurá, Ilha (Rio Branco), 0034 N, 6137.

Ajaratuba (Rio Amazonas), 0337, 6112.

Anta (Rio Branco), 0035 N, 6147.

Aramiã (also Arimã) (Rio Purus), 0547, 6358.

Arauca, Rio, enters the Rio Orinoco (l.b.) at 0724 N, 6635

Ariari, Rio, enters the Rio Guaviare (l.b.) at 0235 N, 7247

Arrau, Refugio de la Tortuga (Rio Orinoco), between 0625 N and 0634 N.

Axioma (Rio Purus), 0645, 6431.

Barreira Branca (Rio Crixás Açu), 1342, 4858.

Branco, Rio , enters the Rio Negro (l.b.) at 0124, 6151.

Cabullarito (Rio Orinoco), 0735 N, 6626.

Capanaparo, Rio, enters the Rio Orinoco (l.b.) at 0701 N, 6707.

Caquetá, Rio, enters the Rio Amazonas (l.b.), with the Brasilian name of Japurá, at 0308, 6446.

Carvoeiro (Rio Negro), 0126, 6201.

Cascalho, Ilha (Rio Araguaia), 1259, 5034.

Centro (Rio Caquetá), 0102, 7129.

Cinaruco, Rio, enters the Rio Orinoco (l.b.) at 0639 N, 6708.

Crixás Açu, Rio, enters the Rio Araguaia (r.b.) at 1319, 5036.

Cunaviche, Rio , enters the Rio Arauca (r.b.) at 0719 N, 6711.

Floresta (Rio Juruá), 0734, 7225.

Gaivota (Rio Branco), not located.

Gaivota (Rio Araguaia), 1306, 5036.

Guadual (Rio Caquetá), 0051, 7133.

Guaporé, Rio , enters the Rio Mamoré (r .b.) at 1154, 6501.

Guaviare, Rio, enters the Rio Orinoco (l.b.) at 0403 N, 6744.

Harmonia (Rio Juruá), 0535, 6736.

Iquitos (Rio Amazonas), 0347, 7313.

Jacaré, Lago (Rio Trombetas), 0118, 5647.

Joanico Central (Rio Juruá), 0352, 6623.

Joanico do Pato (Rio Juruá), 0352, 6623.

Juruá, Rio, enters the Rio Amazonas (r.b.) at 0237, 6550.

Lajeado (Rio Tocantins), 0945, 4821.

Leonardo, Taboleiro (Rio Trombetas), 0120, 5645.

Leticia (Rio Amazonas), 0409, 6957.

Madeira, Rio, enters the Rio Amazonas (r.b.) at 0322, 5845.

Mamoré, Rio, enters the Rio Madeira (r.b.) at 1024, 6563.

GAZETTEER (continuation)

Mandulão (Rio Branco), 0009 N, 6147.

Mapiciarí (Rio Purus), 0705, 6437.

Marová (Rio Negro), 0109, 6235.

Montaria, Fazenda (Rio Araguaia), 1322, 5041.

Monte Cristo (Rio Tapajós), 0404, 5539.

Negro, Rio, enters the Rio Amazonas (l.b.) at 0308, 5955.

Nova Olinda (Rio Juruá), 0412, 6627.

Onça (Rio Juruá), 0609, 6753.

Pacheco (Rio Branco), 0032 N, 6142.

Pararuma (Rio Orinoco), 0629 N, 6708.

Pato (Rio Juruá), 0350, 6621.

Playa Blanca (Rio Orinoco), 0711 N, 6658.

Playa del Medio (Rio Orinoco), 0630 N, 6706.

Pupunha (s) (Rio Juruá), 0506, 6710.

Purus, Rio, enters the Rio Amazonas (r.b.) at 0342, 6128.

Putumayo, Rio, enters the Rio Amazonas (l.b.), with the Brasilian name of Içá, at 0307, 6759.

Rebojinho (Rio Araguaia), 1246, 5042.

Reforma (Rio Juruá), 0828, 7252.

Rolino (Rio Tapajós), 0412, 5555.

Samiria, Rio, enters the Rio Marañon (r.b.) at 0442, 7413.

Santa Fé (Rio Branco), 0028 N, 6145.

Santa Helena (Rio Juruá), 0412, 6627.

São Sebastião (Rio Juruá), 0624, 6750.

Tamanco (Rio Caquetá), 0043, 7147.

Tapajós, Rio, enters the Rio Amazonas (r.b.) at 0224, 5441.

Três Furos (Rio Araguaia), 1300, 5034.

Trombetas, Rio, enters the Rio Amazonas (l.b.) at 0155, 5535.

Ucayali, Rio, enters the Rio Amazonas (r.b.) at 0430, 7327.

Vieja, Isla (Rio Caquetá), 0008, 7412.

Volta Grande (Rio Araguaia), 1249, 5037.

Yarumal (Rio Caquetá), 0056, 7135.

tion of optimization theory to turtle reproduction from another angle. Congdon and Gibbons (l987) show that, in two smaller North American emydids, pelvic structure constrains (and thus increases the variability of) egg size.

Of course, it is not to be hoped that field work on the reproduction of podocnemidid turtles will contribute much to OES, since the latter leans heavily on generalized models of competition theory (Smith and Fretwell 1974, Brockelman 1975) – a dimension signally lacking in podocnemidid research.

It seems to me that a laborious, but simple and

rewarding field of research opens itself, emphasizing concomitant description and interpretation of reproductive strategies of podocnemidid turtles.

RESUMO

Dados sôbre tamanho da ninhada e viabilidade dos ovos foram colhidos na literatura para 7 praias tradicionalmente usadas por *P. expansa* para reprodução, e re-analisados por análise de regressão, do número de ovos sobre o número de fêmeas (ou de ninhos) e de filhotes sobre ovos postos. Todas as regressões foram lineares, passando pela origem, e com altíssimos coeficientes de determinação. O tamanho médio da ninhada variou de 75 a 123, e mostrou diferenciação geográfica: (i) Rio Orenoco, (ii) Rio Trombetas + Rio Branco e (iii) Rio Juruá + Rio Purus. A viabilidade média não mostrou diferenciação geográfica, ficando em cerca de 83%. Em *P. unifilis* também houve diferenciação geográfica, as amostras da região de Iquitos tendo valores muito altos. A viabilidade média foi alta: apenas uma amostra, de Iquitos, teve sucesso inferior a 90%. Os altos valores do coeficiente de determinação levam à consideração do volume dos ovos, que se revelou muito variável em ambas espécies, em contradição com idéias correntes sobre teoria do volume ótimo dos ovos.

Palavras-chave: reprodução de quelônios, viabilidade, tamanho da ninhada, teoria de tamanho ótimo do ovo, *Podocnemis expansa*, *Podocnemis unifilis*.

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