THE HERPETOLOGICAL JOURNAL

BRITISH HERPETOLOGICAL SOCIETY

FRONT COVER: Aberrant *Drymobius rhombifer* from Brazil (S. Elmhurst)

GROWTH CURVE FOR CAPTIVE -REARED GREEN SEA TURTLES, *CHELONIA MYDAS*

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ABSTRACT

Growth of the captive- reared green sea turtle, *Chelonia mydas*, fits a logistic by weight growth equation reaching an asymptotic weight at approximately 12.5 years with an average weight of 156 kg. The relationship of weight to carapace length and width is inter-dependent with age and size of the turtle. Mean age at sexual maturity for the captive green turtle is estimated at 16 years, and it is projected that 96% of a captive population would begin nesting at 25 years of age. Although growth of mature green turtles reaches an asymptote at 12.5 years, captive, mature green turtles continue to increase in weight at a rate of 3 kg/yr.

INTRODUCTION

Cayman Turtle Farm, Cayman Islands, British West Indies, has cultured the green sea turtle *Chelonia mydas* for 25 years. During this period of time, culture techniques have been refined and improved to obtain optimum growth and health of the herd based upon physical and economic parameters. Since 1980, a proportion of the production of the Farm has been released into the waters surrounding the Cayman Islands. Ongoing tag and recapture programmes of the Farm monitor the success of the release programme. An important aspect of this works lies in the comparison of the growth of the released turtles with those maintained in captivity.

Several investigators have fitted data collected from natural populations to various growth equations (Frazer & Ehrhart, 1985; Bjorndal & Bolten, 1988; Frazer & Ladner, 1986). Growth rates and patterns from these investigations are based upon time interval growth data, since the absolute age of the turtles are unknown. In most instances, the size range of the turtles surveyed for any study area is restricted due to the use of the area by the population, i.e. as a feeding ground or breeding area. A complete growth model from hatching to adult for a sea turtle natural population is therefore not available.

Most commonly, growth data from natural populations has been fitted to either logistic or von Bertalanffy growth equations and on the basis of carapace length as compared to weight of the turtle. The age of sexual maturity for any sea turtle species is not clearly defined. Estimates range from 15-50 years for the green sea turtle and various factors appear to influence the projected age at sexual maturity (Groombridge, 1982).

METHODS AND MATERIALS

Turtles at Cayman Turtle Farm, CTF, are maintained in tanks or an excavated pond (Wood, 1991). The turtles are moved through a series of tank sizes and stocking densities to facilitate feeding and handling. Tank size and stocking density increase with the size of the turtle. Hatchlings are kept in small, rectangular tanks with an approximate volume of 600 litres, while the older turtles are kept in circular tanks ranging in volume from 3,000 to 130,000 litres. Tanks are constructed of concrete block or fibreglass walls with concrete bottoms. Unfiltered sea water is pumped continuously into the tanks at an approximate exchange rate of one volume per 20 minutes.

Average daily water temperature ranges from 27°C in January to 30°C in July.

Turtles are fed a floating, pelleted diet. Until the turtles are approximately one year old, they are fed a modified trout chow (Ralston Purina, St. Louis, MO) containing 40% crude protein, 8.0% crude fat and less than 5.0% crude fibre. Older turtles, including the breeding herd, are fed turtle chow (Ralston Purina, St. Louis, MO) containing 35% crude protein, 3.5% crude fat, and less than 5.0% crude fibre. Feed conversion varies from 1.2 to 6.5 units of diet as fed to unit of body weight gain, increasing with the size of the turtle. The hatchlings are fed *ad libitum* while the growing stock over one year of age is fed a regulated daily ration decreasing from 2.0% body weight per day to 0.4% as the turtles grow.

The majority of the size data represented in this paper is the accumulation of stock records collected by CTF personnel under working conditions. The English measuring system is routinely used in the CTF operation. Consequently, in describing the methodology, the English units will be used as applicable. In analysis of the data, data are converted into metric units for presentation. Breeders are weighed individually in February with a commercial, crane mounted scale weighing to within one pound. The curved carapace length, CCL, (from the leading edge of the nuchal scute to the notch between the two supracaudals) and curved carapace width, CCW, (as measured at the widest part of the carapace from the edge of the marginals) are measured with a fibreglass sewing tape to the nearest 0.5 inch.

Periodically, tanks of turtles are weighed to assess the growth of the herd. Any given tank will hold turtles from one age class. As hatching occurs from June through November, the age range within a tank may vary within 6 months. However, 70-80% of the turtles are within two months of age, and the age of each age class is based on the month of hatch of the majority of the group. Turtles within the tank are weighed several at a time and total weight for the tank is used to obtain an average weight per turtle. Farm weight data from May 1985 through October 1990 were used for turtles ranging in age from 5 months to 63 months, as feeding and stocking parameters were constant during this time period.

Weights of turtles less than five months were based on

individual weights of hatchlings, weighed to the nearest 0.1 g.

For comparison of straight line versus curved carapace measurements, straight line carapace length, SCL, (from the leading edge of the nuchal scute to the notch between the supracaudals) and the straight line carapace width, SCW, (as measured at the widest part of the carapace from the edge of the marginals) were measured with callipers to the nearest 1/8 inch.

Individual weights (to the nearest ounce) and SCL, CCL, SCW, and CCW (to the nearest 1/8 inch) were measured for turtles from 5 age classes for the comparison of weight versus length/width measurements within age classes. With repetitive measurements, accuracy of the measurements was estimated to be ±4% (2% error in callipers or scales and 2% error in reproducibility).

Size data are fitted to two growth equations commonly used to describe animal growth (Kaufman, 1981) and which appear to represent empirical data for the green sea turtle. The logistic growth equation is of the general form (Mead & Curnow, 1983):

$$Y = A/(1+Be^{-kt}) \tag{1}$$

The von Bertalanffy growth equation is of the general form (Fabens, 1965):

$$Y = A(1-Be^{-kt}) \tag{2}$$

In both equations Y represents size; A, size at the asymptotic value; B, parameter related to size at birth; e, base of natural logarithm; k, constant rate of growth; t, time.

Statistical procedures were done on an IBM compatible computer utilising a commercially available software package (Statgraphics, Statistical Graphics Corporation, Rockville, MD). Nonlinear regression analysis is based upon the procedure developed by Marquardt (1963) to determine the estimate that minimises the residual sum of squares.
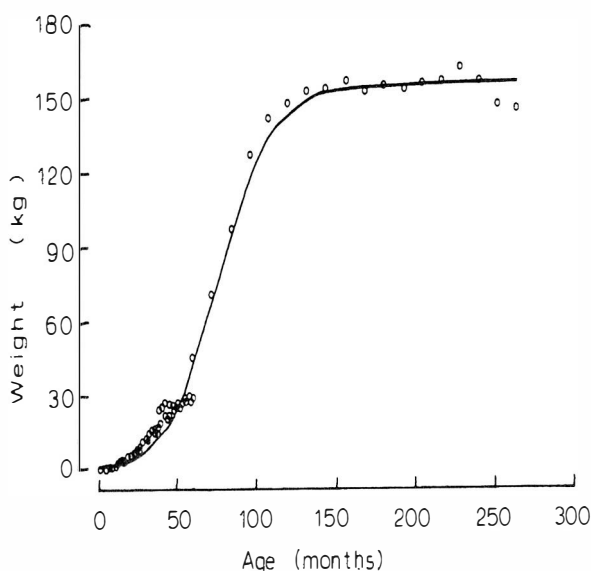

Fig. 1. Logistic by weight growth curve for the captive reared green sea turtle. Circles represent average weight (kg) for each age class (total N for all age classes=127,782). Solid line represents fitted non-linear regression line.

Source	SS	df	MS	F
Logistic:				
Mode	1377450.96	3	125816.99	4750.65 *
Error	1694.99	64	26.48	
Total	379145.95	67		
von Bertalanffy:				
Model	359561.93	3	119853.98	391.68 *
Error	19584.02	64	306.00	
Total	379145.95	67		

TABLE 1. Analysis of variance for the non-linear regression of logistic and von Bertalanffy growth equations for the green sea turtle (*P<.001).

Variable	Weight (kg)	CCL (cm)	CCW (cm)
Average	3.02	29.1	24.9
SD	0.92	3.2	2.9
Range	0.7-6.3	18-38	13-36
Coeff. of Var.	30.6	11.1	11.6

TABLE 2. Size data for 1202, 14 month old green sea turtles.

Analysis of variance utilises the least squares approach to estimate the regression and ANOVA. The Student-Newman-Keuls method was used for multi-range tests.

RESULTS

Fig. 1 shows the growth curve generated using a logistic by weight equation with the equation:

$$Y = 156/(1+105e^{-0.060t}) \tag{3}$$

Table 1 compares the ANOVA for the regression of the data utilising both the logistic and von Bertalanffy equation as both equations have been used in analysis of growth data for sea turtle populations. Each point in Fig. 1 at any given age represents average weight for turtles of that age. Sample size ranges from 8 to 8505 per age class with an average sample size for age class of 1907±2212. No data are presented for the variance in weight within each age class as the majority of the data presented represents group weights as previously explained.

To appreciate the variance that is encountered among turtles of the same age, Table 2 presents data for a group of 14 month old turtles. Individuals of this particular group of turtles are within 30 days of the same age. The coefficient of variation clearly indicates that variability within weights (cv = 30.6) is substantially greater than that within lengths (cv = 11.1).

Table 3 presents weight, SCL, CCL, SCW, and CCW for groups of different age turtles. For the five age groups of immature turtles each sample represents a known age group. For the sample of mature turtles, the sample includes known age, as well as unknown age, turtles, but all are sexually mature.

	Weight (kg)	CCL (cm)	CCW (cm)	SCL (cm)	SCW (cm)
Age = 8 months, N = 2 5					
Mean	1.63	23.3	20.1	22.4	18.8
SD	0.33	1.5	1.3	1.4	1.5
Range	1.08-2.22	21.0-26.0	17.8-22.2	19.7-25.4	16.2-21.9
Coeff. of Var.	20.2	6.3	6.4	6.5	8.0
Age = 20 months, N = 20					
Mean	5.9	36.4	31.4	34.9	28.8
SD	1.76	3.6	2.7	3.3	2.5
Range	3.61-10.31	31.4-44.1	26.7-36.8	29.5-42.2	24.4-3 .3
Coeff. of Var.	29.9	10.0	8.6	9.5	8.7
Age = 32 months, N = 20					
Mean	8.68	42.1	36.3	40.1	32.8
SD	2.37	4.3	3.4	4.1	3.7
Range	5.09-13.66	33.7-50.2	21.4-43.2	32.1-47.3	26.4-39.1
Coeff. of Var.	27.3	10.1	9.2	10.2	11.2
Age = 44 months, N = 20					
Mean	24.6	59.5	52.3	55.7	44.1
SD	10.0	7.3	6.5	7.2	5.7
Range	12.7-46.8	48.6-73.4	43.5-63.8	43.2-68.3	34.3-54.3
Coeff. of Var.	40.6	12.3	12.5	13.0	13.0
Age = 56 months, N = 20					
Mean	26.7	60.6	53.5	55.4	45.6
SD	12.4	9.0	8.4	8.0	7.2
Range	11.4-52.3	46.0-77.8	40.9-68.9	41.9-69.9	33.7-57.9
Coeff. of Var.	46.3	14.9	15.7	14.5	15.8
Mature Breeders, N = 219					
Mean	146.2	102.6	90.6	96.2	72.5
SD	25.6	5.5	6.4	4.6	4.2
Range	8.7-227.7	86.4-114.3	74.9-106.7	81.3-105.4	61.0-82.5
Coeff.of Var.	17.5	5.3	7.1	4.8	5.8

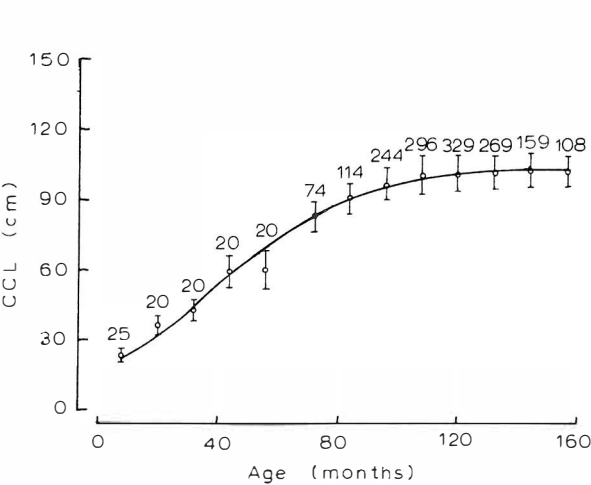TABLE 3. Weight. CCL. CCW. SCL. and SCW for six age classes of green turtles.

Fig. 2. Logistic by length growth curve for the captive green sea turtle. Mean curved carapace length, CCL (cm), ±SD represented by circles with bars for turtles within an age class. Number of turtles in each age class given above mean (total N for all age classes=1.698). Solid line represents fitted non-linear regression line.

Within each sample group. the greatest variability for the size measurement occurs in weight with measurement of carapace size, SCL, CCL, SCW, and CCW, showing similar variability.

The relationships between the different carapace measurements and weight are expressed as ratios in Table 4. An analysis of variance among age classes shows a significant difference ($P < .001$) for each relationship. except CCW to CCL. A Student-Newman-Keuls analysis is used to determine significant differences between means as noted in Table 4. The most obvious correlation is noted in the ratio of weight to either length or width. which increases with increasing size and age.

Using available size measurements for the five groups of immature turtles represented in Table 3 and for older turtles of known age. the CCL and weight can be fitted to a logistic growth equation. as shown in Fig. 2. which includes individual data points. The length data fits the logistic by length equation:

$$Y = 104/(1 + 52.8e^{-0.064t}) \tag{4}$$

Age Class	SCL/CCL	Weight/CCL	Ratio CCW/CCL	SCW/CCW	Weight/CCW
8 months	.962 ± .029[c]	.069 ± .010[a]	.862 ± .020[a]	.938 ± .036[d]	.081 ± .011[a]
20 months	.956 ± .023[c]	.159 ± .030[a,b]	.864 ± .024[a]	.917 ± .038[c,d]	.185 ± .038[a,b]
32 months	.951 ± .021[c]	.203 ± .037[b]	.864 ± .037[a]	.903 ± .045[c]	.235 ± .046[b]
44 months	.934 ± .031[b]	.401 ± .113[c]	.878 ± .019[a]	.843 ± .045[b]	.456 ± .127[c]
56 months	.914 ± .037[a]	.424 ± .131[c]	.883 ± .041[a]	.855 ± .076[b]	.479 ± .144[c]
Breeders	.938 ± .018[b]	1.42 ± 0.20[d]	.883 ± .040[a]	.802 ± .039[a]	1.61 ± 0.24[d]

TABLE 4. Relationship of carapace measurements and weights among age classes. Means ±SD that are significantly different ($P<0.05$) for a given relationship have different superscripts (ANOVA, Student-Newman-Keuls multiple range test).

	Weight (kg)	CCL (cm)	CCW (cm)
Mean	151	101	86
SD	32	7.4	6.4
Minimum	80	81	69
Maximum	232	119	102

TABLE 5. Size of 80 captive reared green sea turtles for the first nesting season.

The weight data for the same turtles fit the logistic by weight equation:

$$Y = 157/(1+119e^{-0.064t}) \qquad (5)$$

Table 5 shows the average size at which 80 females began nesting. The range is considerable, varying from 84 to 232 kg and 82 to 119 cm (CCL). Comparing the size of these females

in years prior to and following first nesting in Table 6, there is a continued pattern of growth following maturity, although at a much lesser rate, in keeping with the growth curve of Fig. 1. The percentage change in length after maturity is less than the percentage change in weight after maturity. Assuming a linear relationship for the narrow range prior to and following maturity, the percent change in weight is 4.7%/yr and 1.3%/yr prior to and after first nesting, respectively. This compares to 1.7%/yr and 0.3%/yr for percent change in length. Table 7 shows a similar pattern of increased size for 1647 female seasons for CTF's stock of females which were obtained as mature adults. The linear regression of weight versus subsequent season following first observed nesting shows an increase in weight of 3.1±0.2 kg/yr and an increase in length of 0.42±0.05 cm/yr. Respective coefficients of correlation are .957 and .917 for weight or length linear regression versus year, respectively.

There is no significant difference among ages for size at sexual maturity ($F=1.024$, $P = 0.42$ and $F=0.884$, $P =0.51$, respectively for weight and CCL) for the 59 known age females nesting for the first time. For these 59 known age

Season	N	Weight (kg)	SD (kg)	CCL (cm)	SD (cm)
0	136	143	31[a]	104.1	7.6[a]
1	145	139	35[a]	104.8	8.3[a]
2	141	142	37[a]	104.8	8.6[a]
3	140	145	37[a]	105.2	8.6[a]
4	138	147	37[a,b]	105.3	8.8[a]
5	133	147	37[a,b]	105.6	8.3[a]
6	129	151	38[a,b]	105.6	8.4[a]
7	125	152	37[a,b]	105.6	8.0[a]
8	101	153	40[a,b]	106.4	8.6[a,b]
9	96	157	40[a,b,c]	106.5	8.5[a,b]
10	88	161	42[a,b,c]	106.7	8.6[a,b]
11	76	161	41[a,b,c]	107.0	8.6[a,b]
12	58	164	41[a,b,c]	107.3	9.4[a,b]
13	46	170	44[b,c,d]	107.7	9.3[a,b]
14	38	178	45[c,d,e]	108.8	9.3[a,b,c]
15	27	188	46[d,e]	111.3	10.1[b,c]
16	20	188	45[d,e]	111.5	10.5[b,c]
17	10	193	51[e]	112.4	11.1[c]

TABLE 7. Comparison of weights for captive wild females following first observed nesting season=0 in captivity. Means with different superscripts are significantly different ($P<0.05$).

Season	N	Weight (kg)	SD (kg)	CCL (cm)	SD (cm)
-7	3	95	27[a]	87.2	8.9[a]
-6	3	118	24[a,b]	93.6	7.0[a,b,c]
-5	4	101	44[a]	88.9	14.2[a,b]
-4	9	118	38[a,b]	94.8	10.9[b,c,d]
-3	18	125	33[a,b,c]	95.9	9.0[b,c,d,e]
-2	38	127	32[a,b,c,d]	96.5	7.9[c,d,e]
-1	61	139	31[b,c,d,e]	99.2	7.5[c,d,e]
0	80	152	32[b,c,d,e]	110.8	7.4[c,d,e]
1	74	144	27[b,c,d,e]	101.4	6.6[c,d,e]
2	68	152	31[b,c,d,e]	101.8	6.8[c,d,e]
3	61	155	32[b,c,d,e]	103.0	6.6[c,d]
4	55	158	31[b,c,d,e]	104.0	6.1[e]
5	49	162	32[c,d,e]	104.5	6.8[e]
6	46	165	34[c,d,e]	104.5	6.9[e]
7	44	163	33[c,d,e]	104.7	6.9[e]
8	43	166	35[c,d,e]	105.0	6.6[e]
9	43	172	36[e]	105.2	6.7[e]
10	37	174	36[e]	105.4	6.6[e]
11	23	169	34[d,e]	103.8	5.8[e]
12	13	173	43[e]	104.1	6.5[e]
13	6	169	37[d,e]	104.6	5.6[e]

TABLE 6. Comparison of weights and CCLs for farmed reared turtles prior to and following first nesting season. Season designated as year preceding or following first nesting season=0. Means with different superscripts are significantly different ($P<0.05$).

females, the average age of first nesting was 10.0 ± 1.5 yr. Herd management at CTF resulted in the culling of all non-nesting females of known age in 1980. Since then additional turtles have been added to the breeding herd. To estimate average age of sexual maturity for captive reared turtles, the percentage of females nesting from a known age class can be calculated and accumulated as shown in Table 8. The coefficient of correlation for the linear regression of percentage mature turtles within an age class versus age is .971. The linear model, $y = a + bx$, yields a value of $a = 34\pm6$ and $b = 5.2\pm0.5$ for y = percentage of females nesting from a known age class and x = age of class (in years). Consequently, at 16 years of age, 50% of the females should begin nesting and at 25 years of age, 96% of the population should begin nesting.

Age (yr)	No. in Age Class	No. Nesting	% Age Class Nesting	Cumulative % Nesting
8	202	7	3.5	3.5
9	192	17	8.9	12.4
10	182	18	9.9	22.3
11	161	9	5.6	27.9
12	96	3	3.1	31.0
13	54	0	0.0	31.0
14	26	2	7.7	38.7
15	21	1	4.8	43.5

TABLE 8. Age at first nesting for 57 farmed reared green sea turtles relative to total no. in respective age class.

DISCUSSION

For the captive green sea turtle, the logistic growth equation best describes the growth of the animal. The logistic curve is sigmoid in shape and represents growth from a very small initial stage, in which growth is proportional to size, to later stages when size approaches an asymptote. In examining the curve of Fig. 1 as described by Equation (3), the following points must be kept clearly in mind. First, the average size of groups of turtles of the same age are used for generating the curve. As Table 2 indicates the variability in these values is considerable with an expected coefficient of variation greater than 30 for weight size data. Practical experience at CTF has shown that smaller turtles will demonstrate the same percentage weight gain as larger turtles. Consequently, the relative size of the turtle is not expected to change the shape of the curve, but whether the individual lies above or below the average.

Secondly, the size data for turtles 63 months and younger are based on stock tank weighings, and for turtles 72 months and older are based on average weights of turtles that have been separated for inclusion in the breeding herd. The effect of this management strategy on the growth rate of the turtles is not defined.

Thirdly, the generated growth curve is based on culture conditions, with regulated diets, controlled water quality and obviously restricted range movements. Although the growth curve is beneficial in economic forecasting for CTF, its application to natural conditions remains comparatively limited. As CTF releases both hatchling and yearling turtles each year, the pattern of growth observed

from recaptures can be compared with what is expected if the turtles had been maintained in captivity.

For herd assessment, weight data is the most beneficial and easiest obtained. However, Table 3 clearly indicates that for monitoring the growth of individuals within a population over a period of time, length or width data would be preferable as the variability within the measurement is considerably less. Bjorndal & Bolten (1988), elaborated on this in their assessment of growth rates of immature green turtles in the southern Bahamas. Practically, curved carapace measurements are the easier to obtain. Length measurements are preferable over width measurements as the points of reference for taking length are more clearly defined than for width.

The relationship of carapace measurements to each other remain reasonably constant for immature turtles, suggesting that conversion from one measure to another would be valid in relation to the expected error in measurement. The relationship of weight to carapace size, however, increases with increasing age or size. A ratio of weight to carapace size has been used at CTF in previous years to assess the development of the breeding herd.

Both fitted logistic by weight equations (3) and (5) and the fitted logistic by length equation (4) over-estimate the size of the green turtle at hatch. The calculated weights and length are 1.47 kg, 1.31 kg, and 16.6 cm (CCL), respectively. Observed weight and length for green hatchlings average 0. 027 kg and 5. 27 cm (SCL) . At 14 months, the calculated weights and length are 3.37 kg, 3.17 kg, and 26.4 cm (CCL), respectively, compared to 3.02 kg and 29.1 cm (CCL) as recorded from Table 2 . Consequently for the first few months of the growth curve, fit is extremely poor. In comparison, the fitted von Bertalanffy equation for the data as presented in Table 1, shows an even poorer fit at $t=0$, with A = -26.7 kg calculated weight at birth.

The data in Tables 6 and 7 suggest that the green sea turtle continues to increase in size following maturity. However, in observing individual turtles in subsequent years, the individual's weight will fluctuate as much as 13%. Consequently, several years are needed to observe this continued growth for mature turtles. There is also no significant difference in

weight or CCL ($P<.05$) between nesting and non-nesting seasons. Although the green sea turtle may lay an egg mass totalling 25% of her body weight, this difference is not detected in her weight as measured in February for nesting in May through August under farm conditions.

Since the culling of known age potential breeders in 1980, additional turtles have been selected from CTF stock for addition to the breeding herd. Presently, 28 females, ages 12-18 years, average age 15 years, form part of this group. Another 29 females, less than 7 years of age, have also been set aside, with additional turtles to be selected each year. Of the 28 females of potential nesting status, 10 have begun nesting. Based on Table 8, 12 of these turtles should have begun nesting. Future seasons will continue to update the reliability of the projections.

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LIFE HISTORY OF THE EUROPEAN PLETHODONTID SALAMANDER
SPELEOMANTES AMBROSII (AMPHIBIA, CAUDATA)

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ABSTRACT

The biology of a *Speleomantes ambrosii* population inhabiting interstitial habitats was studied during two consecutive years in north-western Italy. Surface activity was highest in late spring and early fall and was positively correlated with monthly rainfall. The population structure was analysed on the basis of polymodal size frequency distributions. *S. ambrosii* demographic structure was composed of two juvenile size classes and a mixed component in which subadult and reproductive salamanders were present. Males became sexually mature when >50 mm and females when >58 mm SVL. Estimated age at first reproduction was 3.5 years for males and 5 years for females. Juvenile growth rates, during the first two years of life, ranged from 10 to 13 mm/yr.

INTRODUCTION

European plethodontid salamanders belong to the genus *Speleomantes* (Dubois, 1984) and are found from south-eastern France to central Italy and on the island of Sardinia (Thorn, 1969). To date, six species of *Speleomantes*, two continental and four insular, have been recognized on the basis of morphological and biochemical data (Lanza, Nascetti & Bullini, 1986). All European plethodontids are fully terrestrial; they lay egg clutches in humid rock crevices or in soil, and they have direct development (Stefani & Serra, 1966; Durand, 1967*a,b*).

The Northern Appennine species *Speleomantes ambrosii* (Lanza, 1955) ranges from the French Maritime Alps to eastern Liguria (NW Italy). This species is found in natural and artificial caves and in moist habitats along streams. Some aspects of the biology of this species are already known: thermoregulation (Cherchi, 1952), oviposition, embryogenesis (Durand, 1967*a*; 1967*b*) and diet (Morisi, 1981; Salvidio, 1992). On the other hand, many aspects of life history and population ecology are poorly documented.

The aim of this study was to elucidate the population structure, reproduction and growth rates of a *S. ambrosii* population inhabiting interstitial habitats along a NW Appennine stream.

MATERIALS AND METHODS

THE STUDY AREA

The study site was located in the Bisagno Valley near the village of Davagna, about 15 km NE of Genoa (central Liguria), north-western Italy, at an elevation of 380 m. *S. ambrosii* samples were collected on calcareous rock-faces, in the talus and beneath leaf litter along a 100 m section of a small tributary of the Bisagno river.

The dominant vegetation of the valley is sweet-chestnut woodland (*Castanea sativa*), and a hygrophilous vegetation (*Alnus glutinosa, Ostrya carpinifolia, Fraxinus ornus*) borders the streams. The vegetation cover is thick and the forest soil is moist and rich in organic materials (Montanari, 1988). The climate of the region is submediterranean with relatively high rainfall both in spring and autumn (total rainfall averages and often exceeds 1500 mm per year). The rainfall data utilised in this study were obtained from the pluviometrical station of Scoffera, 5 km north of the sampling area.

SAMPLING

Speleomantes ambrosii seasonal activity was studied from May 1988 to April 1989, except for November and February. A total of 41.5 hours were spent searching for salamanders in the study area, and a standardized index (number of salamanders/hour of search) was used to compare monthly activity patterns.

Monthly samples were collected (in May, October, December 1988 and in May and in October 1989) within 12 days, and were largely non-destructive (Bruce, 1988; 1989). Salamanders were held ventral side up against a transparent plastic ruler and body-size was measured, from the edge of the snout to the posterior end of the cloaca (SVL), to the nearest millimetre. A sample of 36 salamanders was dissected in the laboratory to determine reproductive status. In males the left testis and in females oocytes were counted and measured under a dissecting microscope. Mature males were recognized in the field as they possess a well-developed mental (= chin) gland, the site of production of courtship pheromones. In addition some gravid females were identified without dissection in October and December collections.

Because no egg clutches were found during the study, the time of hatching and body size of new born individuals were inferred from Durand's works (1967*a*; 1967*b*; 1973) on oviposition and embryogenesis of *S. ambrosii* in semi-natural conditions. Correspondence between age and body-size classes was estimated only for immatures, because in sexually mature plethodontids there is high overlap in body size between age classes (Houck & Francillon-Vieillot, 1988).

DATA ANALYSIS

Polymodal body-size distributions of corresponding periods were compared by means of Kolmogorov-Smirnov test for large samples (Sokal & Rohlf, 1981), to determine if the observed differences were statistically significant: then they were pooled and analysed using the maximum likelihood computer program MIX (Ichthus Data System). This method resolves mixed distributions providing estimates of proportions, means and standard errors of the

different components present in the sample. It also evaluates the fit between the observed and theoretical distributions by a chi-square goodness of fit test (Macdonald & Pritcher, 1979; Bruce. 1988).

RESULTS

SEASONAL ACTIVITY

Monthly above-ground activity of the study population varied greatly over the year. Salamanders were most abundant during late spring and early autumn when temperatures were moderate and rainfall was abundant (Fig. 1). Activity decreased in winter when temperatures were low, and during summer when night temperature were >19°C and atmospheric humidity was <75%. Seasonal activity was positively correlated with monthly rainfall: Spearman's rank correlation coefficient $r_s=0.66$, $n=10$, $P<0.05$.

POPULATION STRUCTURE

The SVL distributions of 415 salamanders measured from May 1988 to October 1989 are shown in Fig. 2. The smallest individuals, ranging from 19 to 23 mm SVL, were observed in December. Since hatching begins in September (Durand, 1967b), this size class was undoubtedly composed of newborn individuals, about three months old.

May and October samples from successive years did not differ significantly (Kolmogorov-Smirnov $D=0.190$, $P>0.05$; and $D=0.165$, $P>0.05$ respectively). Thus, corresponding collections were pooled to obtain samples large enough to be analysed. Both spring and autumn SVL distributions were polymodal and were satisfactorily resolved into three normal
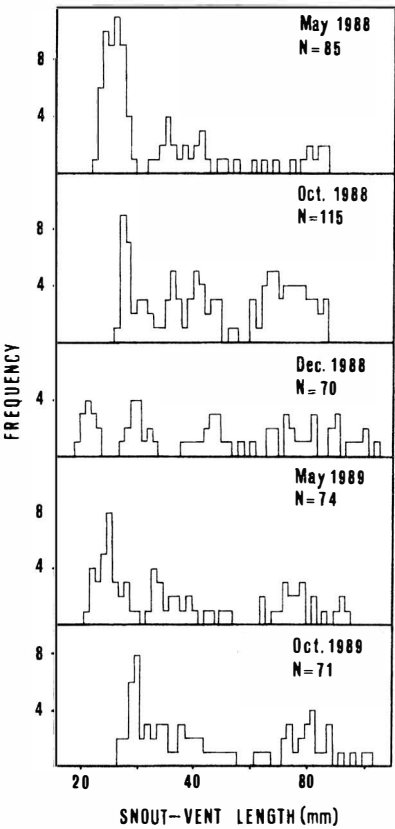

FIG. 2. Snout-vent length (SVL) distribution of 415 *Speleomantes ambrosii* sampled in May, October and December 1988 and May and October 1989.
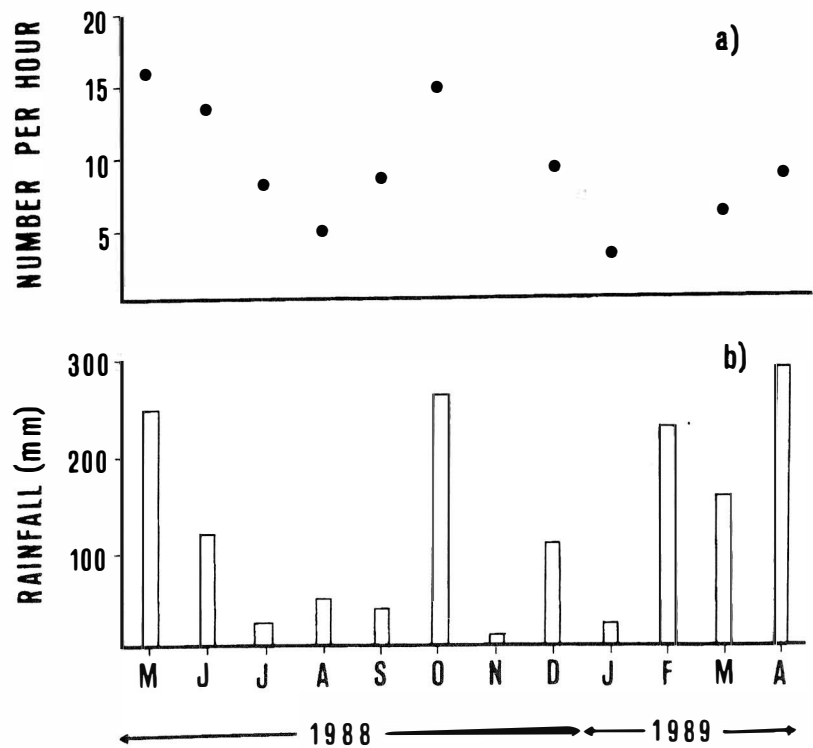

FIG. 1. Relationship between seasonal activity and rainfall in *Speleomantes ambrosii* population. (a) number of salamanders per hour of search. (b) monthly rainfall in mm.

Sample	n	COMPONENTS									Goodness of fit		
		1			2			3					
		%	$\bar{x}$	SE	%	$\bar{x}$	SE	%	$\bar{x}$	SE	χ^2	df	P
May	159	50.4	25.1	0.2	26.6	36.3	1.1	23.0	58.0	1.0	26.8	40	0.94
October	186	23.4	28.7	0.3	34.6	37.9	0.9	42.1	57.2	0.7	28.4	38	0.87

TABLE 1. Composition of May and October *Speleomantes ambrosii* pooled samples provided by the maximum likelihood routine program MIX (Ichthus Data System).

Life-history stage	May		October	
	SVL	growth increment	SVL	growth increment
hatchlings	-		16	
		-		+13
1 yr juveniles	25		29	
		+11		+9
2 yr juveniles	36		38	

TABLE 2. Mean snout-vent length (SVL) and body growth increments (in mm) of juvenile *Speleomantes ambrosii* life-history stages. SVL of hatchlings was obtained from Durand (1973).
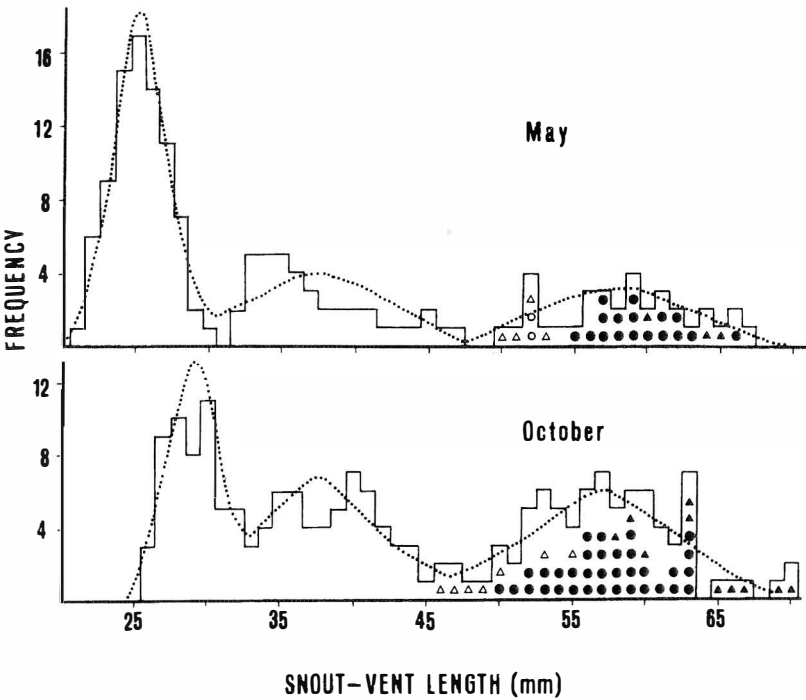

FIG. 3. Snout-vent length (SVL) distribution of May and October *Speleomantes ambrosii* cumulative samples. Open squares represent unsexable individuals, closed circles mature males, open circles immature males, closed triangles mature females, and open triangles immature females. The dotted curves represent theoretical distributions obtained by MIX computer routine program.

components by MIX computer program (Table 1). The analysis of dissected salamanders (see below) indicates that the two smallest body-size classes were composed of immature specimens. An additional subgroup of immature salamanders was included in the larger size class, together with breeding individuals (Fig. 3). In May, when mating occurs, this subsample was composed of subadults of both sexes while, in October, it was made up of subadult individuals in addition to some small mature males.

In autumn, when hatchlings are still underground, the smallest SVL class is about 1 year old, the intermediate juvenile class 2 yr, subadults 3 yr, and the larger mature individuals 4 yr or older.

BODY SIZE AT MATURITY

All dissected specimens smaller than 45 mm (n=10) had small undifferentiated gonads. The smallest male with a swollen mental gland (SVL = 50 mm) and the smallest dissected mature male (SVL = 52 mm) were measured in October. In dissected males (n=10), testes begin to enlarge as the mental gland becomes clearly evident, and the testicular volume was positively correlated with SVL (r=0.79, n=10, P<0.01).

All dissected females 46<SVL<57 mm (n=11) had small translucent follicles (0.2-0.6 mm in diameter) and therefore were not yet mature. In October, a gravid female of 58 mm SVL was measured in the field, and a reproductive female (SVL=59 mm) possessing maturing oocytes was dissected. The mean clutch size, estimated from the number of yolk-filled oocytes observed in mature females, was 13.80±2.05 (n=5, range 12-17).

In May, there were no gravid females, whereas they represented 48% of reproductive females in October (10 of 21) and 58% (7 of 12) in December.

SEXUAL DIMORPHISM

All individuals larger than 58 mm SVL and not possessing the mental gland were considered adult females. The average body length of reproductive females was 64 mm (range 58-72), while mature males average only 58 mm (range 50-67). Only females exceeded a body-length of 68 mm, and the largest individual ever caught was a gravid female (SVL=72 mm, total length *in vivo* = 116 mm). Student's t-test indicates that the observed differences in SVL between sexes were statistically significant in all sampled months (P<0.01 in all cases).

JUVENILE GROWTH RATES

Juvenile growth rates of *S. ambrosii* were estimated indirectly from the mean SVL of different size classes defined by MIX computer routine (see Table 1). Body size of new-born salamanders was obtained comparing their total length (24 mm) reported by Durand (1973) with the smallest individual measured in December collection (SVL=19 mm, total length = 29 mm). Annual growth rates of juvenile SVL classes were estimated to vary from 13 to 10 mm during the first two years of life (Table 2).

DISCUSSION

Two peaks in seasonal activity were observed for the European plethodontid *S. ambrosii*. The first peak occurred during spring (May) when mating takes place, the second during autumn (October). The overall pattern in surface activity was related to monthly rainfall. During the study period, rainfall distribution was consistent with the general trend observed in the region over a 30 yr period (data from the Regional Meteorological Service, 1951-1981).

In the study population, body size frequency distributions were constant over two successive years. Thus, the population structure appeared stable and was suitable for a demographic and ecological study.

In plethodontid salamanders, estimates of age from size-frequency data for juvenile life-stages are accurate if there is no large overlap between size-classes (Houck, 1982; Bruce, 1990). *S. ambrosii* population structure was composed of two distinct juvenile age classes and a mixed component in which large juveniles and adult salamanders were present. In this latter group, an additional age class (subadults), not well defined by size, could be recognized on the basis of sexual immaturity. In autumn, the two small immature classes were made up by individuals aged about 1 and 2 yr respectively, and subadults were 3 yr old. Since breeding occurs during spring, males could be able to reproduce for the first time at an estimated age of 3.5 yr. On the other hand, females were about 8 mm larger than males at sexual maturity, and probably will be able to mate only a year later; thus they will likely deposit their first egg clutches, in winter at an age of 5. That females reproduce for the first time at a larger body-length and at an older age than males is a quite common pattern in plethodontids (Houck, 1982; Herrington & Larsen, 1987; Bruce, 1988, 1989; Ovaska & Gregory, 1989). This seems to be the case in the study *S. ambrosii* population, even if growth differences between males and females could contribute to some of the difference.

Breeding individuals were in their fourth year or older. Because of the wide overlap in SVL of successive age groups, it was impossible to detect discrete classes within the reproductive component. This superposition was probably due to lower adult growth rates and to higher variance in individual growth. In any case, it was impossible to estimate, even roughly, the average age and the oldest age reached by adult *S. ambrosii*.

Juvenile growth rates were estimated to vary from 10 to 13 mm/yr during the first two years of life after hatching. These values fall within the reported range (10-21 mm/yr) for temperate plethodontid salamanders, according to many authors (Houck 1982; Hairston, 1983; Semlitsch & West, 1983; Bruce, 1988, 1990).

This study showed that, apart from a relatively long period of embryonic development (Durand, 1967b), the *S. ambrosii* life-history pattern is comparable to those observed for Nearctic plethodontid salamanders that have direct development. Indeed, the population structure, size and age at sexual maturity and juvenile growth rates appear to be consistent with those characterising many new world temperate species.

ACKNOWLEDGEMENTS

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THE EFFECTS OF HYDRIC AND THERMAL PROPERTIES OF INCUBATION SUBSTRATE ON EMBRYONIC DEVELOPMENT IN THE WATER SNAKE, *NATRIX TESSELLATA*

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ABSTRACT

We studied the effects of incubation substrate and its water content on egg water uptake, incubation duration, and hatchling mass in the diced water snake *Natrix tessellata*. Egg water uptake was highest in sand (the substrate with the highest thermal conductivity) and lowest in air (which had the lowest thermal conductivity). Water uptake was independent of initial egg mass. Incubation duration was correlated with substrate type and water content. Hatchling mass was independent of initial egg mass, but there was a weak negative correlation with total water uptake and with length of incubation. Wet mass of hatchlings incubated in air was greater than those incubated in sand or vermiculite. A greater increase of water uptake by eggs incubated in the most thermally conductive substrate (moist sand) suggests transport of water vapour, rather than liquid water, as the mechanism of transport across the membranes of parchment shelled eggs.

INTRODUCTION

The egg is the most vulnerable stage in a reptile's life. Immobile and often lacking parental care, it is susceptible to predation and exposed to the prevailing environmental conditions. Suitable substrate temperature and moisture are vital for successful development of the embryo and subsequent hatchling performance and behaviour (Packard & Packard, 1988; Burger, 1991).

It has been shown that incubation temperature not only affects incubation duration, but also sex ratios and juvenile behaviour in the pine snake (Burger & Zappalorti, 1988; Burger, 1989) and juvenile behaviour in black racers and king snakes (Burger, 1990). The effects of egg water uptake on hatchling size and physiological characteristics are, however, not clear. Miller, Packard, & Packard (1987) found that hatchling snapping turtles (*Chelydra serpentina*) incubated in moister media (-150 kPa) were larger and heavier and displayed superior locomotory ability relative to those incubated in dryer media (-850 kPa). Similarly, pine snake (*Pituophis melanoleucus*) hatchlings incubated in moister substrates were larger than ones incubated in dryer substrates (Gutzke & Packard, 1987). Some other species, however, showed no such effects (Packard & Packard, 1988). Moreover, the total energy reserves of the hatchlings were only sometimes affected (Gutzke & Packard, 1987), and the incubation period was generally longer for hatchlings incubated in wet substrates (Packard & Packard, 1988). Ratterman & Ackerman (1989), however, found that hatchling mass of the painted turtle *Chrysemys picta* was affected only by the initial egg mass and by incubation duration, but not by the water exchange rate of the egg.

The mechanisms of egg water uptake are controversial. Ackerman, Dmi'el. & Ar (1985), and Ackerman, Seagrave, Dmi'el & Ar (1985) considered water vapour diffusion to be the major mechanism for water transport across reptilian egg membranes. Kam & Ackerman (1990) concluded that the water uptake by *Chelydra* eggs could only be by vapour. Other workers (see Packard & Packard. 1988) have assumed a predominance of liquid water exchange. and Thompson

(1987) maintained that "in natural nests ... sometimes exchanges in the form of water vapour and sometimes exchanges in the form of liquid water would be more significant". Thompson (1987) however, did not demonstrate that liquid water exchange actually occurred, but only that a liquid water connection was present very early in incubation. Whereas experimental evidence (Ar, Koltai, Belinsky & Ackerman, 1990; Ar, Ackerman, Belinsky, Koltai, Blumberg-Binyamini & Dmi'el, in press; Kam & Ackerman, 1990) supports the importance of water vapour exchange, the relative importance of liquid water transport has not yet been established (Packard & Packard, 1988).

Ackerman, Seagrave *et al.* (1985) predicted that the thermal conductivity of the substrate, affected by both its physical properties and its water content, would greatly affect egg water uptake. This prediction was confirmed by Kam & Ackerman (1990) but not supported by Packard *et al.* (1987). If true, maternal choice of oviposition site (e.g. soil type, soil water content and temperature) could profoundly affect the hatchling.

To investigate the relative importance of water vapour versus liquid water transport in parchment shelled eggs, we incubated eggs of the diced water snake *Natrix tessellata* in substrates containing different amounts of water but of similar water potentials. We studied the effects of the different incubation regimes on incubation duration, hatching success and hatchling mass. We also examined the relationship between initial egg mass and hatchling mass under different incubation conditions.

MATERIAL AND METHODS

Gravid female *Natrix tessellata* were collected at Kibbutz Hazorea in northern Israel and transferred to the Canadian Centre for Ecological Zoology at Tel Aviv University. Snakes were housed in large enclosures and fed on fish. A large water bath and ample hiding places were provided in each cage. Cage floors were covered with sawdust; areas that were kept constantly moist served as oviposition sites and were inspected every 1-2 days for fresh eggs.

Thirty one eggs which were obtained from two clutches, were used in this study. The initial egg masses of the two clutches differed significantly ($P<0.001$, t-test). The 15 eggs of the first clutch (mean±SD: 5.98±0.33 g) were distributed randomly to incubate in either sand or vermiculite (sand 1 vs. vermiculite treatment, Table 1), and the 16 eggs of the second clutch (mean±SD: 7.52±0.29 g) were incubated in either sand or air (sand 2 vs. air treatment, Table 1). The relative humidity of all substrates was 100%; both sand 1 & 2 and the vermiculite had similar water potentials (-6 and -12 kPa, respectively). Liquid water contents, however, were drastically different: 0% for eggs incubated in air, 9% in the sand and 200% in vermiculite.

The eggs were incubated in eight plastic containers (20x14x8 cm) with pierced covers to allow adequate gas exchange. Each container was filled with the appropriate substrate. After recording their initial mass, three to four eggs were placed in each container. The eggs assigned to incubate in sand and vermiculite were buried completely in the substrate. Those incubated in air were placed on a plastic mesh, in a trench dug in the surrounding wet (-6 kPa, 9% water content) sand. The eight containers holding the eggs were placed in a temperature-controlled cabinet at 29±0.5°C. During incubation they were weighed (±0.01 g) at intervals of three to four days, and, depending on the change in mass, water was sprayed on the surface to supplement the amount lost. Every seventh day, after weighing the whole container, the eggs were taken out, carefully cleaned and weighed individually, using a Sartorius 1518 (±0.001 g) balance. Before returning the eggs to their containers, the substrate in each container was replaced by a newly prepared one, and water content and water potential were determined in the old substrates.

Sand containing 9% water was prepared by mixing 5 kg oven-dried sand with 450 g distilled water. The vermiculite (heat expanded mica) substrate was prepared by mixing 1.2 kg coarse vermiculite with 2.4 kg distilled water. To determine water contents during incubation, two samples were taken from each container at the end of every week, and were dried to a constant mass at 105°C. The water content level of each experimental medium was fairly stable during the entire incubation period (8.5%-9.3% for sand, 192%-207% for vermiculite). Also, no statistically significant differences were found between the values obtained for the containers of sand 1 and sand 2, nor between them and the sand of the "air" substrate ($F_{2,29}=0.21$, $P>0.8$). The water potential values were obtained by two methods, water retention curve (water potential as a function of water content) and tensiometry (Cassel & Klute, 1986). The characteristic water retention curves of the sand were constructed using the pressure plate method (Klute, 1986). Twelve such curves (two for each container of sand substrate) were constructed in the first and at the end of the fifth week of incubation. The water potentials were estimated from these curves using the measured water content values. In the second method we measured directly the water potential of the sand immediately after the eggs were taken out. This was done several times in each container, using tensiometers with a small, 3 cm long, ceramic cup (Soil Moisture Corp). There was good agreement (±2 kPa) between the two methods. For vermiculite, however, a reliable characteristic water retention curve could not be established. We therefore prepared different mixtures of vermiculite and water, sealed them in wide-mouth 1000 cm³ bottles together with jet-filled tensiometers (Soil Moisture Corp), and measured their corresponding water potential.

We did not measure the thermal conductivities of the

	Number of eggs	Initial egg mass (g)	Average mass change (mg d⁻¹)	Hatchling mass (g)	Ratio of hatchling to initial egg mass	Incubation duration (days)	Hatching success (%)
Sand 1	7	6.051 ±0.315	205 ±29	4.750 ±0.257	0.786 ±0.053	41.90 ±0.38	86
Vermiculite	8	5.920 ±0.423	103 ±17	4.781 ±0.185	0.785 ±0.015	41.10 ±0.38	88
P		NS	<0.005	NS	NS	<0.01	
Sand 2	8	7.477 ±0.223	231 ±28	5.203 ±0.393	0.690 ±0.046	43.00 ±1.15	88
Air	8	7.503 ±0.318	-8 ±0.4	5.597 ±0.358	0.749 ±0.044	42.10 ±0.38	88
P		NS	<0.001	NS	<0.05	<0.05	

TABLE 1. Effects of incubation substrate on egg water uptake, incubation duration, hatchling mass and hatching success in the water snake *Natrix tessellata*. Water potentials and water contents were -6 kPa and 9% in sand 1 & 2, and -12 kPa and 200% in vermiculite. All substrates were saturated with water vapour (100% RH). Incubation temperature was 29°C. Values are mean ± SD; NS = not significant.
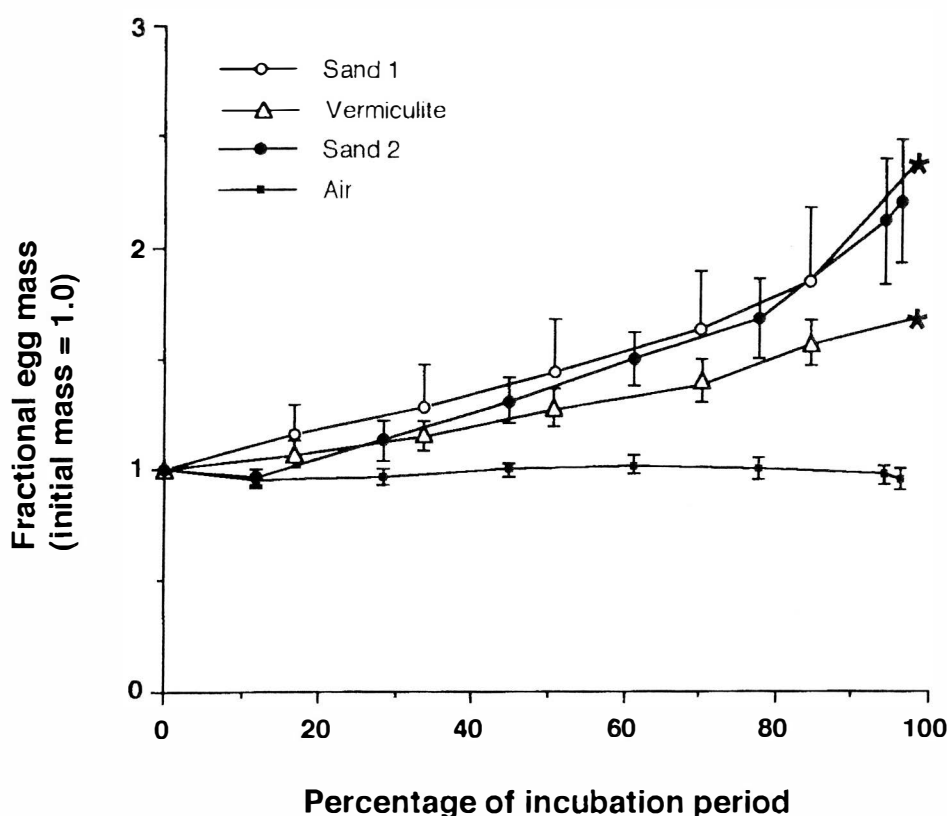
Fig. 1. Increase in the mass of *Natrix tessellata* eggs during incubation in air, sand and vermiculite. Mass change is expressed as egg mass relative to that at laying (initial mass = 1.00). Values are means±1 SD. (vertical bars). Most of the eggs incubated in sand 1 and in vermiculite hatched on the morning they were to be weighed for the last time; the last data point (*) is the mean of two eggs only.

different substrates. From values given in the literature (Ackerman & Seagrave, 1987; Kam & Ackerman, 1990) we estimate, however, that the sand thermal conductivity in our experiments was 6-8 times greater than that of the vermiculite (about 1.6 vs 0.2 W m^{-1} °C^{-1}).

RESULTS

Eggs developed and hatched successfully (88%) in all incubation substrates (Table 1). Water uptake by the eggs was independent of initial egg mass (r=-0.21, P>0.1) but it was dependent on the incubation substrate. The total and daily mass gain was significantly lower in eggs incubated in air than in those incubated in either sand 1 & 2 or vermiculite (Fig. 1; P<0.05. Wilcoxon's signed-ranks test); egg mass gain was highest in sand. The difference between the average rate of mass change (mg day^{-1}) of the eggs incubated in sand 1 and sand 2 (Table 1) was not significant (t=1.64. P>0.1). During the last third of incubation the difference in mass increase between eggs incubated in sand and vermiculite was very marked (Fig. 1). During this period, however. the difference in mass increase between eggs incubated in sand and vermiculite increased (Fig 1).

Incubation duration was related to substrate type and its water content. Eggs incubated in sand 1 hatched significantly later than those incubated in vermiculite (t-test, P<0.01). and those incubated in sand 2 hatched significantly later than those incubated in air (Table 1). These

differences, however, are rather small: less than a day for both treatments (i.e. about 2.5% of the incubation period). Hatchling mass was weakly negatively correlated with egg water uptake during incubation (r=-0.42, P=0.05). Hatchling mass, however, was not correlated with either initial egg mass (r=0.31, P>0.1) or duration of incubation (r=0.17, P>0.1).

DISCUSSION

The model suggested by Ackerman. Seagrave *et al.* (1985) presupposes a predominance of water vapour over liquid water transport across the egg membranes. In this model, environmental and internal water vapour pressures will determine the net movement of water to or from the egg. Water vapour pressure is especially dependent on temperature. If embryonic heat production raises the egg temperature. water vapour pressure inside it will be higher and the egg will lose more (or gain less) water (Ackerman, Seagrave *et al.*, 1985). The temperatures of the egg and its immediate vicinity depend. to a large extent. on the thermal conductivity of the substrate. This. in turn. is mainly determined by substrate moisture content. It is expected. therefore. that eggs incubated in substrates having similar water potentials but different thermal properties should absorb water at different rates. and that at the higher levels of embryonic heat production the differences in water absorption will be greater.

Our data support this model. although we cannot rule out

some exchange of liquid water across the egg membranes. As in Dmi'el (1967) and Ackerman, Seagrave *et al.* (1985), the incubation substrate affected the rate of egg mass increase (Fig. 1). Since all substrates were saturated with water vapour and had similar water potentials, differences in their thermal conductivity probably were responsible for the different rates of mass increase. The greatest change in mass occurred in sand, the most conductive substrate used in this study. Moreover, the highest mass increase was observed during the last third of incubation, when the metabolic heat production of *Natrix* embryos is highest (Dmi'el, 1970). The lowest mass increase occurred in air, the most thermally insulating substrate. Eggs incubated in moist vermiculite, intermediate in conductivity, showed an intermediate mass gain. Parchment-shelled reptile eggs, including those of *Natrix*, have a boundary layer of "dead air", whose resistance to water vapour transport is quantitatively equal to the egg-shell resistance. This layer, however, disappears when the egg is buried in the sand (Ackerman, Dmi'el *et al.*, 1985). The reduced water uptake shown by the eggs incubated in air is therefore probably due to two factors: (1) the low thermal conductivity of the air and (2) high resistance of the air boundary layer around the egg to vapour transport.

The inverse, though weak, relationship of *Natrix* hatchling mass to egg water uptake differs from the results of Gutzke & Packard (1987), who found that bull snakes hatched from eggs which were incubated in wet substrates (and therefore had high rates of water uptake) were heavier than those hatched from eggs incubated in dry conditions. It is also in contrast to Packard & Packard (1988, p. 567), who reported a positive correlation between egg water uptake of parchment shelled eggs and hatchling size. Dmi'el (1967), on the other hand, found no correlation between egg water uptake and hatchling size. Plummer & Snell (1988) also found that hatchling mass of the snake *Opheodrys aestivus* was not related to changes in egg water uptake during incubation.

We found hatchling mass to be independent of initial egg mass. This is in agreement with the findings of Packard & Packard (1987) for the snake *Coluber constrictor*. In the present study, the ratio of hatchling mass to initial egg mass was significantly higher for eggs incubated in air than for those incubated in sand 2 (Mann-Whitney U-test, $P<0.01$). If body size is indeed important to hatchling survival (Ferguson & Fox, 1984; Jayne & Bennett, 1990; Sinervo & Huey, 1990), depositing eggs in a moister substrate than necessary for egg development may be deleterious to the survival of the hatchlings. Excessive water uptake can, however, be avoided, if the female places the egg in saturated air on the surface rather than burying it. Subjecting the egg to dry conditions, on the other hand, will also have adverse effects. Thus, when laying parchment shelled eggs, the female reptile should choose a location where humidity conditions throughout the incubation period are (1) no higher than is necessary for normal development, and (2) not below the tolerance of the egg to dry substrates. These predictions are supported for pine snakes (Burger & Zappalorti, 1988), and by the findings of Perry (1990) and Perry & Dmi'el (1989) for the lizard *Acanthodactylus scutellatus*.

ACKNOWLEDGEMENTS

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SHORT NOTES

A HYPOTHESIS EXPLAINING THE ENIGMATIC DISTRIBUTION OF THE GEOMETRIC TORTOISE, *PSAMMOBATES GEOMETRICUS*, IN SOUTH AFRICA

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The genus *Psammobates* Fitzinger, 1835 comprises three species, namely *Psammobates geometricus*, *P. oculifer* and *P. tentorius* (Loveridge & Williams, 1957; Boycott & Bourquin, 1988; Branch, 1988). *P. geometricus* and *P. oculifer* are monotypic species, while *P. tentorius* is divided into three subspecies, namely *P. t. tentorius*, *P. t. trimeni* and *P. t. verroxii* (Loveridge & Williams, 1957; Greig & Burdett, 1976; Pritchard, 1979; Boycott & Bourquin, 1988). Previously the *P. tentorius* complex was subdivided into as many as 28 different species and subspecies (Hewitt, 1933).

It was suggested by Siebenrock (1904), Duerden (1907), Müller (1939) and Greig & Burdett (1976) that the *Psammobates* taxa fall into two groups, *geometricus* and *oculifer* constituting the one and the *tentorius* complex the other. The proposed sister group relationship between *geometricus* and *oculifer* is, however, based mainly on phenetic principles and does not necessarily reflect the true phylogeny. For phylogeny reconstruction, a cladistic analysis, based on the search for synapomorphies, is called for (Wiley, 1981). A preliminary analysis of phylogenetic affinities within *Psammobates*, forming part of a study on the biology and conservation status of *P. geometricus* (Baard, 1990), corroborated the above grouping.

The present distribution of the three species of *Psammobates* (Boycott & Bourquin, 1988; Branch, 1988), however, seems to contradict this grouping since the two sister species (*P. geometricus* and *P. oculifer*) are geographically separated by *P. tentorius*. Bearing in mind, however, that allopatric speciation is in all probability the most common mode of speciation (Wiley, 1981), it is to be expected that sister species initially will have allopatric distributions. Furthermore, it is not difficult to perceive that *P. tentorius*, through range expansion, could have penetrated into areas left void by a contracting *geometricus-oculifer* ancestral species.

As far as the herpetofauna of southern Africa is concerned, the southwestern Cape is considered the richest centre of endemism (Hewitt, 1910; Poynton, 1964; Poynton & Broadley, 1978). Restricted distribution ranges are characteristic of forms from the southwest, while forms in the northeast tend to have more extensive distributions. The genus *Psammobates* appears to conform to this general pattern in that the species with the smallest range, *P. geometricus*, is a southwestern Cape endemic. Poynton (1989: p.2) describes two contrasting faunas in the southern subcontinent, "the one being more cool-adapted and presently showing relict patterning in areas of high altitude and latitude, the other being warm-adapted with continuous ranges brought about by recent range expansion". He goes on to point out that this led to a "dynamic model involving reciprocal spreading and withdrawing of the interlocking cool- and warm-adapted groups following the cyclic changes in Quaternary climate". Mouton & Oelofsen (1988) discuss the importance of the Cape Fold Mountains, the coastal lowlands and the cold Benguela sea current in speciation events among cordylid lizards in the southwestern Cape. During changing climates these mountains become effective barriers trapping warm-adapted populations along the western coastal lowlands. Due to a supposedly increased influence of the Cold Benguela current on coastal climates during glacial periods, populations along the coastal lowlands become subjected to more adverse climatic conditions than inland sister populations. These coastal populations may become adapted to local conditions, and may eventually speciate.

It is not difficult to picture *P. geometricus* to have originated through a very similar series of events as that proposed for the *Cordylus cordylus* complex by Mouton & Oelofsen (1988). During a warmer interglacial period a warm-adapted ancestral species could have had an extensive range which also included the southwestern coastal lowlands. With the advance of a subsequent glacial period, range contraction and fragmentation could have taken place leaving behind an isolated population along the southwestern coastal lowlands. Due to differential environmental pressures west and east of the Cape Fold Mountains, the western population could eventually have diverged from the original eastern stock in becoming more cool-adapted.

Psammobates geometricus today occurs in three areas which are more or less geographically isolated from one another (Fig. 1). These are the southwestern coastal lowlands (the area from Gordon's Bay in the south to Piketberg in the north), the Worcester-Tulbagh valley and the Ceres valley. These three areas are separated from one another by mountain ranges. Presently *P. geometricus* occurs nowhere on mountainous terrain and it is therefore believed that such areas serve as physical barriers restricting movement of these tortoises and consequently gene flow among the populations. The question to be addressed therefore, is how these isolated populations originated or, in other words, how the populations were formerly geographically linked.

The answer to this depends on knowing the genealogical relationships among the extant populations. Because such information is not available at present, it would be impossible to arrive at any firm conclusions in this regard. It is, however, still possible to discuss the various ways in which the present populations could have been linked in the past.

During periods of lowered sea-levels (Deacon, Hendey & Lambrechts, 1983), the western coastal lowlands and the Worcester-Tulbagh valley could have been linked via the southern coastal forelands of the present day Hangklip area (Fig. 1). For example, Tankard's (1976) time-depth plot of
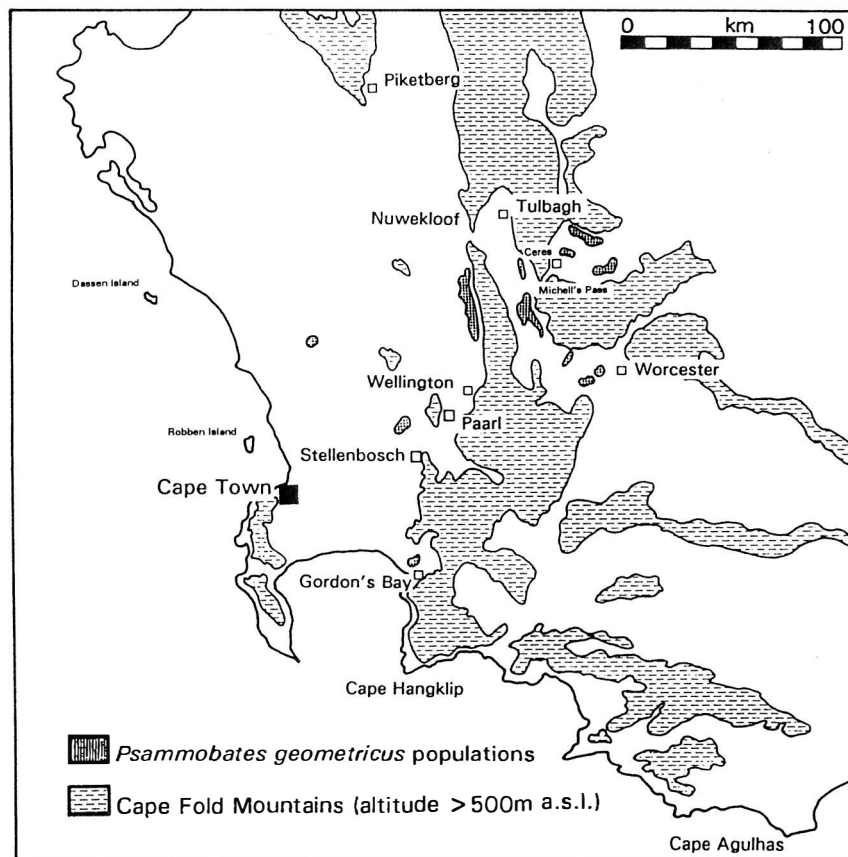
Fig. 1 Map of the southwestern Cape Province, indicating the present location of *Psammobates geometricus* populations, as well as possible communication routes and routes of genetic exchange between populations.

sea-levels for South Africa over the past 47 000 years suggests a rapid fall in sea-level with the advance of the final Wurm glaciation, with a minimum sea-level of -130 m reached at 17 000 to 18 000 years B.P. This implies that a considerable portion of the continental shelf would have been exposed during such times allowing communication between the western coastal lowland and Worcester-Tulbagh valley populations of *P. geometricus*.

Another possible communication route between the coastal and Worcester-Tulbagh valley populations might have been the gap in the Fold Mountains through the present-day Nuwekloof Pass (Fig. 1). At present *P. geometricus* is absent from this ravine and, the terrain being very rugged, it is unlikely that it ever functioned as a link between the two populations.

As regards the Ceres valley population, there are also two possibilities of how this population and the Worcester population could have been linked in the past. A link was possible through the Dwars River ravine (the present-day Michell's Pass) (Fig. 1). At present, this route appears to be impassable for terrestrial tortoises, particularly with the Dwars River and its steep embankments limiting access. However, geological information from this region (Visser, De Villiers, Theron & Hill, 1980; Söhnge & Hälbich, 1983; A. P. G. Söhnge, pers. comm.) suggests that the present drainage patterns in the Ceres and Worcester-Tulbagh valleys differ considerably from those approximately 10 million years B.P. (i.e. during the formation of the gorge, temporary flat areas could possibly have facilitated a link). A more likely communication

route between the Ceres and Worcester-Tulbagh populations would have been via a northeastern, inland route (Fig. 1). The historical inland extension of, firstly, climates favourable to *P. geometricus* and, secondly, its favoured habitat, renosterveld, might possibly have facilitated this inland link via the present-day Karoo.

The natural occurrence of *P. geometricus* in the Ceres valley was questioned by Juvik (1971), who suggested that the population there might have originated from pet tortoises brought in from elsewhere. However, since there are at least six natural populations in the valley, as well as a strong presence of renosterveld habitat, and considering that *P. geometricus* appears to be closely associated with this habitat (Greig, 1984; Boycott & Bourquin, 1988; Branch, 1988; Baard, 1990), we regard it highly unlikely that a fairly large population in the wild could have originated from a few escaped or released individuals.

In conclusion, it is clear that there are various ways in which the three populations could have been linked geographically in the past. More definite conclusions in this regard, however, would only be possible once the relationships among the populations are known. A study to determine these relationships by means of electrophoresis or DNA-analysis is therefore highly recommended.

Unravelling the genealogical relationships between members of *Psammobates* presents an exciting challenge to future workers in this field. A cladistic study of the family Testudinidae, additional to that of Crumly (1984) and

Gaffney & Meylan (1988) is, however, fundamental to this. An analysis of the biogeography of this genus and possibly other genera as well, may contribute significantly to our understanding of the biogeographical patterns already observed in other animal groups in southern Africa.

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CHARACTERISTICS OF NATTERJACK TOAD (*BUFO CALAMITA*) BREEDING SITES ON A SCOTTISH SALTMARSH

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Natterjack toads are associated in Britain with three habitat types: sand-dunes, lowland heaths and upper saltmarshes (Beebee, 1983). Populations on the latter habitat, mostly situated along the northern shores of the Irish Sea, have been relatively little-studied though they include some of the largest in the country (Bridson, 1976; Banks & Beebee, 1988; Beebee, 1989). We have investigated natterjack breeding sites on Priestside Merse, a strip of saltmarsh on the north Solway coast that is about 7 km long and which varies from <50 m to about 500 m in width. The area is dotted with innumerable shallow saltpans, flood-pools and ditches, some of which are used by a natterjack toad population estimated to be in the low hundreds. Common frogs (*Rana temporaria*) and toads (*Bufo bufo*) also occur.

The ponds of Priestside Merse were systematically searched for natterjack adults, spawn and tadpoles during May, the peak of the breeding season, in 1990. Some observations on pond use were also made in earlier years. Water samples were taken from those ponds with healthy spawn or tadpoles (classified as successful breeding sites), ponds with occasional calling males and/or dead spawn (classified as attempted breeding sites) and from a range of ponds with no evidence of natterjack use. Conductivity of these samples was measured using a WPA meter with glass electrode, all at constant temperature, and salinities expressed as percentage seawater (assuming 100% seawater = 2.75% w/v NaCl). During the winter of 1990-1991, further samples were taken from a selection of these ponds at monthly intervals, stored at -20°C, and conductivities subsequently measured as described above.

Natterjack tadpoles and healthy spawn were found in a discrete subset of the saltmarsh ponds (Figure 1A), notably those with relatively low salinities (averaging 7.9% seawater, or about 0.22% w/v NaCl). The highest salt concentration in which breeding looked likely to be successful was 14% seawater (0.39% NaCl); the lowest was about 0.2% seawater (0.06% NaCl, essentially freshwater), but 10 out of the 11 breeding sites showed evidence of some salination and most were in the range 5-10% seawater (0.14-0.28% NaCl) during the May sampling period. Sixteen unused ponds, which were

interspersed with the used ones but often at least slightly closer to the sea, averaged 20% seawater (0.55% NaCl) with a maximum of 34.6% seawater (0.95% NaCl). Two other unused ponds, not included in the analysis of Fig 1A, were essentially 100% seawater. Salinities of used and unused ponds were significantly different by t-test after arcsin transformation ($t=5.29$, $df=17$, $P=0.0001$). There were, in addition, three ponds in which breeding was attempted but in which there was no evidence of success; two of these had occasional calling males (14.6% and 30.2% seawater) and the third had some calling and a single, fungus-infected spawn string (73% seawater).

Sampling the three classes of ponds (successful, attempted and unused) through a winter period confirmed that the differences between them were essentially ones of degree (Fig. 1B). High tides flooded the merse at various times throughout the year, but most acutely during the autumn. Ponds used by natterjacks evidently received these saline flushes, but salt concentrations did not reach the levels seen in unused ponds or in those in which breeding was probably unsuccessful during the spring of 1990. Freshwater, presumably as rain and run-off from inland areas, reduced salinities progressively during the winter months though further, relatively minor inundations were detectable at the height of winter (January-February) and more markedly in spring just before the onset of the natterjack breeding season. Many ponds were dry in May 1991, and no sampling was done in June, but a final July sampling indicated the occurrence of a midsummer inundation of at least some of the saltmarsh pools. We do not know how often midsummer inundation happens at this site, but metamorphosis of toadlets usually occurs in June. Successful ponds averaged about half the salinities of attempted and unused ones (9.5%, 16.4% and 15.9% respectively) throughout the measurement period.

It has been known for many years that natterjacks living in coastal regions, particularly in Scandinavia, often breed in pools exposed to salt spray or to occasional inundation from the sea (e.g. Andren & Nilson, 1979; 1985; Schlyter, Hoglund & Stromberg, 1991) though the degree of salinity has rarely been investigated. Exaggerated impressions of salt tolerance have arisen from accounts of natterjacks breeding in rockpools along the Swedish coast because the low salinity of the Baltic Sea (only about 0.4% NaCl, 15% normal seawater, in bays used by natterjacks) is not always recognised by workers outside Scandinavia. In laboratory trials, early embryogenesis proved more sensitive to salt toxicity than subsequent developmental stages and there were no significant differences in this respect between *B. calamita* and *B. bufo*, nor between inland and coastal populations of *B. calamita* in Britain (Mathias, 1971; Beebee, 1985). Lethal limits for spawn were between 15-20% seawater (0.41-0.55% NaCl), though tadpoles could survive up to about 25% seawater (0.69%) NaCl and possibly higher for short periods. These corresponded closely to the highest salt concentrations at which natterjack reproduction has been recorded in the field, both in this and the earlier studies.

The inundation regime prevalent at Priestside, and probably at other saltmarshes inhabited by natterjacks, may well be crucial to the success of the animal in these habitats. Regular episodes of saline flooding prevent the development of typical freshwater invertebrate communities (Nicol, 1935)
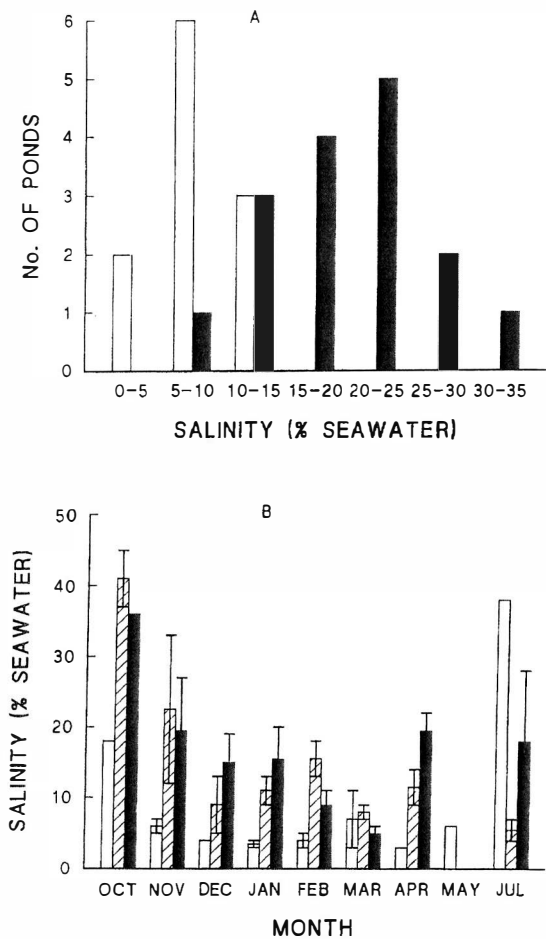
ponds. Furthermore, the spring inundation coincides with the earlier breeding season of the other British anurans (*Rana temporaria* and *Bufo bufo*) and is likely to cause substantial mortality of the eggs and larvae of these competitively superior species. which might otherwise dominate this habitat as they do most others (Banks & Beebee, 1987). Nicol (1935) noted mortality of adult frogs, apparently caught out by high spring tides, in the upper saltmarsh ponds of her study. The inundation pattern is thus ideally suited to natterjack biology, reducing predators and competitors but with a period of lowered salinity in the late spring coinciding with the natterjack breeding season. Any development which altered this pattern, such as a tidal barrage scheme or embankment and reclamation of the upper saltmarsh could well be disastrous for natterjacks in this finely-balanced situation. Finally, our observations indicate that great care is necessary in the creation of new natterjack ponds on saltmarsh habitats to ensure that the appropriate salinity changes are achieved.

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Fig. 1. Characteristics of saltmarsh pools. A: Numbers of ponds successfully used by natterjacks (open bars) or without any evidence of use by natterjacks (solid bars). B: Salinity changes between October 1990 and July 1991 in ponds with natterjack tadpoles or healthy spawn in May 1990 (open bars), ponds with occasional calling natterjacks and/or dead spawn in May 1990 (hatched bars) and ponds with no evidence of use by natterjacks in May 1990 (solid bars). Data are averages from two ponds in each class where error-bars show the ranges of the two estimates; where no error bars are present, only a single pond was sampled on that visit.

and thus maintain low numbers of tadpole predators. This is of vital importance to a species with small larvae highly vulnerable to such predation, and in which metamorphic success rates are inversely proportional to invertebrate predator numbers (Banks & Beebee, 1988). In the Scottish saltmarsh studied by Nicol, invertebrate species diversity was at a minimum and macrophytes virtually absent in the ponds of intermediate salinity and irregular inundation, presumably because neither freshwater nor marine species could establish for long periods. At Priestside at least seven species of tadpole predators have been observed (four species of *Agabus*, *Colymbetes fuscus*, an unspecified *Dytiscus* and *Notenecta glauca*) but numbers were generally low (D. Green, unpublished observations). Aquatic macrophytes were absent from many pools, but water crowfoot (*Ranunculus* species) occurred in some of the most productive natterjack ponds on the upper merse. Overall, faunal and floral diversity was much less than that regularly encountered in dune and heathland

AN ABERRANT SPECIMEN OF DRYMOBIUS RHOMBIFER (COLUBRIDAE: COLUBRINAE) : A NEW GENERIC RECORD FOR BRAZIL

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The neotropical colubrid genus *Drymobius* contains four species of 'racer-type' snakes closely related to the neotropical genera *Dendrophidion*, *Mastigodryas* and *Drymoluber* (Stuart, 1932). Three species, *Drymobius margaritiferus*, *D. chloroticus* and *D. melanotropis* are Central American in their distribution (Wilson, 1970: 1975a-d; Villa, Wilson & Johnson, 1988), although *D. margaritiferus* has also been recorded from the Caribbean coast of Colombia (Pérez-Santos & Moreno, 1988). *D. rhombifer* is primarily a South American species, occurring to the north and west of Amazonia in a Caribbean and Pacific coastal belt extending from French Guiana (Chippaux, 1986) and Venezuela to Ecuador, Peru and Bolivia (Vaeth & Rossman, 1984), on either side of the Andes (Pérez-Santos & Moreno 1991), and into Central America as far as Nicaragua (Villa, 1983).

The first author was conducting a herpetofaunal survey as part of the intensive Anglo-Brazilian, multi-disciplinary, ecological Maracá Rainforest Project (Instituto Nacional de Pesquisas da Amazónia; Royal Geographical Society) on the Ilha de Maracá, a forested riverine island on the Rio Uraricoera, 130 km northwest of Boa Vista, Roraima, northern Brazil (O'Shea, 1989). A single specimen of *Drymobius* was collected on a trail through terra-firme forest near the Cachoeira Fumaça on the northern Furo de Santa Rosa channel of the Rio Uraricoera towards the western end of the 100,000 hectare riverine island. Maracá specimen (field no. MR309): female; 740 mm SVL + 290 mm TL; dorsals (keeled) 19-17-15 rows; ventrals 156; subcaudals 91 (paired); anal plate divided; supralabials 9 (with 4th, 5th and 6th in contact with the orbit, 4th divided by a horizontal suture on both sides); infralabials 10 (with five in contact with first pair of chin shields); preocular 1; postoculars 2; temporals 2+2 (left), 1+2 (right); maxillary teeth 34 (Table 1). Dorsal coloration olive green to brown with patterning confined to scattered black speckling; ventrally off-white with two longitudinal ventrolateral rows of black spots.

Although the ventral and subcaudal scale counts of MR309 (a female) complied with those of typical *D. rhombifer* (Table 1) the characteristeric rhomboid patterning on the dorsum was absent. The head of MR309 also appeared much narrower than that of other specimens of *D. rhombifer* examined. The only other *Drymobius sp.* with similar scale counts is *D. melanotropis* from Nicaragua, Costa Rica and Panama.

	D. rhombifer	*D. melanotropis*	MR309
Ventrals	145-169	149-163	156
Subcaudals	84-103	91-108	91
Maxillary teeth	30-32	33-34	34

TABLE 1. Ventral and subcaudal scale counts for MR309 compared with those obtained from two specimens of *D. melanotropis*, seven specimens of *D. rhombifer* and available literature.
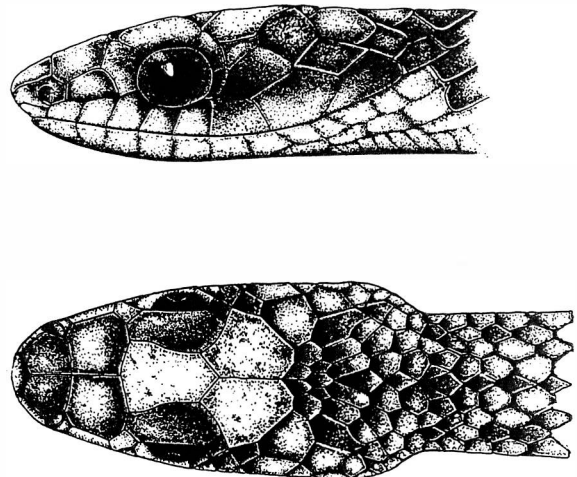

Fig. 1. Dorsal and lateral views of head of MR309 (S. Elmhurst).

The high maxillary tooth count and the uniform dorsal coloration of MR309 resemble the Central American *D. melanotropis* but MR309 lacks the black scale keels usually reported for that species and the presence of a specimen of *D. melanotropis* on Maracá would indicate a range extention of approximately 1800 km. It seems more likely that MR309 represents an aberrant specimen of *D. rhombifer*, the first record of the genus from Brazil, since uniform, unblotched specimens of *D. rhombifer*, although rare, are not unknown (Dixon & Soini, 1977).

Material examined: *D. melanotropis* : UMMZ 79762 (7mi. above Rama, Rio Signia, Nicaragua); UMMZ 131309 (Zapote, Guancaste, Costa Rica); *D. rhombifer* : MNHN 1897-4 (French Guiana); BMNH 74.8.4.24 & 30 (Moyobamba, Peru); BMNH 97.11.12.9 (Medellin, Colombia); BMNH 98.4.28.58 (Paramba, Ecuador); BMNH 1909.4.30.67-68 (Bitaco, S.W. Colombia). MR309 will be deposited in the Museum of Zoology, University of Sao Paulo (MZUSP).

tors and their institutions for the loan of specimens from their collections: Ivan Ineich, Museum National d'Historie Naturelle, Paris; Ronald A. Nussbaum and Greg Schneider, University of Michigan Museum of Zoology. Samantha Elmhurst kindly drew the figure.

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TYPHLOPS BRONGERSMIANUS VANZOLINI AND LIOPHIS ALMADENSIS (WAGLER): TWO NEW RECORDS FOR THE SNAKE FAUNA OF THE PROVINCE OF FORMOSA, ARGENTINA

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El Bagual Ecological Reserve (26° 10' 53" S - 58° 56' 39" W) was created in 1985 to protect northern seasonal moist natural habitats in the eastern part of the province of Formosa. Recent faunistic surveys on the ecology and distribution of snakes at El Bagual conducted by Yanosky and Mercolli, emphasized species composition because of the scarce knowledge of snake species in the province. Bergna & Alvarez (1990) were the first to present a systematic list of 20 snake species for the province of Formosa. Earlier, Yanosky (1989a,b) published two papers on the snakes of El Bagual Reserve, where he cited 19 species. The present contribution adds two additional species to the snake fauna of El Bagual Reserve, Formosa. Both species are new records for the province and Liophis almadensis, recently cited as a new record for Argentina by Bergna & Alvarez (1990), confirms its presence at the southern end of the "wet" Chaco of Argentina.

Typhlops brongersmianus Vanzolini. This species is represented by two specimens taken at El Bagual Reserve in September 1989 and 1991 by Yanosky and Mercolli. The 1989 specimen is now catalogued in the Texas Cooperative Wildlife Collection (TCWC 69413), the 1991 specimen is in El Bagual Herpetological Collection (REB-TO 002). Neither animal has been sexed. Both specimens were found on the surface among grasses of the genus Paspalum during daylight hours in a mixed low forest-savanna habitat. Both specimens have 20-20-20 dorsal scale rows, 287 dorsals from rear of snout shield to tip of tail, streaked rostral and no tail ring. The average number of pigmented dorsal scale rows is 11 (Dixon & Hendricks, 1979). Our specimens have 13 pigmented dorsal scale rows, and Cruz & Scrocchi (1989) reported a specimen assignable to T. brongersmianus with 15 rows of pigmented dorsal scales.

Typhlops brongersmianus has been recorded from the Argentine provinces of Buenos Aires, Córdoba, Corrientes, Entre Ríos, Misiones, Salta, Santa Fé, and Tucumán by Dixon & Hendricks (1979). The species was later recorded from the province of Chaco by Cruz & Scrocchi (1989). The latter province and the province of La Rioja were later included in the species distribution in a checklist of Argentine snakes by Williams & Francini (1991).

Liophis almadensis (Wagler). This species record is based upon six specimens taken at El Bagual Reserve in the months of October and November 1991. One specimen was donated to the Corrientes Herpetological Collection (CHC), one to the Texas Cooperative Wildlife Collection (TCWC) and four remain in El Bagual Herpetological Collection (REB-LA). Three specimens are female, one is a male, and two remain unsexed. The habitat where five specimens were taken is highly varied. One came from beneath a potted plant in a human dwelling, one from within a termite mound one meter deep, and four came from savannas where Paspalum sp. is the common grass with an overstory of Leguminosae.

Measurements taken from five specimens showed a body mass of 16.7±8.34 g (range 11.5-31.5); snout-vent length of 31.5±4.07 cm (range 28.5-38.5) and total length of 37.7±1.56 cm (range 36.0-40.0). Scale characters of the head, body and tail are typical of the species presented by Dixon (1991) and easily assigned to specific level by Dixon's (1989) key.

Liophis almadensis is known to occur from Marajo Island, Brazil, south along the Atlantic coast to Rio Grande do Sul, westward to northern Bolivia and south to the Paraguayan Chaco (Dixon, 1991). Dixon's (1991) distribution of the species invalidated the specimens referred to as Liophis almadensis by Abalos & Mischis (1975), because no specimens existed in collections housing Liophis species from Argentina. Based upon Dixon's (1991) distribution map, Williams & Francini (1991) excluded Liophis almadensis from the Argentine snake fauna. Bergna & Alvarez (1990) cited the first recent records of Liophis almadensis from the provinces of Chaco and Misiones, Argentina.

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FORUM

HYPOTHESIS: FUNCTIONAL SIGNIFICANCE OF COLOUR AND PATTERN OF ANURAN TADPOLES

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In the absence of sexual selection, the modest array of colours and patterns of anuran tadpoles function primarily in camouflage and specific intra- (e.g. school cohesion) and interspecific (e.g. antipredator) interations. We suggest that the paucity of observations (e.g. Voris & Bacon, 1966) and tests (e.g. Caldwell, 1982) involving tadpole colours result in part from the lack of a summarisation and synthesis of the variations present. We present such a summary and submit three general hypotheses concerning the colours and patterns of tadpoles.

An effective terminology must represent preserved and live specimens and distinguish among patterns formed by the presence, absence and dispersion of both melanic (persist in preservative) and non-melanic (mostly disappear in preservative) pigments. Non-melanic pigments often overlie gaps in melanic patterns, and patterns commonly are formed, sometimes almost entirely in younger stages, by pigment deposited in subintegumentary structures.

(1) Dorsal and ventral colour and pattern correlate with the ecology and behaviour of tadpoles. Patterns of tadpoles are more diverse than the relatively low variety of colours. We divided these patterns that are assumed to function in various forms of crypsis in specific macro- and microhabitats into 11 components that often occur in combinations. (1) Both uniformly dark (e.g. many *Bufo*, some *Rana*, some *Rhinophrynus*, some *Scaphiopus*) and light (e.g. various microhylids, some *Rhinophrynus*, some *Scaphiopus*, some *Xenopus*) dorsal colourations are common. Sparse pigmentation (e.g. some *Scaphiopus*, *Rhinophrynus* and *Xenopus*) or transparency of all (e.g. some hylids, some microhylids) or part (e.g., some phyllomedusine hylids) of the body are common in midwater forms. Multiple objects, such as gut and eyes surrounded by translucent areas move together but appear separated, and tracking such objects is more difficult because receptive eyes look at the parts alternately. Ventral colouration varies from uniformly dark to translucent (benthic forms) or white (= countershading) in nektonic forms. (2) Stripes (i.e. longitudinal or oblique) may be positioned on the sagittal line of the body (e.g. *Hypopachus variolosus, Kaloula rugifera* and *Rana pleuraden*), laterally on the tail (e.g. *Hemisus guttatum, Hyla andersoni, H.*

femoralis, Phrynohyas venulosa, Semnodactylus weali) or obliquely from eye to naris (e.g. *Hyla avivoca*) or extend from the body onto the tail and often through the eye (e.g. *Hyla microcephala* group, *H. picta*). Both melanic and non-melanic pigments may be involved, and a bicoloured tail muscle (upper dark, lower light, many *bufo*) is a type of stripe. Faint dots formed by pigment around neuromasts (e.g. *Rana grylio, R. virgatipes*) can form a discontinuous, faint stripe. (3) Bands (i.e. transverse or vertical; across body, between eyes, or vertical, height of tail muscle and fins) may occur on the tail (e.g. *Atelophrynus chrysophorus* and *Litoria micromembrana*, Fig. 1B, *Litoria "bicolor"*) or body (e.g. between eyes of *Hyla avivoca*; tail of small *Rana palmipes*, tail and body of small *Pseudis*). (4) Saddles, partial bands limited to the dorsum of the tail muscle, may be single (e.g., young *H. gratiosa*) or multiple (e.g. *Acris* spp., *Bufo valliceps*, *Hyla avivoca*, Fig. 1C, *Pseudacris crucifer*). Stripes, bands and saddles probably serve to break up the body outline in different views. Stripes may provide camouflage or disruptive effects in linearly arranged habitats (e.g. submerged grasses) and probably modify a predatory attack because the speed of striped objects is often over-estimated. Bands offer crypsis by disruption of outline and confusion during movement because of the inability to track specific bands. (5) Mottling, dark reticulations and irregular blotches on light ground colour or vice versa, occurs in many species (e.g. *Rana*). (6) Maculate (i.e., multiple, dark, isolated spots, dots and blotches on light background or vice versa (e.g. *Boophis microtympanum, Rana catesbeiana*, Fig. 1D) and (7) freckled (i.e. smaller, usually evenly distributed spots or dots; *Boophis tephraeomystax, Phyllomedusa marginata* and large *Hyla cinerea*) differs only in the size of mark. Mottling, spots and dots all function as camouflage in a dappled environment caused by vegetation. (8) Light or dark lip-lines extend posteriorly to posteroventrally from near the lateral base of the oral disc. (9) Light fins with darkened areas at or near the edges and lighter or unpigmented zones adjacent to the tail muscle (*Phrynomerus bifasciatus, Calluella yunnanensis*, and *Rana heckscheri*, Fig. 1E) probably serve a disruptive function. (10) Fake eyes or ocelli, light, usually circular areas surrounded at least partially by darker borders or vice versa, are assumed to be deflection marks. Crude ocelli with indistinct proximal borders occur on the tail tips of suctorial tadpoles of *Ascaphus* (Fig. 1F) and *Staurois* that move relatively little; attacks from within the water presumably come from the rear, and aerial attacks would presumably be directed at the tail rather than the cryptically coloured body. The large (c. 100 mm) gregarious tadpoles of *Rana alticola* have a single (Sahu & Khare, 1984) or multiple (Annandale, 1912) bright enamel yellow rings surrounding intense black situated on each side of the tail muscle (Fig. 2B). The ocellus may make the tadpole look like the head of a much larger, big-eyed beast, and large glands occur dorsolaterally and ventrolaterally on the body. Selection should favour characteristics of ocelli that enhance apparent size or prominence of the "eye." Over-estimation of the size of the inner of concentric circles (= large "pupil") and underestimation of the outer circle is greatest when the two diameters are in a ratio of 1.5:1 (Oyama, 1962). High contrast enhances the effect. The ratio of ocellar components of four specimens of *R. alticola* (CAS 111532) ranged from 1.15 - 1.29. Black tail tips without surrounding light areas are assumed to serve as deflection patterns (e.g. *Acris* (Fig. 2A), *Chirixalus doriae, Hemisus*
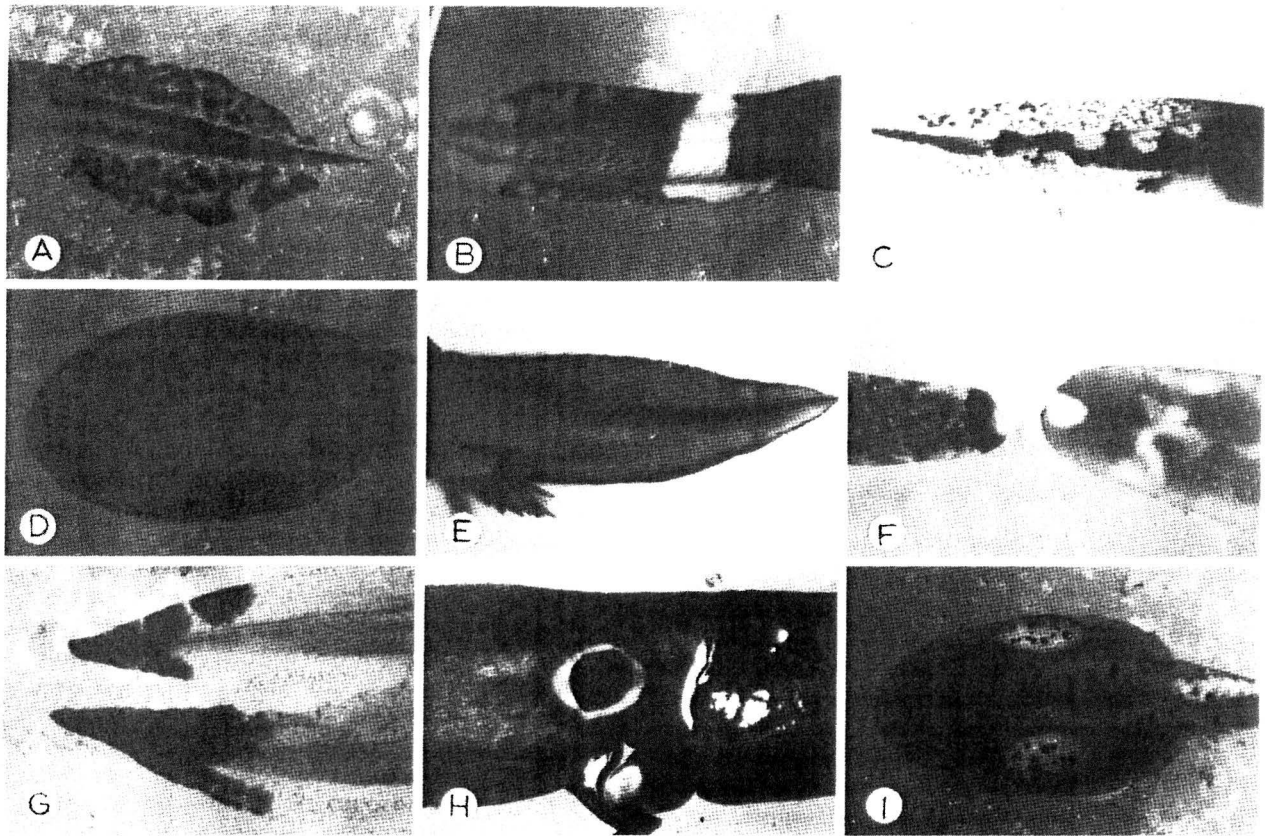
Fig. 1. Pigment patterns of selected tadpoles: (A) striped tail muscle of *Hyla femoralis*; (B) banded tail of *Litoria micromembrana*; (C) saddles on tail of *Hyla avivoca*; (D) maculate body of *Rana catesbeiana*; (E) dark margin on the tail fins of *Rana heckscheri*; (F) tail tip ocellus of *Ascaphus truei*; (G) black tail tip of *Acris gryllus*; (H) yellow ocelli at the base of the tail of *Rana alticola*; and (I) integumentary glands of an Indian ranid tadpole.

guttatum, Hyla smithii, some *Hyperolius*, some *Lysapsus* and some *Rana*; Caldwell, 1982). (11) Isolated clear areas along the periphery of the tail fin (e.g. *Hyla berthalutzae*) and isolated dark spots, often in the tail fins and usually surrounded by transparent or lightly-pigmented tissue (e.g. phyllomedusine hylids) in tail fins and muscle may serve as ocelli but more likely serve for outline disruption. Tadpoles of *Hyla hutchinsi* have a pinkish tail with a single large black spot with diffuse margins at about midlength. Unicoloured dark (benthic) or light (mobile nektonic) ventral coloration are common. Tadpoles that remain motionless in midwater, often among dense vegetation, commonly have banded (e.g. *Megophrys carinensis*), mottled (e.g. *Gastrophryne*, some *Microhyla*, some phyllomedusine hylids) or striped (*Hyla leucophyllata* and *H. parviceps* groups) throats and bellies.

(2) Changes in colour and pattern as a function of time of day, ontogeny and site are accompanied by changes in behaviour and ecology. Diel changes usually involved nocturnal blanching of all or part of the body, but the distal third of the tail of large tadpoles of *H. gratiosa* (Altig, 1972) becomes darker at night. Changes in intensity of the diffuse spot in the middle of the ventral fin of some phyllomedusine hylids is correlated with light intensity.

Ontogenetic colour changes usually occur between hatchling and tadpole stages or between small and large tadpoles. Tail saddles of many hatchlings are lost by the time the tadpole is free-swimming but retained throughout larval life in *Acris, Hyla avivoca, Pseudacris cadaverina* and some *Bufo*. The yellow body band of young tadpoles of *Rana grylio*

and *R. heckscheri* disappears in the benthic tadpoles of *R. grylio* (Altig, 1972) but remains throughout larval life in the nektonic, schooling tadpoles of *R. heckscheri*. Likewise, small tadpoles of *R. heckscheri* lack the dark edges on the fins that are present in larger tadpoles. Until about a third grown, tadpoles of *Hyla gratiosa* have a single dark saddle at midlength of the tail muscle that is not derived from the pattern of hatchlings; these small tadpoles tend to stay among vegetation. After this saddle dissipates, a sharp demarcation between proximal punctate and distal stellate melanophores becomes apparent, and the tadpoles are more pelagic in open water. Small tadpoles of *Rana palmipes* have bands at midbody and at the tail-body junction that disappear in larger tadpoles, and young tadpoles of *Pseudis paradoxa* are boldly banded on the body and tail, while large specimens are rather uniformly greenish-black to faintly mottled. Multiple ocelli on the tails of *Rana alticola* tadpoles disappear with age until only one remains (Annandale, 1912). Some pigmentary traits respond as dominants in F_1 progeny (Fortman & Altig, 1973), but there are no definitive data on the genetics of larval colours.

The implications of colour differences among sites largely are enigmatic. Successive cohorts of *Rhinophrynus dorsalis* in the same pond in Costa Rica were uniformly light or almost black (R. W. McDiarmid, pers. comm.). *Rana alticola* tadpoles from streams were lighter than those from ponds (Sahu & Khare, 1984). Tadpoles growing in clear water, especially if darkly stained by tannins, are more prominently coloured than individuals in turbid water (e.g. Bragg, 1957), and the red tail colouration of tadpoles in the *Hyla versicolour* group only

occurs when the tadpoles live in clear waters; if this colouration functions in chromostereopsis (inability of a lenticular system to focus all wavelengths in one plane simultaneously), the red and melanic pigments should appear at different distances from the viewer. The normally darkly-pigmented tadpoles of *Spea* living in turbid water appear silvery in life and largely transparent in preservative.

(3) Associated structures and behaviours are correlated with colour and pattern. A fright reaction in response to cutaneous substances has been shown only for ranid (Altig & Christensen, 1981) and bufonid (Hews & Blaustein, 1985; Pheiffer, 1974) tadpoles. The intense blackness of most *Bufo* tadpoles may be an aposematic colouration associated with a tendency to aggregate and cutaneous toxicity during part of larval ontogeny (Brodie & Formanowicz, 1987). The organized schools of golden, nektonic tadpoles of *Phyllomedusa vaillanti* are segregated by size, and school formation is governed by ambient light (Branch, 1983). Large mobile aggregations of tadpoles of *Rana heckscheri* appear unorganized, contain hundreds of individuals, occupy a number of cubic meters, and along a bank they move in a rotational manner as described by Duellman & Lescure (1973) for tadpoles of *Osteocephalus taurinus*. Tadpoles in stationary or slowly-moving, mid-water schools of small tadpoles of *R. heckscheri* all face one direction, and the schools appear spatially organized (pers. observ.). Bursts of swimming interspersed with quiet periods appear to occur after a neighbour moves and stops, and it is tempting to suggest that the golden band contrasted against the black body serves as a motivational cue to sustain orientation within the group.

Escape by swimming or immobility are viable modes of defence for individuals or a group that are presumed to vary with colour, age and site. Escape behaviours are poorly understood but usually involve moving away and often downward from the stimulus regardless of the starting position. Ending positions usually are at or near the bottom or within bottom debris. Large tadpoles of *Hyla gratiosa* and *Pseudacris nigrita* commonly escape temporarily to the surface in clear water at night, and tadpoles of *Rana sphenocephala* often escape upward in turbid water during the day or night. Skin glands assumed to produce toxic or noxious substances upon contact occur in hylids (e.g. *Hyla fimbrimembra*), leptodactylids (e.g. *Physalaemus petersi*), ranids (e.g. *Amolops* spp. *sensu lato*, *Rana alticola*, *R. chalconota*) and rhacophorids (e.g. *Boophis* cf. *majori*). Some *Amolops sensu lato* have epidermal spines on the dorsum.

Judged relative to human visual perception and based on the contingencies of lens, sensory structures and interpretative centres, probably no visual interpretation is exactly the way the scene exists. The primary functions of colour in tadpoles probably involve: (1) background matching, (2) disruptive patterns and (3) countershading for crypsis plus (4) deflection marks and (5) perhaps mimicry or aposematic colouration. Benefits of colour and pattern probably stem from (1) failure of a predator to detect or recognize the prey, (2) a delay in a predatory attack while proper identification and location of the prey is evaluated, and (3) misdirection of attack. A colour pattern of a given tadpole may employ more than one technique and function differently with (1) different predators, (2) at different times of day, (3) in different habitats, and (4) at different ages. The success of anti-predator features need not be totally effective to enhance selection. The effects of foraging strategies (e.g. sit-and-wait vs. pursuit hunters; attacking from above or within

water column) and sensory abilities (e.g. binocular vs. monocular vision, foveate vs. non-foveate eyes, electroreceptive vs. not, colour vs. black and white vision, and olfactory acuity) of predators are poorly understood modifiers.

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BOOK REVIEWS

Atlas de Répartition des Batraciens et Reptiles de Corse.
Michel Delaugerre & Marc Cheylan. (1992), Parc Natural Régional de Corse. 128 pp.

Corsica is the fourth largest and the second highest island in the Mediterranean. It has a particularly original fauna, with, especially in the herpetofauna, quite a series of endemic species and forms. With this book on the amphibians and reptiles of Corsica the authors offer considerably more than the title suggests. Besides the distribution maps which could be expected it gives a wealth of data on Corsica, its special fauna and biogeographic position. All this is richly illustrated by really beautiful photographs, clear data-tables and insight-supporting drawings.

A short treatment of the vegetation, geology, geography, climate and human influence on Corsica is followed by a thorough discussion of each species as the heart of the book. Here the two authors are supported by six French and Italian specialists in the field of amphibians and reptiles. As could be expected in an atlas, distribution maps are given in this chapter. They are based on more than 2600 recent observations and they are all supplied with clear histograms showing altitude distribution. After a critical discussion of these data follows a thorough survey of known but also often newly collected data on all sorts of biological aspects of the animal, such as its precise taxonomic position and ecological and ethological data such as habitat selection, courtship and mating, reproduction and activity times. For the more special species this even leads to a treatment of the whole genus *(Euproctus, Algyroides)*. Also the recently described *Discoglossus montalentii* is scholarly discussed.

After this treatment of every species separately there are some chapters which render this book considerably more than an "atlas". First there is a chapter on the micro-insular distribution around Corsica (data about 111 islands and satellite islets!), in which morphological differences between the various populations are also dealt with (e.g. in body size, colouration and sexual dimorphism). Then there is a separate synthesis of all ecological data given with the species discussions and matters such as development of the animal communities. Here the Corsican and Tyrrhenean endemics are considered the originals and the rest as later invaders, partly not yet having reached their definite position on the island. Moreover, it is shown that even for the original species shifts in distribution are still in progress. Finally there is a very good biogeographic synthesis dealing with the complete western Mediterranean and partly also other vertebrate groups (mammals and birds). These last few chapters are written in a stimulating and hypothesis-generating manner, rendering this book into a "must" for anyone interested in geography or animal ecology. But also for those who just love Corsica's beautiful scenery this book contains a wealth of information, especially by the ample use of the wide margin for explaining "difficult" words and concepts.

H. Strijbosch
University of Nijmegen

Venomous Reptiles of North America. Carl H. Ernst. (1992). Smithsonian Institution Press, Washington. 236 pp. $35.00, cloth.

The North American herpetofauna is almost certainly the most intensively studied in the world, due to the large number of North American herpetologists, both professional and amateur. For obvious reason, the venomous species have attracted a disproportionate amount of attention. Consequently, one of the problems for herpetologists first starting to take an interest in these animals is simply seeing the wood for the trees, and finding their way through the enormous volume of literature.

Ernst's book is a valuable attempt to survey and summarise the literature on the natural history of these creatures. The stated aim of the book is to present the current knowledge of the biology of all North American venomous reptiles, with the particular aim of providing necessary information for conservation programs. Furthermore, the book aims to promote further research by pointing out the numerous gaps in our knowledge of these animals.

The introduction briefly covers general aspects of the biology of the North American venomous reptiles, as well as giving brief instructions for procedures to follow after bites. The introduction is followed by a key to the venomous species occurring north of Mexico. This primarily relies on colour pattern features, or large, obvious scalation characters, allowing its use on live specimens in the field. However, for a few rattlesnakes, the chosen characters concern rather small features of the head scalation, which I personally would not want to have to examine on an unrestrained live specimen.

The remainder of the book consists of individual species accounts of the Gila monster (*Heloderma suspectum*), the yellow-bellied sea snake (*Pelamis platurus*), and the 19 North American species of front-fanged land snake. The length of the accounts varies from 5 to 20 pages, depending on how much is known about the relevant species. The species are described and their natural history discussed under the largely self-explanatory headings of *Recognition, Karyotype, Fossil Record, Distribution* (a map is provided), *Geographic Variation* (including a listing of the subspecies, and their distributions), *Confusing Species, Habitat, Behaviour, Reproduction, Growth and Longevity, Food and Feeding, Venom and Bites, Predators and Defence, Populations, and Remarks.* The text consists largely of lists of facts about the animals gathered from the recent (mostly post-1955) literature, sometimes supplemented with the author's personal observations. References are cited copiously throughout, and the bibliography contains an impressive total of approximately 1000 references. Gaps in our knowledge of various facets of the biology of these animals are pointed out everywhere, and a concern for the conservation status of various species is expressed in the accounts.

There are a few minor niggles. The distribution maps cover only the range of the species, but do not show the ranges of the subspecies, which might have been useful. However, since many of these subspecies are likely to be biologically irrelevant non-entities, this is hardly a serious omission. More seriously, the author appears to have confused the distributions of *Crotalus mitchelli pyrrhus* and *C. m. stephensi*: it is

the latter that is restricted to SW Nevada and adjacent eastern California, and the former which occurs from Utah to southern California and Arizona. However, the distinguishing characters are correct, and the colour plates of the two forms are correctly labelled.

The book is illustrated with 55 colour plates, displaying all species and subspecies, with several plates for some taxa. There are also black and white photographs of most species scattered through the text. The standard of the photographs is variable, but overall, I was disappointed. Several colour plates are severely faded, resulting in poor colour rendition, and some are poorly focused. In the case of the black and white photographs, the contrast of the printing is too high, obliterating many details. Due to the enormous amount of attention lavished on the venomous reptiles of North America by professional and amateur photographers alike, superb quality photographs are available for all, or practically all, taxa; it is a pity that many of the photographs chosen for this book are of a standard that one would expect from a publication from the 1960s rather than the 1990s.

However, overall, this book is a very valuable and welcome summary of current knowledge of the natural history of the venomous reptiles of North America. The extremely comprehensive literature survey and bibliography will be invaluable to anyone seeking to become acquainted with these animals. The author is to be commended for constantly pointing out how much we do not yet know, rather than glossing over the gaps to emphasise the progress that has been made. I would recommend this book to anyone with an interest in the North American herpetofauna, or in the natural history of venomous reptiles in general.

Wolfgang Wüster
University of Aberdeen

Handbook to Middle East amphibians and reptiles. Leviton, A. E., Anderson, S. C., Adler, K. & Minton, S. A. (1992). 252pp. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA. US$28.00 (cloth).

Prompted by Iraq's invasion of Kuwait in August 1990, the handbook was appropriately conceived as an interim replacement to Kamel Khalaf's (1959) *The reptiles of Iraq, with some notes on the amphibians.* With the increased need, the handbook with its section included on snakebite and recognition was designed as a useful work of reference in the field for the troops and ancillary civilian groups serving in the area of military operations. The conflict ended, however, and most military personnel were withdrawn before the book could be produced, but the environmental chaos and damage caused by the Gulf War ensured a continuing need in the context of biodiversity assessment and conservation. With these points in mind, and the urgency for making a handbook available within a reasonable period of time, certain limitations were imposed upon the authors, obliging them to depend on documented records and museum specimens immediately available to them without the opportunity to verify the occurrence of all species in the region recorded in the literature.

Notwithstanding these limitations, it should be said immediately that to my mind the authors have done an excellent job

and produced a work that is likely to be of use for many years, if not several decades to come. If discord between nations must reach the level of conflict, then at least a useful outcome has been the application and scientific endeavour that went into this handbook!

The geographical area delimited by the handbook encompasses that of allied operations during the Gulf War. It has no particular significance in terms of physical, environmental or political geography. This somewhat arbitrary selection is perhaps regrettable for it renders the work's title a misnomic. Although the whole of Iraq and Kuwait have been included, the area extends only into parts of Iran and Saudi Arabia, and embracing also Bahrain, Qatar and part of the United Arab Emirates. Fully appreciating the time constraints imposed upon the team of authors and the magnitude of the task that would have been involved, I was personally sorry not to see Syria, Lebanon, Jordan, Israel and the whole of Iran also within the area of coverage if one is going to go to the trouble of producing a handbook in the first place. I realise that it would be difficult to include all of the countries of the Arabian Peninsula for national boundaries are uncertain and the herpetology not well known - in fact the Arabian Peninsula would require a separate handbook. The handbook is therefore less one for the Middle East *per se* than for the Gulf zone, that is Iraq, Kuwait and adjoining areas.

The handbook otherwise is praiseworthy. Nomenclature of species has as far as possible been updated; useful keys have been included: 80% of the species listed have been illustrated by at least one plate (some also showing habitat as well as intraspecific variation) - only two of which in the whole book are not in colour - and most are of specimens from within or adjacent to the handbook's geographical area of coverage. Contributors of photographs have been very carefully acknowledged and great care has been taken over the accuracy of captions. However, in a handbook, some information on size in either the text or as a scale in the captions could have been helpful for non-herpetologists in the case of most species, even if perfectly obvious to enthusiasts for genera that are well-known and described in other, readily available standard works. I felt this was a particular deficiency for the non-venomous snakes (dimensions are included in the special section on venomous species) and amphibians. Perhaps as compensation for this short-fall, there is a thorough and comprehensive bibliographic section with coverage ranging from general works on amphibians and reptiles to technical references that also include check lists and keys under groups and countries. Indeed, the work strongly reflects the authors' contacts with herpetologists worldwide, the excellence of cooperation achieved with them and the highly constructive pooling of resources from whatever source. This kind of international involvement is inevitably an outcome of the First, and will be of subsequent World Congresses of Herpetology - to bring together the world's exponents in the field to further the present state of the art!

The useful sections on the venomous snakes, and on snake venoms and snakebite in the Middle East, will concern and be of interest to non-specialists as a whole. On the basis that the handbook will hopefully engender enthusiam amongst naturalists generally and be an inspiration for aspiring herpetologists, a useful section on collecting and preserving amphibians and reptiles by John E. Simmons has been in-

cluded as an Appendix respectively to support and assuage the hopes and desires of museum specialists.

Notwithstanding the limited area coverage, my congratulations to the Leviton/Anderson/Adler/Minton team. I regard this handbook as invaluable to the field worker in Middle Eastern countries and for a book with proper, durable hardback being marketed at around £16 sterling it will not at the same time break your bank balance! Yes, get it if you are anticipating a visit to the Middle East and require enlightenment on the species you are likely to observe there.

M. R. K. Lambert
Natural Resources Institute

Guide to the Reptiles and Amphibians of the Savannah River Site. J. Whitfield Gibbons and Raymond R. Semlitsch. (1991). 131 pp. University of Georgia Press, Athens, Georgia. $20.00, cloth.

This is a uniquely-conceived book, which does not readily lend itself to comparisons with other herpetological works. Although the herpetological literature abounds with site-specific and regional inventories, as well as relatively short-term ecological studies, there are only a handful of localities where long-term population monitoring of amphibians and reptiles has been consistently conducted. One of these is the 780 km^2 Savannah River Site, located in west-central South Carolina. It provides an unparalleled ecological laboratory, encompassing a diversity of habitat types, secure from public intrusion, and a network of roads which provide ready access to study areas. This site has provided ecologists with opportunities to study life histories, natural population cycles, and the effects of habitat alteration and disturbance upon herpetological communities.

Those looking for a "field guide" to the herpetofauna of South Carolina may be disappointed by the lack of illustrations and the book's narrow geographic scope. The title may be a bit misleading - in reality it is not a [field] guide but a well-annotated guide to several decades of herpetological research conducted at the Savannah River Site, by a succession of ecologists and their students. The introductory chapters provide an overview of the area, as well as more detailed descriptions of specific study sites, followed by a checklist and key to the amphibians and reptiles recorded from the Savannah River Site. These chapters are followed by short accounts concisely summarizing each species' distribution and abundance at the Savannah River Site and detailing any site-specific research pertaining to that species. Specific references are listed by number, which corresponds to a numerically-coded bibliography of the Savannah Research Ecology Laboratory's herpetological publications. The final chapter of the book is an exhaustive, cross-referenced, numerically-coded bibliography of herpetological research conducted at the Savannah River Site, divided into subject categories which span a broad range of biological disciplines, including systematics, ecology and physiology.

Recent, well-publicised concerns that populations of amphibians are declining must be evaluated in light of the scientific evidence documenting these species' natural population fluctuations. As public pressure to conserve

amphibians (and reptiles) increases, the importance of the Savannah Research Ecology Laboratory's long-term ecological research programme will become ever-more apparent. I hope that the authors intend to periodically update this volume. The book is printed on high quality paper, the cloth binding is rugged, and the design and layout, while spartan, are pleasing and very functional. For herpetologists, ecologists and conservation biologists, this book is excellent value. It is a modestly-priced, information-packed reference volume.

Michael W. Klemens
American Museum of Natural History

Herpetology: Current Research on the Biology of Amphibians and Reptiles. Kraig Adler (ed.). (1992). Society for the Study of Amphibians and Reptiles. Oxford, Ohio. US$28.00, cloth.

The decision to hold the First World Congress of Herpetology in England was made at meetings in Raleigh, North Carolina, and in London and was largely due to the generous vision of US herpetologists. They feared that herpetologists from what were then Communist countries might be unwilling or unable to travel to the USA at the time of the (then) cold war. Kraig Adler took a leading part in these early and later negotiations and it is fitting that he should be the Editor of the present volume.

The book itself, 245 A4 pages, is intended as a record of the First World Congress of Herpetology which was held at the University of Kent, Canterbury, on September 11-19, 1989. There are the final drafts of the nine plenary lectures (171 pages) followed by full details of the congress organisation.

The plenary lectures are valuable if inevitably somewhat dated summaries of important herpetological subjects. The first by Carl Gans (USA) entitled *The status of herpetology* is a thought-provoking, humourous and wide-ranging review, as one would expect from one who, if anybody, can be considered the doyen of the subject. The other lectures are: *Evolution and ecology of parthenogenesis in reptiles* by I. S. Darevsky (Russia); *Tempo and pattern in anuran speciation and phylogeny: an albumin perspective* by L. R. Maxson (USA); *Conservation of amphibians and reptiles* by R. A. Mittermeier, J. L. Carr, I. R. Swingland, T. B. Werner and R. B. Mast (USA and UK); *Sexual selection in amphibians and reptiles: theoretical issues and new directions* by T. R. Halliday (UK); *Paleoherpetology now: a point of view* by A. J. de Ricqlès (France); *Ecophysiology of desert reptiles* by S. D. Bradshaw (Australia); *The state of the art in community ecology* by E. R. Pianka (USA) and *An integrated approach to evolutionary studies of salamanders* by D. B. Wake (USA). Together with the references given, these articles constitute required reading for anyone who wishes to pursue the relevant subject and could be part of the education of any herpetologist.

The remainder of the volume gives complete details of all those concerned in the Congress, a list of the many symposia, workshops and lectures and an account of the other activities in Canterbury. There is also a list of the registered attendants with their addresses. Finally, as this was the first Congress, a

Constitution was agreed and is here published. It is hard to imagine a more comprehensive account of what was in effect the coming of age of herpetology as a discrete zoological subject.

The book is well illustrated with photographs and reproductions of the various memorabilia. including the charming colour print of a watercolour by D. M. Dennis of *Terrapene carolina* gazing at blueberries. copies of which were given to every registered member and can still be purchased. In its format. printing and binding the book is a first class artefact. It will surely become a collector's item. 800 copies only have been printed so you'd better hurry. The address given for puchase is: Robert D. Aldridge. Department of Biology, St. Louis University, 3507 Laclede, St. Louis. Missouri 63103. USA.

G. A. D. Haslewood
British Herpetological Society

BOOKS RECEIVED

Herpetofauna of Costa Rica. Jay M. Savage & Jaime Villa R. (1986). 207 pp. Society for the Study of Amphibians and Reptiles, Athens. Ohio.

A fully revised and bilingual (English and Spanish) edition of Savage's *A Checklist with Preliminary Keys to the Herpetofauna of Costa Rica.*

Biologia Centrali-Americana. Reptilia and Batrachia. Albert C. L. G. Gunther (with Introductions by H. M. Smith & A. E. Gunther). (1987). 326 pp. + 76 plates. Society for the Study of Amphibians and Reptiles, Athens, Ohio.

A facsimile reprint of Gunther's extensive account of the herpetology of Middle America, published to commemorate SSAR's first meeting outside the USA, in Mexico in 1987.

Snakes of the Agkistrodon Complex. A Monographic Review. Howard K. Gloyd & Roger Conant. (1990). 614 pp. Contributions to Herpetology No. 6. Society for the Study of Amphibians and Reptiles, Athens, Ohio.

Comprehensive and systematic account of the evolution. systematics. natural history , and distribution of this group of venomous snakes.

Plazi - Reptilia. Vlastimil Barus & Ota Oliva. (1992). 222 pp. Ceskoslovenska Akademie Ved, Prague.

A systematic account of the reptiles of Czechoslovakia. illustrated with line -drawings and b/w photographs.

Sensorimotor Integration. Biology of the Reptilia vol. 17. Neurology C. Carl Gans & Philip S. Ulinski (Eds.). The University of Chicago Press, Chicago and London.

The third in series of volumes dealing with the reptilian nervous system. this book contains eight contributed papers covering visual systems. infrared sensitivity. muscles. tendons. receptors. the cerebellum and neuropeptides.

ANNOUNCEMENT

The following application was published on 17 December 1992 in Vol. 49, Part 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on this Application is invited for publication in the *Bulletin.* and should be sent to the Executive Secretary. I.C.Z.N., c/o The Natural History Museum. Cromwell Road, London, SW7 5BD, UK.

Case 2814

Pseudoxyrhopus **Günther, 1881 (Reptilia, Serpentes): proposed conservation**

Hobart M. Smith.*Department of Environmental, Populational and Organismic Biology, University of Colorado, Boulder, Colorado 80309-0334, USA.*

Kenneth L. Williams. *Department of Life Science, Northwestern State University, Natchitoches, Louisiana 71497, USA.*

Van Wallach. *Department of Herpetology, Museum of Comparative Zoology, Harvard University, Cambridge. Massachusetts 02138, USA.*

David Chiszar. *Department of Psychology, University of Colorado, Boulder, Colorado 80309-0345, USA.*

Abstract. The purpose of this application is to conserve the generic name *Pseudoxyrhopus* Günther, 1881. The name is in current universal usage for a genus of snakes from Madagascar but was originally published as an unnecessary replacement for *Homalocephalus* Jan, 1863, which has not been used for over 100 years.

SEH MEETING 1993

The 7th Ordinary General Meeting of Societas Europaea Herpetologica will be held on 15-19 September 1993 at the University of Barcelona, Spain. Further details of the scientific programme and registration forms are available from Dr Gustavo Llorente, Dept. of Animal Biology, University of Barcelona, Av. Diagonal, 645, 08028 Barcelona, Spain.

EDITOR'S NOTE

The Editor is grateful to the following for refereeing manuscripts in 1992:

C. Andrèn. R. Avery, J. Baker. T. Beebee. T. Birkhead. K. Bjorndal. W. Branch. D. Broadley, G. Brown. J. Burger, J. Caldwell, C. Ciofi, B. Clarke. J. Cooper, C. Cummins. R. van Damme. J. Davenport. W. Duellman. W. Dunson. S. Eckert. L. Edsman. M. Ferguson. A. Foà, N. Frazer. J. van Gelder. M. Gil. A. Hailey. T. Halliday. J. Harry. C. Hawkey. W. Heyer. W. Hödl. R. Huey. A. Lewis. A. Malhotra. D. Mebs. R. Meek. C. McCarthy. T. Madsen. W. Magnusson. A. Milner. G. Naulleau. R. Oldham, B. Pierce. M. Plummer. W. Pyburn. A. S. Rand. R. Semlitsch. R. Shine. A. Smart. U. Sinsch. H. Strijbosch. R. Theakston. R. Tinsley. G. Underwood. P. Verrell. L. Vitt. R. Wassersug. D. Yalden.

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1992)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.

2. *Three* copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees

3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).

4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.

5. The usual rules of zoological nomenclature apply.

6. Tables are numbered in arabic numerals, e.g. Table l; they should be typed double spaced on separate sheets with a title/short explanatory paragraph underneath.

7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. Fig. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

8. References in the text should be given as in the following examples: "Smith (1964) stated ..."; "...as observed by Smith & Jones (1963)." "...as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. The following examples will serve to illustrate the style and presentation used by the Journal.

> Bellairs, A. d'A. (1957). *Reptiles.* London: Hutchinson.
> Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins *(Pseudemys scripta elegans)* in the laboratory. *British Journal of Herpetology* **2**, 206–210.
> Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.
> Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995–1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.

10. Proofs should be returned to the Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.

11. Twenty-five offprints and one complimentary copy of the Journal are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.

12. All submissions are liable to assessment by the editorial board for ethical considerations, and publication may be refused on the recommendation of this committee. Contributors may therefore need to justify killing or the use of other animal procedures, if these have been involved in the execution of the work.

THE HERPETOLOGICAL JOURNAL

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