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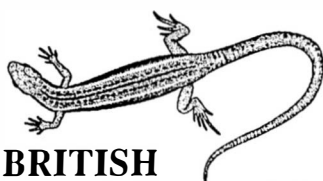
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FRONT COVER: Fire salamander larva (*Salamandra salamandra*) (P. Benson)

ASSESSMENT OF THE OMAN GREEN TURTLE (*CHELONIA MYDAS*) STOCK USING A STAGE-CLASS MATRIX MODEL

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We applied the stage-class matrix model to published data to investigate the population growth rate of Oman female green turtles (*Chelonia mydas*) under different simulated biological and fishery conditions. Juveniles dominated the stable stage-class population vector. Juveniles and adults contributed most to the potential reproductive output. The present total fishing deaths consisted of approximately 2280 hunted and 2000 accidentally drowned (in fishing nets) female turtles. The model suggested a maximum hunting quota of approximately 143 females to maintain a stable population. In addition to protecting eggs and hatchlings, reduction in the juvenile mortality significantly increased the population growth rate. Simulated reduction in the current annual 4280 female fishing deaths to 268 produced a positive population growth rate within feasible stock parameter values. Previous studies have indicated a size at first maturity below 85 cm curved carapace length (CCL). Thus, restricting the number of hunting and accidental drowning deaths to less than 268 females and enforcing a minimum size limit of 85 cm CCL in the traditional turtle fishery appeared necessary to reverse the population decline. More studies on stock abundance, sex composition, stage specific growth, survival, and reproductive rates are needed to refine the model.

INTRODUCTION

Omani fishermen have hunted green turtles (*Chelonia mydas*) for their meat and eggs for many thousands of years, and the practice continues today (Salm, 1991). Lack of data has hindered delineation of stocks. Consequently, the population of nesting and feeding green turtles in Oman waters has been identified as part of the large Indo-Pacific stock (Mager, Jr., 1985). Turtle investigations in Oman started in the late 1970s with the primary purpose of conservation and sustainable exploitation (Ross, 1979). These investigations indicated that green turtles nested on many beaches all along the 1700 km stretch of Oman coastline, with Ra's Al-Hadd being the primary nesting area, followed by Masirah Island (Fig. 1). Active hunting of green turtles for food was limited to a few areas (e.g. Masirah Island and Al Halaniyat Islands) in Oman (Hirth & Hollingworth, 1973; Ross, 1979). However, a significant number of deaths occurred due to accidental drowning in trawl and gill nets (Hare, 1991; Salm, 1991). Although accurate catch statistics were non-existent in Oman, there were a few estimates of annual green turtle deaths within the range 1000 - 6000 individuals (Table 1).

Turtle fisheries have collapsed in many parts of the world largely due to excessive fishing pressure (Mager, Jr., 1985; Ehrhardt & Witham, 1992). Based on the distribution of straight carapace length of female nesters in Ra's Al-Hadd in 1978, Ross (1979) esti-

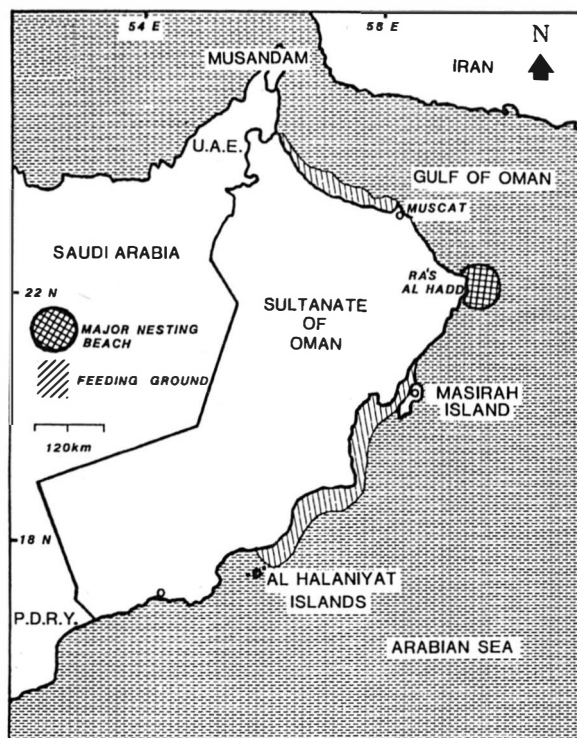


FIG. 1. Map of Oman showing important green turtle nesting and feeding areas.

mated a much lower population of new nesters than the level necessary to maintain a steady population level. Salm's (1991) estimates of Oman's annual breeding female green turtle stock size and number of fishing deaths (hunting plus accidental drowning in fishing nets) for 1990 were the most recent and comprehensive (Table 1). He concluded that the prevailing rate of removal would systematically reduce the population. Thus, Oman requires scientifically-based management policies to conserve the dwindling green turtle population. Ross (1979) and Salm (1991) provided rough estimates of optimal harvesting levels based on approximate turtle population growth rate values. Our primary goal was to improve Salm's (1991) estimate of optimal harvest level (300-450 female green turtles) utilizing a rigorous stage-class matrix model (Lefkovitch, 1965).

Matrix projection technique has been used by many researchers to predict future population trends and responses to different management options on turtle populations (Crouse, Crowder & Caswell, 1987; Crowder, Crouse, Heppell & Martin, 1994). The population vector in the stage-class matrix model consists of biologically distinct stages rather than ages. Thus, one stage may consist of many age groups. We also simulated population growth rates under different, but feasible, biological and fishery conditions, to identify the management options that will reverse population decline. No proven methods of turtle ageing are available and upper age limits of turtles are unknown. Moreover, age specific growth, mortality, and reproduction parameters are largely unavailable for Oman green turtles or any other green turtle population. Under these circumstances a stage-based population model is more appropriate than any age-based model

TABLE 1. Estimates of annual fishing (capture and accidental drowning in fishing nets) deaths and annual female nesting population sizes of green turtles in Oman in 1978 and 1990 (The 1978 values are not comprehensive). R.A.-H.: Ra's Al-Hadd. Sources: (1) Ross & Barwani (1981), Ross (1979, 1985); (2) Salm (1991).

Period	No. fishing deaths		No. nesting females			Source
	females	total	R.A.-H.	Masirah	Oman	
1978	630	1,000	6,000-18,000	200-500	-	(1)
1990	4,280	6,000	-	-	20,000-30,000	(2)

METHODS AND MATERIALS

NOTATIONS USED IN THE TEXT

M = instantaneous annual natural mortality.
 F = instantaneous annual fishing mortality.
 Z = instantaneous annual total mortality, $Z = F + M$.

C = number of annual fishing deaths.
 V_t = stage-class population vector of dimension $n \times 1$ at time t .
 n = number of biologically distinct stage classes in the population.
 N_i = average number of females in the i -th stage.
 N_0 = average number of 0-year old female hatchlings.
 t_1 = start age of i -th stage in years.
 t_2 = final age of i -th stage in years.
 n_{i0} = percentage of individuals in i -th stage at the start time.
 n_{i1} = percentage of individuals in i -th stage after 1 year.
 Fc_i = fecundity of i th stage (equivalent to number of female hatchlings reaching the sea per breeding female in i -th stage per year).
 σ_i = specific annual survival probability of individuals in i th stage.
 d_i = stage duration in years.
 P_i = probability of surviving and staying in i -th stage.
 G_i = probability of surviving and growing into $(i+1)$ -th stage.
 R_i = reproductive output by individuals in i -th stage (Fc_i values adjusted by P_i and G_i).
 A = population projection matrix of dimension $n \times n$ (the elements of A are the stage-specific reproductive outputs (R_i), the probability of individuals in each stage-class that survive and remain in that stage (P_i), and those that survive and enter the next stage (G_i) in a given period of time (see Crowder *et al.* (1994) for details)).
 λ_1 = Same rate of increase of each stage-class at the new stable stage distribution (this is the overall population growth rate and is equivalent to the dominant eigenvalue of the stage class matrix, ($\lambda_1 = e^r$)).
 r = intrinsic rate of population increase in the equation $N_{t+1} = N_t e^r$, where N_t = population size at time t .
 V_e = new stable stage-class distribution vector (right eigenvector).
 V_f = stage-specific reproductive value vector (this is the expected per capita contribution of individuals in each stage to population growth and is equivalent to the left eigenvector corresponding to the dominant eigenvalue, λ_1).

STAGE-CLASS MATRIX MODEL

The Lefkovitch (1965) stage-class matrix model can be written as:

$$AV_t = V_{t+1} \quad (1)$$

Multiplying the population projection matrix by the population vector at time t produces the population state at time $t+1$. Because the projection matrix considered here is primitive (some powers of A have only

positive entries (Doubleday, 1975)) repeated projection of any initial stage-class population vector by this projection matrix tends towards a stable stage-class distribution, V_e , where each stage-class increases at the same rate, λ_1 (Pielou, 1977) such that:

$$AV_e = \lambda_1 V_e \quad (2)$$

Thus, the stable population size remains constant, increases or decreases depending on $\lambda_1 = 1$, $\lambda_1 > 1$ or $\lambda_1 < 1$. The corresponding intrinsic rate of population increase, r , is then 0 , > 0 or < 0 , respectively ($\ln(\lambda_1)=r$).

The stage-specific reproductive value is the relative contribution of an individual of a given stage to population growth. A newly laid egg receives a potential reproductive value of 1, and all the other stages are given values relative to that. The product of stage-class strength and the corresponding stage-specific reproductive value provides a measure of the relative contribution of a stage-class to population growth. The life stage with the highest value of this product is the one for which greater protection can contribute most to the maintenance or recovery of the population (National Research Council, 1990). The elements of V_f in the following equation provide potential reproductive values for each stage:

$$V_f A = \lambda_1 V_f \quad (3)$$

GREEN TURTLE POPULATION PARAMETERS

Reproduction. Green turtles nest at Ra's Al-Hadd and Masirah Island throughout the year with a peak between July and October. Each female made one to four nests per year, with an average of three (Ross, 1979). Carr, Carr & Meylan (1978) and Salm & Salm (1991) reported that females return to nest on the same beaches every two to four years at an average interval of three years. Thus, on average, one mature female produced one nest per year during her active reproductive life. Mean clutch size (number of eggs per nest) for Masirah green turtle nesters was 97 ± 5.6 (2 SD) and that for Ra's Al - Hadd was 103.5 ± 8.0 (Ross & Barwani, 1981). Using the minimum stock sizes of female nesters in Ra's Al-Hadd and Masirah (Table 1) we obtained the weighted average value of 103 eggs per clutch for Oman green turtles.

High mortality occurs during egg and hatchling stages on nesting beaches. Floods, beach erosion, four-wheel drive vehicles, artificial light, and fires contribute to a substantial decrease in number of eggs and hatchlings surviving in a breeding season. Foxes, wolves, hyenas, rats, dogs, and people dig eggs; fishing nets spread to dry on the beach trap many emerging hatchlings; and ghost crabs, sea birds and fish eat a large number of emerging hatchlings. Considering mortality percentages provided by Ross (1979), 103 eggs resulted in 37 zero + age hatchlings entering the

sea. In the absence of actual hatchlings' sex composition data, we assumed a theoretical sex ratio of 1:1 applicable for the entire Oman green turtle stock (Ross, 1985), and estimated the effective F_c (in terms of numbers of female hatchlings reaching the sea) to be 18. Salm & Salm (1991) suggested the age at first maturity to lie between 30 and 50 years, with a maximum nesting age of 70 years. Present estimates consider 30 years as the first maturity age and 69 years as the final reproductive age for discriminating the stage-classes in the population vector.

Stage-class population vector. The total life span of female green turtles from birth to the maximum reproductive age provided four biologically distinct stages measured in years: hatchlings (0*), juveniles (1 to 29), novice nesters (30), and adults (31 to 69). Out of the total of green turtles nesting every year on Oman beaches, approximately 15% were novice nesters (i.e. first time egg-layers) (Salm, 1991). Taking the lower nesting population size of 20,000 (Table 1), this was equivalent to 3000 novice nesters. Theoretically, four hatchlings per 1000 must survive to adulthood to maintain a steady population size (Ross, 1979). An arbitrary average adulthood age of 50 (maximum first maturity age) provided an upper limit to adults' annual M . Thus, using the relation, $e^{-50M} = 4/1000$, $M = 0.11$. Hatchlings and juveniles suffer higher natural mortality than do adults. Therefore, hatchlings' and juveniles' annual M were assumed to be 0.3935 and 0.1900, respectively (see the following section for justification). The data on the number of novice nesters helped to construct the initial stage-class stock size using the following formula:

$$N_i = \frac{N_0}{Z} e^{-Zt} [1 - e^{-Z(t+1)}] \quad (4)$$

In the absence of accurate stage-specific annual F and M , the above stage-specific high M values replaced Z in the estimation of initial stage-class stock size (Table 2).

TABLE 2. Current stage-class stock size and stage-class distribution (%) (stage-class population vector) for Oman female green turtles with stage-class abundance and relative strength estimated based on the number of novice nesters=3,000 and stage-specific annual M values (col. 2).

Stage	Stage-specific annual M	Est. stage-class size	Stage-class distribution (%)
Hatchlings	0.3935	959,394	18.84
Juveniles	0.1900	4,104,278	80.60
Novice nesters	0.1100	3,000	0.06
Adults	0.1100	25,447	0.5

Survival probability. Information on 0⁺ year-class (hatchlings) and juvenile specific annual survivals were lacking for green turtles. Therefore, we used 0.6747 ($M=0.3935$) reported for 0⁺ year-class loggerhead turtles (*Caretta caretta*) in the Atlantic Ocean (Frazer, 1983a) for hatchlings. Crowder *et al.* (1994) quoting C. Limpus reported that the specific annual survivals of unexploited large juveniles and sub-adult loggerhead turtles on Heron Island, Queensland were 0.83 and 0.885, respectively. Because our classification of the juvenile stage consists of individuals ranging from small juveniles to sub-adults, we assumed the specific annual survival of unexploited individuals in the juvenile stage to be 0.83 ($M=0.19$).

The number of fishing deaths in 1990 (Table 1) helped to estimate approximate F for respective stages using initial stage-specific stock sizes (Table 2). Out of 4280 fishing deaths, 2280 were due to hunting and the rest due to accidental drowning in fishing nets (Salm, 1991). Since fishermen prefer large green turtles with abundant green fat and harvest them in shallow feeding grounds (Ross, 1979), the hunted animals consisted almost entirely of adults. On the other hand, there was no size selection on accidentally caught turtles in nets. The size frequency data on accidentally caught turtles were also lacking for grouping them into separate stage-classes. Nevertheless, limited field observations on the carcasses of accidentally drowned turtles on the central Oman coast indicated an approximate 1:1 ratio between juveniles and adults (Salm, 1991). Using this ratio we partitioned the total female green turtle fishing deaths into 1000 juveniles and 3280 adults. These estimates provided the current annual F of juveniles and adults using the following formula:

$$C = FN_i \quad (5)$$

Thus, juveniles' and adults' F were 0.00024 and 0.1153, respectively, and the corresponding juveniles' and adults' specific annual survival rates ($e^{-F \cdot M}$) were 0.8268 and 0.7983, respectively. Therefore, juvenile and adult stages' specific annual survivals assumed these values (i.e., $\sigma_2 = 0.8268$, $\sigma_3 = 0.7983$ and $\sigma_4 = 0.7983$). In the absence of actual field results, we believe that these values are reasonable first approximations.

STAGE-CLASS POPULATION PROJECTION MATRIX MODEL FOR OMAN GREEN TURTLE

The complete model was as follows:

$$\begin{bmatrix} P_1 & R_2 & R_3 & R_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix} \begin{bmatrix} n_{10} \\ n_{20} \\ n_{30} \\ n_{40} \end{bmatrix} = \begin{bmatrix} n_{11} \\ n_{21} \\ n_{31} \\ n_{41} \end{bmatrix}$$

The following formula (Crowder *et al.*, 1994) provided the matrix A elements:

$$P_i = \frac{(1 - (\sigma_i / \lambda)^{d_i-1})}{(1 - (\sigma_i / \lambda)^{d_i})} \sigma_i \quad (6)$$

$$G_i = \frac{(\sigma_i / \lambda)^{d_i-1} (1 - (\sigma_i / \lambda))}{(1 - (\sigma_i / \lambda)^{d_i})} \sigma_i \quad (7)$$

$$R_i = F_{c_i} P_i + F_{c_{i+1}} G_i \quad (8)$$

We wrote a FORTRAN program for this purpose, which estimated the population projection matrix elements based on σ_i and an initial estimate of λ , and then final λ_1 , V_e and V_f . The program first estimated the matrix elements based on an initial λ value and then estimated the dominant eigenvalue (λ_1) for the given matrix. The λ was iterated using this dominant eigenvalue until the difference between the initial λ and the final λ_1 was less than 0.0001. Then, the stage-class distribution vector (V_e) and the stage-specific reproductive value vector (V_f) were determined for the final λ_1 value. At the stable stage-class distribution the population reaches stability and each stage of the self reproducing population increases at the same rate, λ_1 .

RESULTS

CURRENT POPULATION GROWTH RATE, STABLE STAGE-CLASS POPULATION VECTOR, AND REPRODUCTIVE VALUES

The current estimated population projection matrix using fecundity and survival data provided in the section 'Green Turtle Population Parameters' and an overall population growth rate estimate (λ_1) are given in Table 3. The λ_1 and the corresponding r for this projection matrix were 0.9596 and -0.0413, respectively. Thus, the current F appeared to have reduced the female green turtle population. Juveniles dominated the corresponding stable stage-class population vector, whereas reproductive values were large for novice nesters and adults (Table 4). The products of stage-class strength and stage-specific reproductive

TABLE 3. Population projection matrix for Oman female green turtles based on current fecundity and survival values provided in the text, and an overall population growth (λ_1) value of 0.9596.

Hatchlings	Juveniles	Novice nesters	Adults
0	0.0322	14.3690	14.3668
0.6747	0.8250	0	0
0	0.0018	0	0
0	0	0.7983	0.7982

TABLE 4. Stable stage-class population distribution vector, stage-specific reproductive value vector, and the product of reproductive value and stage-class strength of Oman female green turtles for the original population projection matrix.

Stage	Stable stage-class distrib. (%)	Stage-specific reproductive value	Stage-class strength x repro. value
Hatchlings	16.4790	1.0000	16.4790
Juveniles	82.6055	1.4222	117.4815
Nov. nesters	0.1540	88.9571	13.6994
Adults	0.7615	89.0026	67.7755

value were high for juveniles and adults (Table 4) indicating their dominant contributions to overall population growth rate.

SIMULATIONS

We varied σ_i and F_{ci} and produced new population projection matrices with new overall population growth rates (λ_1). This helped to explore the variation in r under different, but feasible, biological and fishery conditions.

Variation in fishing death. Various proportions of the current fishing deaths (i.e., total number of female fishing deaths in 1990 (Table 1)) provided different F (using formula (5)) for estimating new specific annual survival, hence new projection matrix elements. The resultant matrices provided r for a plausible set of first

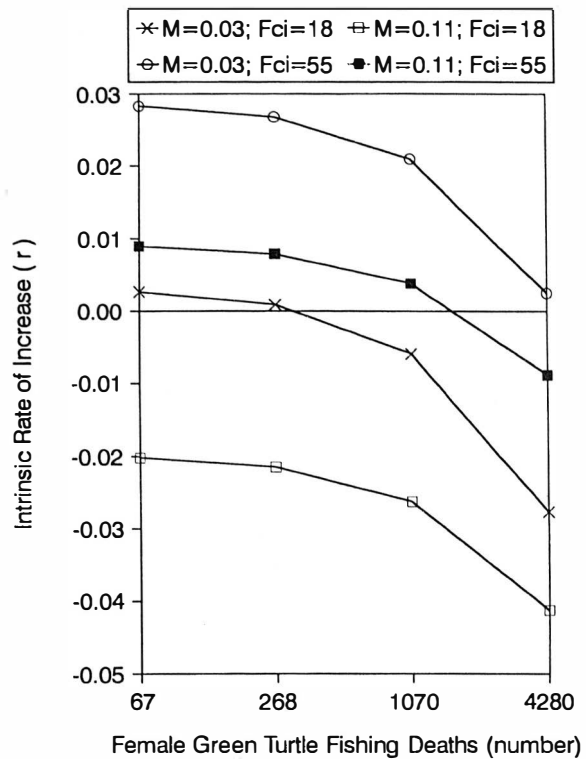


FIG. 2. The relationship between female turtle fishing deaths and intrinsic rate of increase (r). r was estimated at the first nesting age of 30-year and two values of adults' annual natural mortality ($M=0.03$ and 0.11) and fecundity ($F_{ci}=18$ and 55).

TABLE 5. Values of parameters used in the simulations with different sets of adults' survival for (a) $M=0.03$ and (b) $M=0.11$ (C =no. female annual fishing deaths, F_{ci} =fecundity, M =adult female natural mortality, and σ_i =female stage-specific annual survival probability). * values in parentheses indicate that simulations were carried out separately for each value for the same set of values of the other parameters.

Item	Systematic reduction in no. fishing deaths				Systematic increase in first reproduction age		Systematic reduction in total mortality or increment in fecundity			
Adult C	3,280	820	205	51.2	820	205	0%	25%	50%	75%
Juvenile C	1,000	250	62.5	15.6	250	62				
Total C	4,280	1,070	267.5	66.8	1,070	267				
First reproduction Age	30	30	30	30	(30, 40, 50)*	30	30	30	30	30
F_{ci}		(18, 55)			(18, 55)	18	22.5	27	31.5	
(a) $M=0.03$										
σ_1	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.7835	0.8499	0.9219
σ_2	0.8268	0.8269	0.8270	0.8270	0.8269	0.8270	0.8268	0.8782	0.9170	0.9576
σ_3	0.8648	0.9429	0.9635	0.9687	0.9429	0.9635	0.8648	0.9035	0.9346	0.9668
σ_4	0.8648	0.9429	0.9635	0.9687	0.9429	0.9635	0.8648	0.9035	0.9346	0.9668
(b) $M=0.11$										
σ_1	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.6747	0.7835	0.8499	0.9219
σ_2	0.8268	0.8269	0.8270	0.8270	0.8269	0.8270	0.8268	0.8782	0.9170	0.9576
σ_3	0.7983	0.8704	0.8894	0.8942	0.8704	0.8894	0.7983	0.8596	0.9041	0.9508
σ_4	0.7983	0.8704	0.8894	0.8942	0.8704	0.8894	0.7983	0.8596	0.9041	0.9508

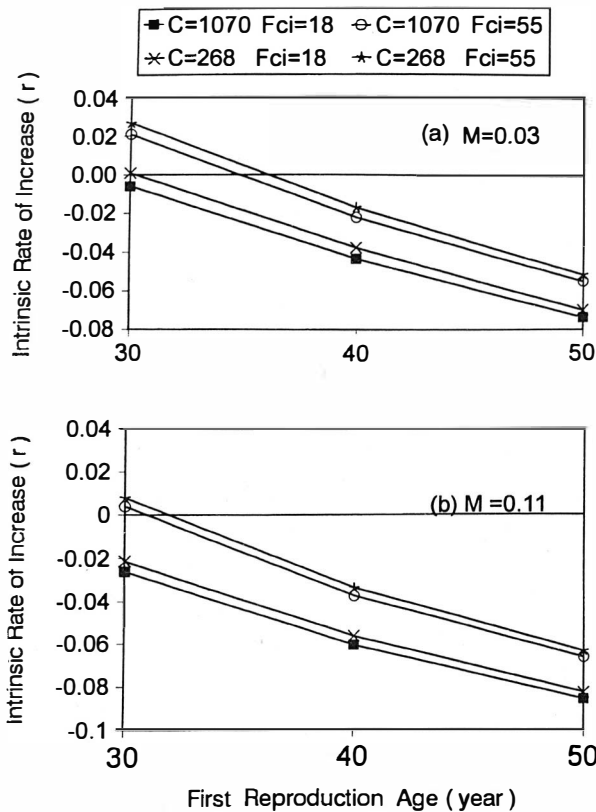


FIG. 3. The relationship between intrinsic rate of increase (r) and first reproduction age for female green turtles. r was estimated for two values of the number of annual fishing deaths ($C=268$ and 1070) and fecundity ($F_{ci}=18$ and 55) at two values of adults' annual natural mortality ((a) $M=0.03$ and (b) $M=0.11$)

maturity age, F_{ci} and stage-specific annual M values (Table 5). Frazer (1983b) and Crouse *et al.* (1987) considered a lower rate of annual population decline, 3% (equivalent to an approximate average annual M value of 0.03), than the recent estimate of 5% (equivalent to an approximate average annual M value of 0.05) by Crowder *et al.* (1994) for an Atlantic loggerhead turtle population. Thus, the M range, 0.03-0.11, was plausible for the tropical green turtle population. The F_{ci} range, 18-55, appeared to be conservative (see the following section), but reasonable.

Reducing the current C from 4280 to 1070 (75% reduction) resulted in positive r within the probable adults' M range only for the higher F_{ci} ; whereas, reducing fishing deaths to 268 (93.75% reduction) produced positive r at both low and high F_{ci} only for the lower adults' M (Fig. 2).

Variation in first reproductive age. Variation in the first reproductive age between 30 and 50 years provided different r at the above two C values for the two extreme F_{ci} and adults' M values (Table 5). At adults' $M=0.03$, r was positive for $C \leq 1070$ only at higher F_{ci} and first reproductive age ≤ 35 . However, when first maturity age was ≤ 30 , r was positive at this M and the lower F_{ci} value (Fig. 3(a)). On the other hand, when

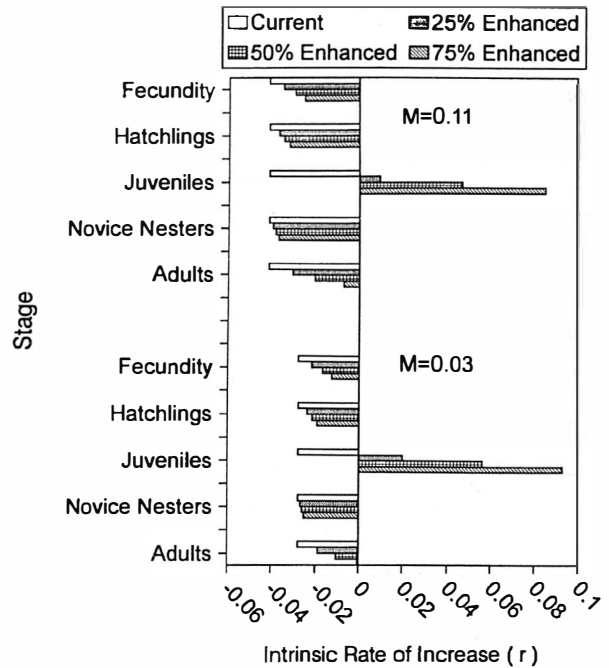


FIG. 4. Comparison of current intrinsic rate of increase (r) of female green turtles with those estimated under favourable (enhanced) simulated conditions. Enhanced conditions in stage-specific survival were created by reducing current stage-specific mortality rates, stage by stage, by 25, 50 and 75% while keeping the rest at the current level. Enhanced conditions in fecundity were created by increasing fecundity by 25, 50 and 75% while keeping the rest at the current level (see Table 5).

adults' $M=0.11$, r was positive for $C \leq 1070$ only at the higher F_{ci} value and first reproductive age closer to 30 (Fig 3(b)).

Because of probable delayed maturity of Oman green turtles due to poor diet (Ross, 1985), we simulated the effect of various fishing mortality rates on r assuming a high first maturity age of 35 and a moderate adults' M of 0.055 (half of the upper limit of adults' M). We evaluated r at the two extreme F_{ci} values, 18 and 55. The r were negative for all C values, including $C=0$. Because our assumption of 1:1 sex ratio among hatchlings was largely theoretical and Salm (1991) reported a female to male ratio of 2:1 on accidentally drowned green turtles, we evaluated r for a higher F_{ci} value of 69 ($= 103 \times (2/3)$). At this F_{ci} value, r was 0.0014 for $C=268$. Because of uncertainties in the model input values, this conservative C value would be safe to maintain a positive population growth rate.

Variation in reproductive output or survival probability at different stages. We compared estimated r at the current level with those estimated by reducing annual total mortality ($1 - \text{annual survival}$) by 25, 50 and 75% of the current level or increasing F_{ci} by the same percentages from the current level (Table 5),

stage by stage. This helped to identify those stages that needed protection to reverse population decline. For example, increasing F_{c_i} by 25% while keeping σ_i at the current level explored the effect of increasing F_{c_i} on r . Reducing the hatchling mortality by 25% while keeping the F_{c_i} and specific survival rates of the rest at the base level investigated the impact of increased hatchling specific survival on r . Reducing juveniles' and adults' total mortalities, stage by stage, by 25% of their original values explored the impact of reduced total mortality (includes F) of juveniles and adults on r . The r increased tremendously as a result of a reduction in the juveniles' mortality. The r also enhanced due to a reduction in the adults' mortality, but the increment was not as dramatic as that of the juveniles. Increased F_{c_i} or reduced mortality of the other stages, however, had very little effect on r (Fig. 4). These findings were indeed not surprising, having already observed juveniles' and adults' relatively high contributions to overall population growth.

DISCUSSION

The simulations suggested that if the first maturity age was 30 years, reducing the current annual 4280 female green turtle fishing deaths to 268 prevented population decline within the probable F_{c_i} and adults' M ranges except the unlikely event of high M and low F_{c_i} . However, if the first maturity age and adults' M were moderately high, 35 and 0.055, respectively, a higher F_{c_i} value of 69 induced a positive population growth for 268 fishing deaths. Wood & Wood (1993) reported that 96% of female green turtles farmed in the Cayman Islands (West Indies) sexually matured at 25 years. The age at first maturity of farmed female green turtles in Florida ranged 19 - 24 years (Ehrhardt & Witham, 1992). However, food limitation resulted in low growth rate and delayed sexual maturity in the Caribbean wild green turtle population (Bjorndal, 1981). This appeared to be the case for the wild Oman green turtle population as well. Ross (1985) observed poor diets in Oman green turtle feeding grounds and suggested that this may have affected the reproductive output. Consequently, it was possible that Oman green turtles attained first maturity at a higher age than 30 years. The sex composition of accidentally drowned turtles (Salm, 1991) suggested a possibility of a higher F_{c_i} value. Thus, the conservative estimate of 268 determined at these higher values of first maturity age, adults' M , and F_{c_i} was appropriate as the permissible maximum number of female fishing deaths. This optimum was less than the rough estimate, 300 - 450 females, suggested by Salm (1991). Considering the relative contribution of hunting deaths to total fishing deaths, an upper limit of 143 hunting deaths was appropriate to sustain the traditional turtle fishery while maintaining the population at a safer level.

The primary management measures practiced in many parts of the world in preventing turtle population depletion are protecting eggs, hatchlings, and females on nesting beaches (National Research Council, 1990). However, the population size could be significantly increased by reducing juvenile mortality in addition to protecting very early stages. Crouse *et al.* (1987) derived the same conclusion for Atlantic Ocean loggerhead turtles. Ross (1979) identified a distinct subgroup of small green turtles of 88 - 90 cm curved carapace length (CCL) in a large length frequency sample, and suggested that it consisted of novice nesters. The exact upper size limit for juveniles in Oman was difficult to determine. However, recent data indicated that the sizes of nesting female green turtles in Oman ranged from 85 - 120 cm CCL (Ali Amer Al-Kiyumi, personal communication, 12 July 1994). Mature farmed green turtle sizes in the Cayman Islands ranged from 86.4 - 114.3 cm CCL (Wood & Wood, 1993). Both these sets of data suggested that the size at maturity is below 85 cm CCL. Thus, an arbitrary 85 cm CCL as the minimum capture size in the traditional fishery was appropriate for reducing juveniles' F . However, restricting numbers of turtles caught was considered a high priority because concentrating harvest on (feeding) adults could increase adults' F and prevent females from nesting more than once in their lifetime. Furthermore, strict enforcement of a fishing ban in shallow (turtle feeding) waters for industrial fish trawl and drift gill net vessels, mandatory inclusion of turtle excluder devices (TED) in industrial fish trawl nets (National Research Council, 1990), and obligatory release of accidentally caught live turtles in the artisanal drift and bottom gill nets, and industrial drift gill nets would minimize unwanted fishing deaths.

The F_{c_i} , σ_i , and first maturity age values used in this paper were estimated from either published data on Oman green turtles (Ross, 1979; Salm & Salm, 1991) or reports of well studied, related loggerhead turtles (Frazer, 1983a,b; Crouse *et al.*, 1987; Crowder *et al.*, 1994) of similar growth and life span. However, the juveniles' and adults' F evaluations were based on the lowest female population sizes, thereby possibly overestimating F and underestimating specific-survivals. Consequently, the original population projection matrix may have underestimated r . However, the current r is very likely to be negative for the following reason: Fig. 2 shows that with a stock size of 28,447 adult females, more than 1070 female fishing deaths (consists of 820 adult females) produce a negative r except for the unlikely combination of the lowest adults' M and highest F_{c_i} . Thus, 4280 total female fishing deaths (consists of 3280 adult females) would require a stock size of at least 113,788 adult females to break-even at the same r . However, there were no data to suggest that the actual Oman adult female green turtle stock could be as high as 113,788.

Field data on many aspects of population dynamics of the green turtle population in general and the Oman population in particular are scarce, and we suggest collecting those demographic data in the future. We do not address the problem of resilience (i.e. tendency for r to change inversely with stock size) because of lack of a time series of demographic data. Estimating the absolute size and sex composition of an open sea turtle population is a difficult task (Witham, 1985); Therefore, studies are needed to evaluate stage- and sex-specific growth and mortality rates by other methods, such as tagging. Extensive tagging experiments on Oman sea turtles have been conducted since the late 1970s, which may provide sufficient information to refine this model.

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**ADVERTISEMENT CALL OF THE MIDWIFE TOAD FROM THE SIERRAS
BÉTICAS *ALYTES DICKHILLIENI* ARNTZEN & GARCÍA-PARIS, 1995
(AMPHIBIA, ANURA, DISCOGLOSSIDAE)**

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The advertisement calls of the recently described species of midwife toad (*Alytes dickhilleni*) are described, and a characteristic audiospectrogram and waveform of the call are presented. We also provide numerical data about the spectral and temporal features of the calls. Information about calling behaviour and the relationship between call parameters, size, and temperature are provided as well.

INTRODUCTION

Anuran mating calls are important taxonomic determinants due to their role as pre-zygotic species isolating mechanisms. Their analysis has provided valuable material for quantitative comparisons which can be of use to elucidate taxonomic problems such as determining cryptic sister species, (e.g., Blair, 1955, 1958, 1959; Littlejohn, 1959; Littlejohn, Fouquette Jr. & Johnson, 1960; Loftus-Hills & Littlejohn, 1971; Littlejohn & Loftus-Hills, 1968; Gerhardt, 1988; Schneider & Sinsch, 1991; Paillette, Oliveira, Rosa & Crespo, 1992) analyse gradients along hybrid zones, and even test crucial hypotheses in evolutionary biology such as reproductive character displacement or reinforcement (Sanderson, Szymura & Barton, 1992; Littlejohn & Watson, 1985; Littlejohn, 1988). Therefore, since the development of sound analysis techniques, there has been a concerted effort to describe accurately and quantitatively the advertisement calls of most anuran species in tropical areas (e.g., Schlüter, 1979, 1980, 1981; Zimmerman & Bogart, 1984; Márquez, De la Riva & Bosch, 1993, 1995; De la Riva, Márquez & Bosch, 1994; Sánchez-Herrera, Márquez, Barbadillo & Bosch, 1995; Alcalá, Joermann, & Brzoska, 1986; Kuramoto, 1986) as well as in the temperate zone (e.g., Schneider, 1966, 1971, 1973, 1974; Lörcher, 1969; Paillette, 1967, 1977; Schneider & Sofianidou, 1985; Schneider, Hussein, & Akef, 1986).

In the Iberian Peninsula, two species of midwife toads were previously recognised. The first species, the Iberian midwife toad (*Alytes cisternasii* Boscá, 1879), is endemic to and distributed throughout the south-western third of the peninsula. The second species is the common midwife toad (*A. obstetricans boscai*, Lataste 1879), which is more widely distributed in continental Europe and occupies the northern third of the peninsula and reaches further down along the coasts and on the mountains of central and south-eastern Spain. The populations of midwife toads from the south-eastern mountain ranges (Sierras Béticas and Sub-Béticas) have recently been described as a differ-

ent species: *Alytes dickhilleni* Arntzen and García-París, 1995. While the vocalisations of the two previously recognized species of midwife toads from the Iberian Peninsula have already been described (Crespo, 1981; Crespo, Oliveira, Rosa, & Paillette, 1989; Márquez & Verrell, 1991), the calls of the new species remain unknown because none of the previous descriptions of the calls included recordings from the distribution area of *A. dickhilleni*. In this paper, we contribute to the knowledge of Spanish herpetofauna by describing the advertisement calls of *A. dickhilleni*. This bioacoustical information complements the description of the new species, which is based on genetic and morphological characters (Arntzen & García-París, 1995).

MATERIAL AND METHODS

Male advertisement calls were recorded in 1992 from populations of *Alytes dickhilleni* in Sierra de Baza (UTM 30SWG13), Sierra Nevada (UTM 30SWG50), Sierra de Cazorla (UTM 30SWG09) (Andalucía), and one population from Sierra de Alcaraz (UTM 30SWH45) (Castilla-La Mancha), all in south-eastern Spain. Recordings were obtained with Sennheiser ME 80 directional microphones and a Sony WM D3 or a Marantz PMD 221 tape recorder. When a male could be observed calling, immediately after recording, its cloacal temperature was measured to the nearest 0.1 °C with a Fluke 52 thermocouple thermometer, and the snout-vent length (SVL) was measured to the nearest mm by pressing the toad flat (ventral side) against a ruler.

Recordings were processed with an Apple Macintosh-based digital signal analysis system. Digitalisation and editing were completed at a sampling frequency of 44.1 kHz and 16-bit resolution with Sound Tools software and hardware (version 2.5, by Digidesign Inc.). Signalyze software (version 3.12, by Infosignal Inc.) was used to obtain numerical information from audiospectrograms and waveforms. Frequency information was obtained through fast Fourier transform (FFT) (width, 1024 points; fre-

quency resolution, 22 Hz). Given the lack of energy of the harmonics above the fundamental, only three variables were measured: fundamental (= dominant) frequency, call duration, and duration of interval between calls.

RESULTS

Males could be found calling throughout the period of the study (May, June, and July 1992), although they are likely to be active at other times of the year given the developmental stages of the larvae found in the different sites. Like other species of *Alytes* in the Iberian Peninsula (Crespo, 1981; Crespo *et al.*, 1989; Márquez & Verrell, 1991; Márquez, 1995a, 1995b), males called primarily at night from the open, near their refuges (holes in the ground or under rocks often in banks or near eroded sections of the ground). Males could also call extensively from within their burrows, and in some particularly undisturbed sites, males could be heard during the day calling buried in the ground. Male calling-sites were always in the vicinity of a permanent or near-permanent body of water: mountain springs (natural, or modified by humans), man-made water catchments, troughs, and permanent streams.

A sample of 2 to 17 calls was analysed, comprising 50 males (480 calls total), from four populations. In Table 1 we present, for each population studied, the numerical parameters (mean, standard deviation, and range) of call duration, dominant frequency, and interval between calls. For the sound parameters, means of all the calls obtained from each individual were used. Table 1 also includes the mean recording temperature and the mean snout-vent length (SVL) of the calling individuals, as well as the mean and range of the within-recording coefficients of variation of the three sound parameters.

A characteristic waveform and audiospectrogram of the call are shown in Fig. 1. The calls are extremely simple tonal notes, with most power concentrated in the fundamental (dominant) frequency.

A Kruskal-Wallis Anova test indicated that between-individual variability was larger than within-individual variability for all of the acoustical

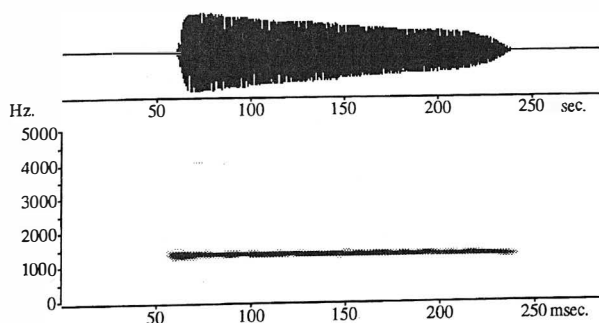
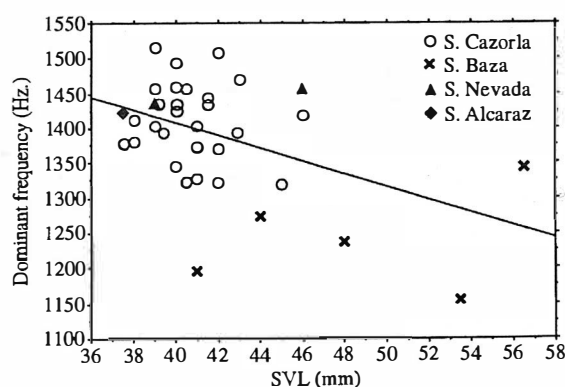


FIG. 1. Waveform (upper) and audiospectrogram (lower) of a characteristic call of a male *Alytes dickhilleni* (male recorded in Sierra de Cazorla, SVL 42 mm, cloacal temperature 9.9°C. Note that the ordinate for the waveform is relative and linear, and therefore a scale is not provided.

parameters measured (fundamental frequency, $N_{\text{calls}} = 480$, $N_{\text{males}} = 50$, $H = 438.23$, $P < 0.001$; duration, $N_{\text{calls}} = 444$, $N_{\text{males}} = 50$, $H = 394.57$, $P < 0.001$; call interval, $N_{\text{call intervals}} = 365$, $N_{\text{males}} = 49$, $H = 157.8$, $P < 0.001$). This result suggests that all parameters could provide information on the calling individual at the particular time of calling. The within-recording coefficients of variation of the three sound parameters are low ($< 9\%$) suggesting that call duration and dominant frequency would be a "static" (*sensu* Gerhardt, 1991) characteristic of the call, while interval between calls would be a "dynamic" characteristic having high coefficients of variation ($> 39\%$).

Because the numbers of recordings from most populations taken individually were not sufficient to establish a significant association between sound parameters and male size or temperature, the data from all the populations were used to study the relationships between male size and temperature and call parameters. On the one hand, call dominant (=fundamental) frequency was significantly correlated with male SVL ($N = 36$, $R = 0.46$, $P < 0.0046$, $y = -9.1x + 1772.5$) (Fig. 2a.). However, in a multiple regression between male size and temperature vs. call dominant frequency, only male size was significantly correlated ($N = 35$; SVL, partial $F = 4.6$, $P < 0.0396$; temperature, partial

A



B

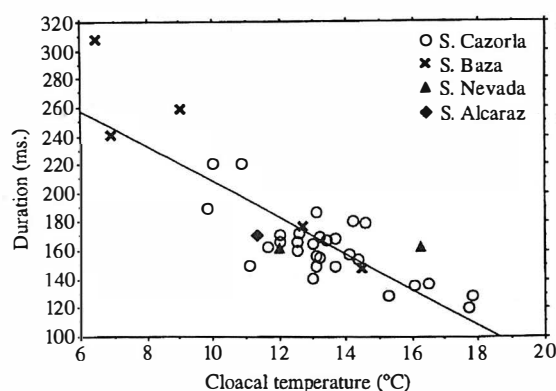


FIG. 2. A: Linear regression of male size (SVL) and call dominant frequency for the recorded individuals captured in the four populations studied. B: Linear regression of cloacal temperature of the animal recorded and call duration of the recorded individuals captured in the four populations studied.

TABLE 1. Mean, standard deviation (in parenthesis), and range, of male size (SVL), cloacal temperature, and three call parameters from the calls of male *Alytes dickhilleni* for each population studied. The data for the acoustical parameters include all animals recorded, while size and cloacal temperature was measured only on those recorded animals that were subsequently captured. The coefficients of variation of the sound parameters included (CV) are within-recording coefficients of variation (expressed as percentages).

Population	Individuals recorded	Individuals captured	SVL (mm)	Cloacal temp. (°C)	Duration (msec.)	Dominant frequency (Hz.)	Interval between calls (msec.)
Sierra de Cazorla	38	31	40.8 (2.2) 37.5-46.0	13.2 (2.1) 9.8-17.8	161.0 (24.7) 114.9-220.0 CV 4.2 CV _{range} 0.4-14.5	1404 (61) 1298-1560 CV 0.8 CV _{range} 0.0-3.5	5989.9 (1836.1) 3084.0-10201.2 CV 39.6 CV _{range} 8.4-93.9
Sierra de Baza	5	5	48.6 (6.4) 41.0-56.5	9.9 (14.5) 6.5-14.5	226.4 (64.1) 148.6-307.9 CV 8.5 CV _{range} 2.7-18.2	1241 (73) 1154-1343 CV 2.9 CV _{range} 1.2-7.9	5435.2 (2299.8) 3313.5-8975.0 CV 47.9 CV _{range} 22.0-74.9
Sierra Nevada	5	2	42.5 (4.9) 39.0-46.0	14.5 (3.0) 12.0-16.3	150.0 (28.1) 113.7-179.6 CV 5.2 CV _{range} 2.0-7.1	1371 (125) 1151-1457 CV 0.5 CV _{range} 0.0-1.1	4313.6 (2166.8) 1148.7-6889.64 CV 48.7 CV _{range} 23.3-83.9
Sierra de Alcaraz	2	1	37.5	11.3	156.5 (20.8) 141.8-171.2 CV 3.5 CV _{range} 2.5-4.4	1364 (83) 1305-1422 CV 1.2 CV _{range} 0.8-1.6	4636.6 (37.2) 4610.3-4662.9 CV 61.35 CV _{range} 36.2-86.5

$F=1.34$, $P < 0.26$). On the other hand, call duration was significantly correlated with recording temperature ($N=38$, $R=0.836$, $P < 0.001$, $y = -12.4x + 332$; Fig. 2b.); however, a multiple regression of male size and temperature vs. call duration showed that male size was also significantly correlated with call duration ($N=35$; SVL, partial $F=10.58$, $P < 0.0027$; temperature, partial $F=45.61$, $P < 0.001$). The significance of the relationship between male size and call duration disappears if the five data points from the recordings of individuals from Sierra de Baza are excluded. Therefore, this result has to be taken with caution because the individuals from Sierra de Baza were markedly larger than the rest.

DISCUSSION

The advertisement calls of the other three known species of *Alytes* are short (100-160 ms long), extremely soft, tonal notes repeated at relatively long intervals (0.5 - 10 s) (Crespo, 1981; Crespo *et al.*, 1989; Márquez & Verrell, 1991; Heinzmann, 1970; Bush, 1993).

The range of fundamental frequencies for the four populations of *A. dickhilleni* (1151 - 1560 Hz.) is wider than that found previously for any single species of continental *Alytes*. Heinzmann (1970) reported that the range of frequencies was 1240-1495 Hz in individuals of *A. o. obstetricans* of different sizes from a population near Tübingen (Germany). Crespo *et al.* (1989) reported a range of 1.25 - 1.47 kHz. for *A. obstetricans boscai* from three populations in northern Portugal. They also reported a range of 1.35 - 1.57 kHz. for *A. cisternasii* from central and southern Portuguese populations. Márquez (1995a) reported a range of 1009 - 1373 Hz. for a montane population of *A. obstetricans boscai* from Sierra de Guadarrama, in central Spain and a range of 1362 - 1645 Hz. for a population of *A. cisternasii* from Mérida, in Extremadura, Spain. Moreover, Márquez (1995b) found that a montane population of *A. obstetricans* from Formigal, in the Spanish Pyrenean Mountains had a range of 1080-1428 Hz. Similarly, the range of call durations found in our study is large (113.7-220.0 ms.), wider than most ranges reported to date, although the distribution of this parameter may be related to the good correlation between call duration and temperature in *Alytes* (Heinzmann, 1970; Márquez, 1995) and other Discoglossidae or Bombinatoridae (Zweifel, 1959; Schneider *et al.*, 1986).

The two static call characteristics appear to have different roles in the communication of *Alytes*. Given the published information on the calls of other species in the genus, it appears that the most obvious parameter in the frequency domain (dominant or fundamental frequency) plays an important role in sexual selection. In two populations of midwife toads and one of Iberian midwife toads, low-frequency calls

(relative to the population average) are more attractive to females than are high-frequency calls (Márquez, 1995a, 1995b). Alternatively, species identity appears to be more closely related to temporal parameters in the populations of discoglossid frogs studied. Among the different species and subspecies of *Alytes* that occur in the Iberian Peninsula, it appears that call duration relative to temperature is the most effective discriminating parameter (Márquez & Bosch, in prep.). In other related taxa, the study of the advertisement calls of males from two sympatric species of *Bombina* Oken 1816, in central Europe showed that calling rate was the most important discriminating parameter between the species (Lörcher, 1969; Schneider *et al.*, 1986; Sanderson *et al.*, 1992). Curiously enough, the variability obtained in our recordings suggests that call repetition rate is a dynamic characteristic for this species and therefore it could hardly be effective as a species discrimination characteristic. Similarly, in an extensive comparative study of advertisement calls of green frogs, Schneider & Sinsch (1991) found that such temporal parameters (corrected by temperature) were the most important characters for discriminating between major taxonomic groups.

The geographic distribution of *A. dickhilleni* is extremely fragmented. All populations occur on the mountaintops of southeastern Spain, in different ranges isolated by large sections of extremely dry lowland. Moreover, even within a given range, there are often extremely long distances between the nearest locations with permanent or near permanent bodies of water (Márquez, García-París & Tejedo, 1994; Arntzen & García-París, 1995). Therefore, a more detailed comparative study of the bioacoustical characteristics of different populations with different degrees of isolation between them, may prove fruitful for understanding the effect of isolation on a character crucial for species recognition.

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INTRASPECIFIC AGGRESSIVE BEHAVIOUR IN FIRE SALAMANDER LARVAE (*SALAMANDRA SALAMANDRA*): THE EFFECTS OF DENSITY AND BODY SIZE

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The most striking social behaviour in urodele tadpoles is overt aggression against conspecific or heterospecific larvae that may result in harmful injuries, predation or cannibalism. In this study we analysed under laboratory conditions aggressive behaviour in fire salamander, *Salamandra salamandra*, larvae. The aims of our study were: (1) to analyse the function of visual and movement displays in the context of agonistic behaviour; (2) to examine whether relative body size between individuals influences the frequency of aggressive interactions; and, (3) to determine the effect of larval density on the frequency of these aggressive interactions. The analysis of patterns that preceded a direct act of aggression (i.e. lunge or bite) revealed that the initiator of the contest exhibited more attacking patterns and that the receiver displayed more escape acts. Relative body size significantly affected the frequency of aggressive acts. The proportion of aggressive acts performed by the larger larva was positively related to relative larval body size. Density significantly affected the number of aggressive interactions observed. Significantly more aggressive acts were received or displayed by the focal larva at high density. Body size seems to be an important cue which is correlated with the outcome of aggressive interactions in *Salamandra salamandra* larvae. By visually assessing size asymmetry, individuals are able to use this difference to assess fighting ability, and can adjust their behaviour accordingly to avoid escalation of the aggressive encounter.

INTRODUCTION

Social behaviour has been widely studied in anuran tadpoles, especially schooling and sibling recognition (Blaustein *et al.*, 1987; Blaustein, 1988; Waldman, 1991). However, this is not the case for tailed amphibians and only recently have some studies dealt with social behaviour of larval caudates (Walls and Roudebush, 1991; Walls & Semlitsch, 1991; Pfennig & Collins, 1993). The most striking social behaviour in caudate larvae is overt aggression against conspecific or heterospecific larvae. These behaviours are regarded as mechanisms of interference competition that may regulate populations of larval salamanders (Smith, 1990; Van Buskirk & Smith, 1991). Sometimes, the outcome of overt aggression may lead to harmful injuries (Walls & Jaeger, 1987; Semlitsch & Reichling, 1989), or even predation (Wilbur, 1972; Stenhouse *et al.*, 1983; Stenhouse, 1985), or cannibalism (Degani *et al.*, 1980; Kusano *et al.*, 1985; Harris, 1987). The inherent cost of aggression is a potential decrease in survival and growth rates, which would favour the evolution of ritualized behaviour patterns and ameliorate these costs. The relative size of contestants is important in the decision to escalate encounters to overt and aggressive behaviour, and game theory predicts an increase in escalation when relative fighting abilities do not differ between opponents (Parker, 1974). Population density may affect the degree of aggressive interactions, i.e.

injury rates increase in high-density experimental and natural populations of larval salamanders (Semlitsch & Reichling, 1989; van Buskirk & Smith, 1991).

In this study, we experimentally analysed aggressive behaviour of larval fire salamanders, *Salamandra salamandra*, under laboratory conditions. This species is a widespread salamandrid occurring from Western Europe to the Middle-East and North Africa (Thiesmeier, 1992). In the southernmost part of its distribution, the fire salamander breeds in temporary ponds that typically fill after autumn or winter rains and become dry at the end of spring (Degani & Warburg, 1978; Bas-López, 1982; Díaz-Paniagua, 1986; Warburg, 1986a,b, 1992). Breeding activity is not continuous but is limited to some peaks, which depend mainly on rainfall (Warburg, 1992; personal observations). This pulse pattern produces variation in larval density across the season and discrete age cohorts that differ in size. Moreover, differential growth rates among tadpoles may increase the range in body size. Aggressive interactions during the larval stage may be frequent, based on the high frequency of injuries observed in the ponds, although other predators may induce it (personal observations). Moreover, cannibalism has been reported in larval fire salamanders (Degani *et al.*, 1980; Warburg, 1992; personal observations) and therefore, aggression may be important in the regulation and dynamics of salamander populations. The objectives of our study were to: (1) analyse the function of visual and movement displays

in the context of agonistic behaviour; (2) examine whether relative body size between individuals influences the frequency of aggressive interactions; and (3) analyse the effect of larval density on the frequency of these aggressive interactions.

MATERIAL AND METHODS

EXPERIMENTAL DESIGN

During early January 1992, we captured salamander larvae from a pond located in Sierra Morena (Córdoba province, Spain). Larvae were of approximately similar age, about one month old. Births were synchronized at this site, coinciding with rains which filled the pond during the first week of December. After that peak, low night temperature prevented female migrations to the pond. Average larval snout-vent-length (SVL) was 22.6 ± 3.3 mm (mean \pm 1 SD; $n = 114$). All larvae were kept in the laboratory in two aquaria of 90 l that were aerated and maintained at room temperature (water temperature $10.5 \pm 2.1^\circ\text{C}$), and maintained under a natural photoperiod. Salamanders were kept in large glass aquaria (50 l) feeding them with pond zooplankton *ad libitum* prior to and during the experiments.

We designed two sets of experiments. Firstly, we addressed whether relative body size affected the frequency of aggressive interactions and whether larger animals performed most of the aggressive acts. We conducted 21 trials, and for each trial two larvae were randomly selected from the storage tanks and introduced in 20 x 15 cm glass aquaria filled with 3 l of pond water. We did not provide any vegetation or hiding places. After 15 min of acclimation, we recorded the sequence and frequency of behavioural patterns for each individual, using spot patterns to distinguish the larvae. No larva was tested more than once. In a second experiment, we asked whether the frequency of aggression events was influenced by larval density. We used two density levels: two or four larvae were introduced into a 30 x 20 cm aquaria filled with 6 l of pond water. For each trial, we randomly selected the larvae from the storage aquaria. After acclimation for 15 min, we randomly selected an individual salamander and recorded all aggressive acts (Bite and Lunge) that it received or performed. Each trial lasted 30 min. Each density was replicated 12 times, and no larva was tested more than once.

QUANTIFICATION OF BEHAVIOUR PATTERNS

We found six different behaviour patterns in larval *S. salamandra* that were similar to those reported by Walls & Jaeger (1987) in ambystomatid larvae. We operationally defined the following: (1) Move toward (MT), one salamander moves by walking in the direction of another; (2) Look toward (LT), one salamander turns its head in the direction of another salamander; (3) Move away (MA), as a consequence of move to-

ward by a second larva, a salamander avoids the contact and increases the distance from it; (4) Look away (LA), a salamander turns its head away from an approaching larva. Two forms of overt aggression were found: (5) Bite (B), one salamander grasps another on the tail, mouth, legs, etc.; and (6) Lunge (L), one salamander moves by fast swimming, not walking, to a second salamander and moved its mouth as in grasping. Bite is an obvious act of aggression (Jaeger, 1984), and Lunge may be considered an unsuccessful bite because the salamander opens and closes its mouth when approaching its opponent (Walls & Semlitsch, 1991). The function of other patterns were categorized as aggressive behaviour (MT and LT) or submissive behaviour (MA) in larval *Ambystoma* (Walls & Semlitsch, 1991). To ascertain whether *Salamandra* has similar patterns of behaviour to that reported for *Ambystoma*, we analysed the acts previous to and subsequent to an act of overt aggression (L or B). We hypothesized that the individual producing the overt aggression would exhibit other aggressive behaviour both before and after the act, and the recipient would show submissive behaviour (Jaeger, 1984; Walls & Semlitsch, 1991). The behaviour of both aggressor and recipient were compared using two-tailed Binomial tests (Siegel, 1956). To avoid pseudoreplication we only analysed the first aggressive act for each trial. The effect of relative body size (SVL of larger salamander/SVL of smaller) on the frequency of aggressions (B and L) was analysed by Spearman rank correlations. All trials lasted 30 min after which the SVL of each larva was measured to the nearest 0.5 mm. No larva was tested more than once.

RESULTS

On average, larger individuals within a pair exhibited a greater number of patterns per trial (large larvae mean = 11.5, SD = 4.4 patterns; small larvae, mean = 8.3, SD = 4.9 patterns; Mann-Whitney *U*-test, $U=122$, $Z=2.48$, $P=0.007$). When the mean frequency of patterns per trial were compared between small and large larvae, significantly more Bites and Lunges were performed by larger larvae. Moreover, greater numbers of LT and MT patterns were displayed by larger larvae. In contrast, smaller salamanders showed higher average frequencies of LA and MA patterns, (Mann-Whitney *U*-test, $P < 0.05$, Fig. 1). Relative body size significantly affected the frequency of aggressive acts ($r_s = -0.655$, $P = 0.0015$, $N = 21$). Higher frequencies were found when the larvae were more similar in size, and frequencies of behaviours dropped to a relatively constant value when the size ratio was greater than 1.2 (Fig. 2a). The proportion of aggressive patterns displayed by the larger larva was positively related to relative larval body size ($r_s = 0.655$, $P = 0.0011$, $N = 21$, Fig. 2b). Larger individuals monopolized aggressive interactions when larvae differed in size. With the exception of three trials, all aggression was performed

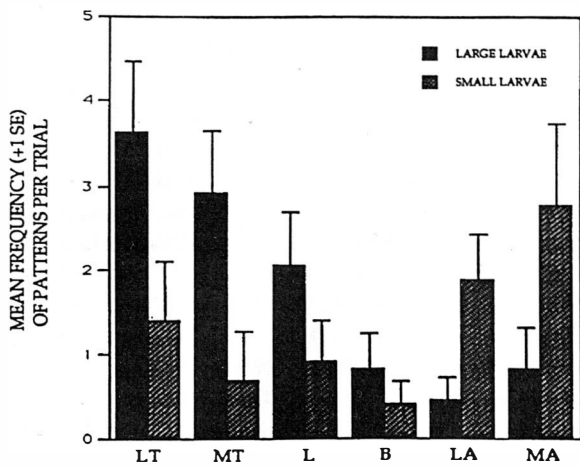


FIG. 1. The mean frequency of patterns in 30 minutes trials ($N=21$) (+ 1 SE) between large and small larvae of *Salamandra salamandra*. LT, look toward; MT, move toward; L, lunge; B, bite; LA, look away; MA, move away.

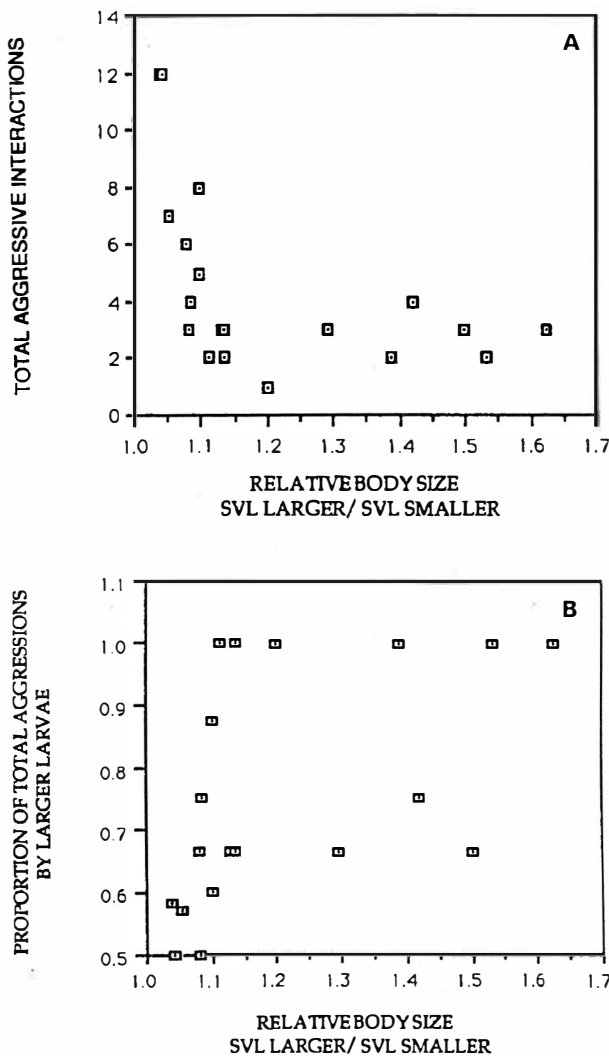


FIG. 2. A, Total number of aggressive acts (Lunge and Bites) per trial as a function of relative body size of larval salamanders (SVL larger/ SVL smaller) ($r_s = -0.655$, $P = 0.0013$, $N = 21$). B, Proportion of total aggressive acts by larger larvae (Lunge and Bites) per trial as a function of relative body size of larval salamanders (SVL larger/ SVL smaller), ($r_s = 0.632$, $P = 0.0021$, $N = 21$).

TABLE 1. Analysis of agonistic patterns before or after to (1) Lunge or (2) Bite. P : probabilities associated with a two-tailed Binomial tests. Missing cells correspond to comparisons with insufficient sample size for assigning probabilities. $N=21$ trials. Ag: aggressor; Re: recipient.

	Before LUNGE			After LUNGE		
	Ag	Re	P	Ag	Re	P
Look Toward	14	3	0.003	6	0	0.032
Move Toward	7	2	0.180	10	1	0.012
Look Away	0	9	0.040	1	2	—
Move Away	0	5	0.062	0	14	<0.001

	Before BITE			After BITE		
	Ag	Re	P	Ag	Re	P
Look Toward	3	2	>0.05	3	1	>0.05
Move Toward	7	1	0.070	3	0	—
Look Away	0	3	—	0	2	—
Move Away	0	2	—	0	7	0.016

by the larger individual above the 1.2 size ratio. This same trend was found when we analysed only frequency of Bite. Bite also exhibits a negative correlation with relative body size ($r_s = -0.476$, $P = 0.029$, $N = 21$), and the proportion of bites given by larger larvae was positively related to relative larval body size ($r_s = 0.70$, $P = 0.016$, $N = 11$). The analysis of the patterns that preceded a Lunge revealed that the aggressor of the contest exhibited significantly more LT than LA and MA acts. Moreover, the recipient displayed more LA and MA acts prior to the Lunge (Table 1a). The analysis of behaviour before and after a Bite was limited because this behaviour occurred infrequently. Before a Bite, only MT differed significantly between aggressors and recipients. Larvae that were bitten subsequently displayed significantly more MA than did the attacker (Table 1b).

Density significantly affected the number of aggressive interactions (Bites and Lunges) observed. Significantly more aggressive behaviours were received or displayed by the focal larva at high density (mean = 9.5, SD = 5.4, $N = 12$) than at low density (mean = 2.5, SD = 1.97, $N = 12$; Mann-Whitney U -test, $Z = 3.138$, $P = 0.0017$, $N = 24$). Therefore, an increase in density promoted higher encounter rates leading to the higher observed rates of aggressive behaviour.

DISCUSSION

Relative body size is an important variable correlated with the outcome of aggressive interactions in larval *Salamandra salamandra*. By visually assessing size asymmetries, individuals are able to use this difference to assess fighting ability, behaving accordingly and not escalating (Maynard Smith & Parker, 1976). The functional aspect of Move Away pattern seems to be a response to aggressive behaviour. After an attack, Lunge or Bite, the recipient usually followed with a Move Away, thus avoiding additional aggression. It is more difficult to ascertain the aggressive role of Move Toward before an attack. Obviously, a larva has to approach another to engage in a Bite or Lunge but, sometimes, the receiver behaved in the same way before it received a Bite or Lunge. In this sense, the function of this pattern may not be clearly dissuasive. This behaviour may be in some sense unavoidable since salamanders react actively to any movement produced in the water and Move Towards pattern may be part of larval predatory behaviour. Larger individuals more frequently exhibited Bite and Lunge than did their smaller opponents, and the relative body size of contestants affected both the total number and proportion of attacks performed by the larger of the pair. Larger larvae were able to monopolize nearly all attacks when the size ratio was greater than 1.2; smaller larvae tended to avoid counter-attacking when the difference in size with its opponent was higher. When size asymmetry decreased the opportunity of being the initiator of an attack did not differ from chance. In ambystomatids, unidirectional aggression was observed when larvae differed largely in size but reciprocated attacks were common when the difference in size between larvae was not significant (Walls & Semlitsch, 1991).

Level of aggression increased significantly with density. The total number of aggressive acts performed or attacks received by focal individuals was greater at the higher density. In natural ponds, situations of crowding may be common and aggression may be frequent. The cost of aggression may be higher due to intrinsic energetic costs associated with it and, moreover, the cost associated with injuries (Harris, 1987). Injuries may result in lower growth rates (Semlitsch & Reichling, 1989), increased susceptibility to predation (Wilbur & Semlitsch, 1990) and/or lower survival due to infections (Walls & Jaeger, 1987). Aggression may function as a mechanism of spacing, but agonistic behaviour against conspecifics may also be a form of predation or cannibalism that has been observed in some salamander populations (Degani *et al.*, 1980; Warburg, 1992; Thiesmeier, 1992; personal observations). In temporary ponds, any advantage derived from larger body size such as superior competitive ability and rapid growth may influence larval fitness traits such as time and size at metamorphosis (Wilbur & Collins, 1973). Some studies have suggested that

larger animals are superior to smaller ones in interference competition (Schoener, 1983; Persson, 1985). Smith (1990) studied the effect of relative body size on the outcome of interference competition in larval salamanders. In these laboratory experiments, Smith found that growth rates were higher for those individuals raised with similar-sized larvae whereas lower growth was found for those larvae raised with larger ones. He could control the level of exploitative competition and interference, through aggressive interactions, was the only mechanism responsible for the depressed growth of smaller larvae. In contrast, our results with *Salamandra* indicate that less aggression was involved as the size difference of larvae increased. If we assume that aggressive behaviour incurs a cost which is a function of the number of interactions, we can expect that the effect of interference competition would be less intense as larvae diverge in size. However, this suggestion does not take into account that the cost of injury may depend on the size-ratio of competing larvae. The fact that smaller larvae did not escalate to injurious attacks when the size of the opponent was relatively high would indicate that the cost induced by injuries is significantly high. Experiments in laboratory or in artificial enclosures are necessary to address the effect of variation in body size has on competition in *Salamandra salamandra* larvae.

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REPRODUCTIVE AND FAT BODY CYCLES OF THE LACERTID LIZARD *PODARCIS BOCAGEI*

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This paper presents data on reproductive and fat body cycles of the oviparous lacertid lizard *Podarcis bocagei* in northwest Spain. Testes exhibited their maximal volume during December-March and decreased in size throughout the summer. This pattern agrees with the "mixed type" of spermatogenetic cycle proposed by Saint Girons (1963, 1982). Vitellogenesis started at the end of March or April. Females with oviductal eggs were found from mid-April to mid-July. Oviposition occurs between mid-May and the end of July. Fat bodies of males were smallest during the spring mating period. Female fat body volumes declined during vitellogenesis. No significant decline of lipid stores was detected during the winter period (October-March).

INTRODUCTION

Since the pioneer studies of Tinkle (1969) and Tinkle *et al.* (1970), lizard life histories have received considerable attention. Life history traits can vary within a single population over time (Ballinger, 1977; Dunham, 1978, 1981; Ferguson *et al.*, 1980; Jones *et al.*, 1987; Castilla *et al.*, 1992) as well as among populations of a single species (Tinkle & Ballinger, 1972; Dunham, 1982; Ballinger, 1983; Tinkle & Dunham, 1983). Numerous studies document such temporal variation and spatial differences in life histories among lizards.

Among the components of an organism's life history, reproduction is perhaps the most fundamentally important process (Gillis & Ballinger, 1992). An important indicator of the reproductive biology of a species is the determination of its reproductive cycle (e.g. Fitch, 1970; Ramírez-Pinilla, 1991a, 1991b; etc.). Reproductive cyclicity has been studied in numerous temperate zone lizards. Nevertheless, the literature on species of the genera *Podarcis* (family Lacertidae) is sparse and restricted to a few species (e.g. Saint Girons & Duguy, 1970; Botte *et al.*, 1976; Braña, 1984; Kwiat & Gist, 1987; Barbault & Mou, 1988; Henle, 1988; Llorente, 1988; García-Fernández, 1990; etc.).

The genus *Podarcis*, with 15 species (Arnold, 1989; see also Böhme, 1986), occupies a wide variety of habitats over its geographic distribution (south Europe and northwest Africa), particularly in the Mediterranean range, in which it shows great ecological versatility (Arnold, 1987). The reproductive biology of *Podarcis bocagei*, an endemic species with a restricted distribution in the Northwest of the Iberian Peninsula, is poorly known (Pérez-Mellado, 1982; Braña, 1983, 1984; Braña *et al.*, 1992; Galán, 1994). The present study provides data on seasonal changes in gross gonadal morphology and fat body sizes of *P. bocagei* collected in a population from NW Spain.

MATERIALS AND METHODS

A total of 73 adult males and 69 adult females of *Podarcis bocagei* were collected in San Vicente de Vigo, Carral (La Coruña province, Spain; 43° 14' N, 8° 17' W; UTM 29T NH5687; 90 m elevation). Lizards were captured by hand at monthly intervals, from January to December 1990.

The study area experiences a characteristic wet oceanic climate, which is common in coastal areas of the northwestern Iberian Peninsula. Average annual rainfall is 1200 mm and average annual sunshine is about 2000 h. Annual temperature oscillation is very small, about 10° C between the coldest month (January, mean temperature: 8°C) and the hottest month (July, mean temperature: 18°C).

For each lizard, the following measurements were taken: SVL (to the nearest 0.1 mm); body mass (0.1 g); longest and shortest axes of the right testis; maximum diameter of the right epithelio-epididymis; diameter of the largest ovarian follicle; length, width and height of the right abdominal fat body; stage of follicular development (non-vitellogenic, vitellogenic, luteal) and presence of oviductal eggs.

An estimate of testicular volume was obtained using the formula for the volume of an ellipsoid ($V = \frac{4}{3}\pi a^2b$, where $a = \frac{1}{2}$ shortest diameter and $b = \frac{1}{2}$ largest diameter). Although fat bodies vary in shape, their general form was approximated as the longitudinal half of a flat ellipsoid with unequal lengths for the three axes. Accordingly, we calculated an estimate of fat body volume by the formula $V = \frac{2}{3}\pi abc$, where $a = \frac{1}{2}$ length, $b = \frac{1}{2}$ width and $c = \frac{1}{2}$ height (see Castilla & Bauwens, 1990).

Testicular volume, maximum diameter of the epididymis and fat body volume increased significantly with SVL. An index of SVL-adjusted dimensions of each organ was calculated using residuals from the least-squares regression line between organ size and SVL (both variables log-transformed). To assess differences

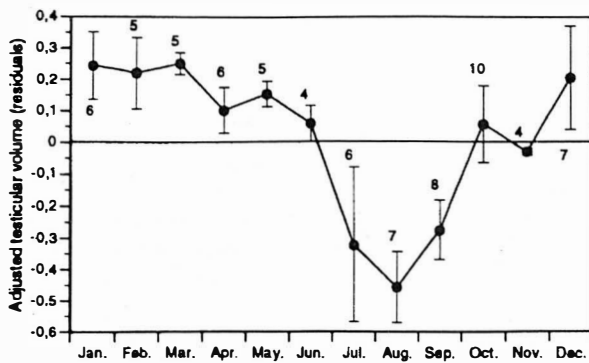


FIG. 1. Monthly changes (mean \pm SD and sample size) in SVL-adjusted testicular volume (residuals) of *Podarcis bocagei* throughout 1990.

between means a one-way analysis of variance (ANOVA) was used followed by Scheffe's *a posteriori* test. When the data did not meet assumptions of normality, I used a Kruskal-Wallis analysis of variance, followed by Mann-Whitney *U*-tests for comparison among pairs of means.

As part of a demographic study (Galán, 1994), other lizards were marked and recaptured at regular intervals on a 0.27 ha study area adjacent to the sites for collecting specimens for autopsy. Data from this portion of the study were used as corroborative evidence of clutch frequency and timing.

The snout-vent lengths (SVL) of the smallest sexually mature specimens examined in this population were 48.1 mm in males and 45.3 mm in females (Galán, 1994). The mean SVL of male lizards used for this study was 56.1 ± 0.35 mm (range: 50.2-64.5 mm; $n = 73$) and of females was 53.8 ± 0.27 mm (range: 45.9-60.5 mm; $n = 69$).

RESULTS

GONADAL CYCLES

Testicular volume cycle. There were significant differences among months in SVL-adjusted testicular volume (residuals of the regression of testicular volume on male SVL; ANOVA: $F = 25.82$; $df = 11, 72$; $P < 0.001$; Fig. 1). An *a posteriori* analysis (Scheffe-test) revealed two principal groups in SVL-adjusted testicular volume. The first is July-September (negative residuals) and the second is October-May (without November). A third group was formed by June (not significantly different from October-May) and November (only significantly different from August).

Testicular volume began to increase in September, was maximal in December-March and decreased thereafter (Fig. 1). Minimal volume was in July-August. Increasing testicular volume in autumn appeared to be correlated with decreasing photoperiod and temperature, and increasing rainfall.

Epididymis diameter cycle. Maximum diameter of the epididymis, adjusted for SVL, also exhibited seasonal changes during 1990 (Fig. 2; ANOVA: $F = 19.62$; $df = 11, 69$; $P < 0.001$). *A posteriori* analysis of

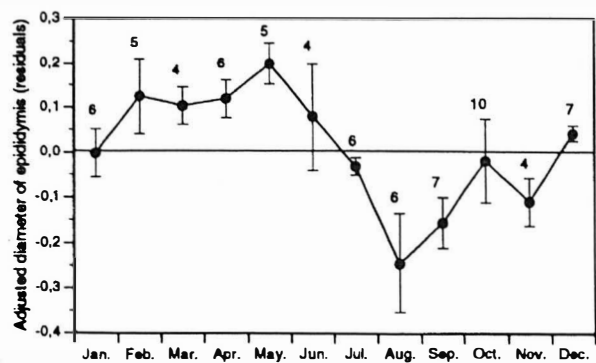


FIG. 2. Monthly changes (mean \pm SD and sample size) in SVL-adjusted maximum diameter of the epididymis (residuals) of *Podarcis bocagei* throughout 1990.

the data by Scheffe-test shows two principal groups of the monthly values: December-June (without January; positive residuals) and August, September and November (highly negative residuals). June and October did not differ significantly from these two groups.

Maximal epididymis diameter was reached in May and diameter began to decrease in June. Minimal diameter was reached in August, at the end of the reproductive season.

Female gonadal cycle. Females with immature ovaries that contained many transparent grey-to-translucent white follicles less than 1.6 mm in diameter were found between August and March. Vitellogenesis began at the end of March (always in bigger females; $SVL > 56$ mm) and ovarian follicles increased in size to a maximum diameter of about 7.0 mm prior to ovulation (Fig. 3). Ovulations occurred in late April (1990) or early May (1991) so that females produced the first clutch before the end of May. The second clutch was deposited in June. In some females, the third clutch was deposited in July. Oviductal eggs were seen on three occasions after mid-July. Most females collected on these dates and all females collected later were post-reproductive.

Apparently there was asynchrony among females during the reproductive season. For example, between 1 and 5 June, 1990, three individuals had oviductal eggs whereas four had vitellogenic follicles (about 5.5 mm diameter) and one had just completed oviposition.

Data on clutches shown in Fig. 3 were obtained from females collected in the study area that later laid clutches in terraria. These ovipositions were recorded between May 12 and July 22, 1990.

FAT BODY CYCLES

Male and female abdominal fat body volumes related to SVL showed a clear seasonal cycle (Fig. 4). There were significant differences between months (Kruskal-Wallis: males: $H = 48.25$; $P < 0.001$; females: $H = 45.78$; $P < 0.0001$).

In males, we detected two principal clusters of monthly values (differences not significant in each group, Mann-Whitney *U*-test $P > 0.05$). On the one

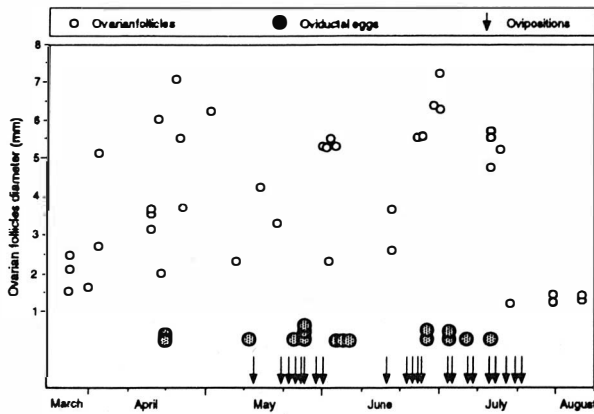
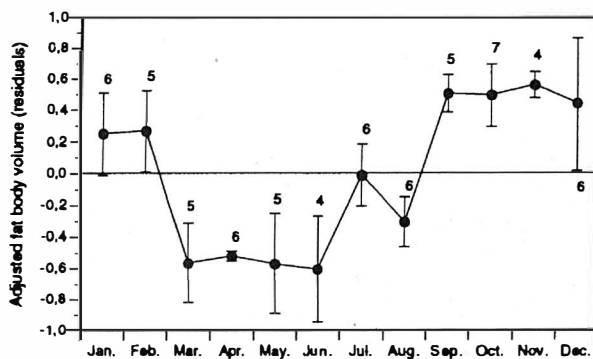


FIG. 3. Gonadal cycle of female *Podarcis bocagei* in the study area during the reproductive season of 1990. Open circles: diameter of the largest ovarian follicle from both ovaries. Shaded circles: oviductal eggs; arrows: oviposition.

MALES



FEMALES

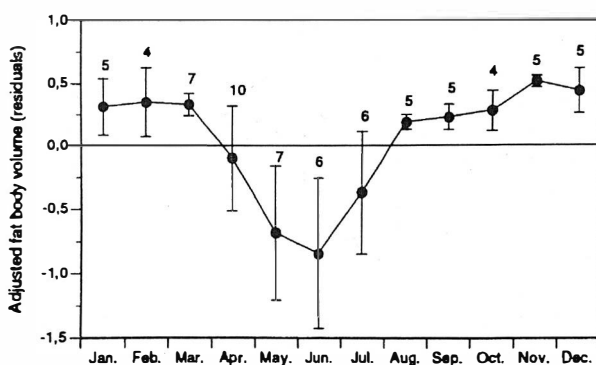


FIG. 4. Monthly changes (mean \pm SD and sample size) in SVL-adjusted fat body volume (residuals) on male and female *Podarcis bocagei* throughout 1990.

hand, September to February (positive residuals), and on the other, March to June (negative residuals). July and August do not differ significantly in these two groups. Fat stores of the males decreased rapidly in volume between February and March and were at their lowest levels during March to June.

The fat bodies of females were lightest in June, began to be deposited in July and reached a peak in November. As can be observed in Fig. 3 and 4, there

was an inverse relationship between vitellogenesis and fat body lipid deposits in females.

DISCUSSION

The reproductive cycle of *Podarcis bocagei* is similar to that of many other temperate zone lizards. The spermatogenic cycle is of the "mixed type", in the terminology of Saint Girons (1963, 1982). Testicular recrudescence began in September and proceeded until the onset of hibernation. Testes attained their maximum volume from January-March, decreased in volume during April-July and reached their minimum size during August. All European lacertids studied to date, except *Acanthodactylus erythrurus* from central Spain (see Castilla *et al.*, 1992), exhibit a mixed type reproductive cycle (e.g. Pérez-Mellado, 1982; Bons & Saint Girons, 1982; Pascual-González & Pérez-Mellado, 1989; Castilla & Bauwens, 1990).

The annual epididymis cycle observed in this population is similar to the cycle of this organ shown by *Lacerta monticola cantabrica* in populations from high and low altitudes in Asturias (northern Spain), principally the latter (Braña *et al.*, 1990). Nevertheless, it differs from the other Mediterranean Lacertidae such as *Lacerta laevis* (Hraoui-Bloquet & Bloquet, 1988), *Lacerta lepida* (Castilla, 1989; Castilla & Bauwens, 1990) and *Psammodromus algirus* (Carretero & Llorente, 1991). In these species, the maximum diameter of the epididymis is not attained in spring, as in *Podarcis bocagei*, but in autumn instead, and the organ remains hypertrophied until the end of the mating season. As pointed out by Braña *et al.* (1990), a possible explanation of these differences may be the contrasted environmental characteristics of these populations (Mediterranean versus Atlantic). Mediterranean lizards are exposed to higher maximal temperatures and a greater thermal amplitude than the Northwestern (Atlantic) Iberian lizard populations. These environmental conditions allowed some winter activity and an early beginning of the mating season (Amores *et al.*, 1980; Mellado & Olmedo, 1987; Hraoui-Bloquet, 1987; Hraoui-Bloquet & Bloquet, 1988). Nevertheless, this 'Mediterranean' type of epididymis annual cycle cannot be considered as a general pattern for all Mediterranean Lacertidae (see Angelini *et al.*, 1978).

The female gonadal cycle is also similar to that of other Iberian Lacertidae. Nevertheless, ovarian activity lasts longer in this population of *Podarcis bocagei* than in other Lacertidae which inhabit areas with continental climate or high altitudes (Pérez-Mellado, 1982; Braña, 1983; Busack & Klosterman, 1987; Pascual-González & Pérez-Mellado, 1989; Pollo & Pérez-Mellado, 1990; Braña *et al.*, 1992; Castilla *et al.*, 1992). Vitellogenesis began in late-March or April. The ovarian follicles are translucent and small (maximum about 1.6 mm) in juvenile lizards and in adult females between August and March. Large fe-

males (SVL more than 56 mm) were the first to start vitellogenesis and, consequently, began reproduction earlier than small females. Ovulations occurred from mid-April until mid-July and oviposition from May until late July. A mature female at the onset of reproduction, in April, could produce three clutches by the end of the season in July. (Galán, 1994; see also Braña, 1983). Reproduction ended in July, after which time all females examined were post-reproductive.

This prolonged female reproductive cycle is similar to that of other strictly Mediterranean *Podarcis* species, such as *P. sicula* from south Italy (Botte *et al.*, 1976; Limatola *et al.*, 1989). It is also like the female gonadal cycle of populations of *Lacerta monticola cantabrica* from low altitudes in La Coruña province, the other unique species of small lacertid that inhabits this area (Galán, 1991).

The general model of continuous reproduction throughout the breeding season, with three phases of ovulation and laying, shown by this population, is only valid at the population level. At the individual level, there is high variability. For example, at equal size and age, females with a high level of lipid inguinal storage begin reproduction early and can lay several clutches (Galán, 1994). If there are differences in size between females, the variability in timing, clutch characteristics and clutch frequencies are very high.

There may be a close relation between the temperate environmental conditions of the study area (low temperature oscillation, absence of dry season) and the duration of the reproductive period. Moderate temperatures at the end of winter and in early spring permitted the beginning of the mating season in March and, on the other hand, the absence of a dry summer period permitted oviposition to be prolonged until late-July.

The fat body cycles were closely coupled with the timing of reproductive events in both sexes. As pointed out by Castilla & Bauwens (1990), in estimating fat body volumes, we unrealistically assume that these have uniform and fixed shape. Therefore, these estimates are subject to error that would increase variance within the sampling period. Even so, a fat body cycle emerges which is consistent with those of other temperate zone lizards (Ballinger & Schrank, 1972; Avery, 1974; Derickson, 1976a; Etheridge *et al.*, 1986; Castilla & Bauwens, 1990; Castilla *et al.*, 1992).

Mature females have distinctly larger fat bodies than males and there is a decrease in stores throughout the reproductive season, as happen in many species of lizards from temperate areas (e.g. Derickson, 1976a; Ballinger, 1973; Diller & Wallace, 1984; Braña *et al.*, 1992). The inverse relationship between follicular development and inguinal fat body volume has been demonstrated in other populations of *Podarcis bocagei* from northern Spain (Asturias) by Braña *et al.* (1992). A large fraction of the energy invested in the development of the ovarian follicles come from the lipids stored in the inguinal fat bodies, as in many lizard spe-

cies (Hahn & Tinkle, 1965; Derickson, 1976b; Guillette & Sullivan, 1985; Vitt & Cooper, 1985) and other reptiles (Congdon & Tinkle, 1982; Diller & Wallace, 1984). Nevertheless, these lipid stores are useful mainly in the first clutch, remaining vestigial during the rest of the breeding season. Thus, energy allocated to vitellogenesis in later clutches seems to be obtained from food consumed during that period (Braña *et al.*, 1992).

The fat body stores of males show an abrupt decrease at the beginning of the reproductive season (March). These stores remain low throughout the mating period. As pointed out by Castilla *et al.* (1992) for another lacertid species, *Acanthodactylus erythrurus*, the abrupt depletion of the males' fat body stores at the beginning of the activity season probably reflects high energy requirements associated with the acquisition and defence of a territory, searching for and guarding a mate, and courtship during this period. This relation is also observed in other lizard species (e. g. Vitt *et al.*, 1978; Ortega & Barbault, 1986; Méndez de la Cruz *et al.*, 1988; Braña *et al.*, 1990).

In both sexes fat body volumes remain high during winter. Therefore, the energy requirements during the winter diapause appear to be only a rather small fraction of the fall lipid stores, as reported in other temperate lizard species (Derickson, 1976a). This pattern can be observed in this population, although they show some winter activity during periods of favourable weather (Galán, 1994).

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SHORT NOTES

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THERMOREGULATION OR OSMOTIC CONTROL? SOME PRELIMINARY OBSERVATIONS ON THE FUNCTION OF EMERSION IN THE DIAMONDBACK TERRAPIN *MALACLEMYS TERRAPIN* (LATREILLE)

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The diamondback terrapin *Malaclemys terrapin* Latreille is a medium-sized emydid turtle that inhabits salt marshes and other brackish-water habitats on the east coast of the USA. (Pritchard, 1979). The osmotic physiology of the species has attracted much study, especially by Dunson and his co-workers (Dunson, 1970, 1976, 1985, 1986; Dunson & Dunson, 1975; Dunson & Mazzotti, 1989; Robinson & Dunson, 1976). *Malaclemys* spends much of the summer in an essentially marine environment, yet does not have such powerful salt glands as the marine turtles (Robinson & Dunson, 1976). When exposed to high salinity the turtles survive by virtue of an extremely low integumentary permeability to salts, a low permeability to water, a large interstitial fluid volume, (Robinson & Dunson, 1976) an ability to secrete salts from the lachrymal glands (Cowan, 1971), plus behavioural responses that allow them to select low salinity drinking water and to detect and exploit rainwater (Dunson, *op.cit.*; Davenport & Macedo, 1990; Bels *et al.*, 1995). They also exhibit a reduced appetite in sea water (Davenport & Ward, 1993) thereby minimizing uptake of salt in their invertebrate diet and by incidental swallowing of sea water whilst feeding (Dunson & Mazzotti, 1989).

The present study arose from three observations. Pritchard (1979) and Seigel (1984) both noted that diamondback terrapins are often to be seen in large basking aggregations on mudbanks. Davenport & Ward (unpublished data) found that terrapins used in feeding experiments spent increasing amounts of time out of sea water when deprived of access to fresh water; this observation was made under conditions of constant light and temperature.

Basking for thermoregulatory purposes is an extremely common phenomenon in reptiles, particularly in lizards (e.g. Cowles & Bogert, 1947; Bartholomew, 1966; Pearson & Bradford, 1976), but also in aquatic turtles (e.g. Spotila *et al.*, 1990). It has ecological costs (in terms of time unavailable for other activities, enhanced risk of predation etc), but the benefits in terms of maintenance of heightened body temperature

and possibly the inhibition of epiphytic growths on the shell, outweigh these disadvantages. For lizards and snakes a heightened body temperature will facilitate food capture and processing, but in aquatic turtles, basking can also be associated with quicker digestion of meals acquired in water at lower temperature (Hutchison, 1979).

Because Davenport & Ward had observed that animals deprived of fresh water spent increasing periods out of water, even though held at constant temperature, it seemed possible that 'basking' in *Malaclemys* might be in part a behavioural response to dehydration, rather than being solely a thermoregulatory response. This preliminary study tests this hypothesis.

Ten male diamondbacks (211 - 300 g) were used in these experiments. They were fed twice weekly, *ad lib.*, on flesh of scallops (*Chlamys opercularis*). They were held in a tank of circulating sea water (34‰) held at 25°C. The tank had a wooden platform onto which the animals could readily climb; it was fitted with a fixed drinking vessel that normally contained fresh water, but was filled with sea water during periods of experimental water deprivation. The tank was sited in a dimly-lit room where the air temperature ranged from 14 - 19°C; that is always at least 6°C cooler than the tank sea water.

To assess 'basking' (= emersion) frequency during experiments the terrapins were observed at 09.00 hr., 12.00 hr and 17.00 hr each day. The number out of water on the platform was counted and summed for the day (maximum possible frequency 30).

During 1992 and 1993, four experiments were performed. The first was a pilot experiment. The turtles had access to fresh water for several weeks. They were observed for basking frequency for five days, then deprived of fresh drinking water for ten days. In the light of this first trial, three further long experiments were performed, each lasting 36-40 days and separated from each other by 1-2 months of standard maintenance. In each case, turtles were observed for 9-10 days when fresh water was available, then for 13-16 days when it was not, followed by a further period of 10-14 days after fresh water access was restored.

To allow an assessment of the relative importance of respiratory and cutaneous water exchange, the following experiments were carried out in 1993-94. First, three groups, each of three well-fed terrapins, were fasted for 12 days. One group was held in fresh water, one in sea water and one in air (at 25°C). Their holding vessels were mounted next to one another to ensure a similar atmospheric humidity, but daily readings of relative humidity (RH) were taken by hygrometer (5 mm above the water surface in the case of the fresh water and seawater vessels). Animals were weighed each day, those held in water being thoroughly dried with paper towels before weighing (accuracy ± 0.05 g). Second, after several weeks during which the terrapins were again well fed and had access to fresh water, three ani-

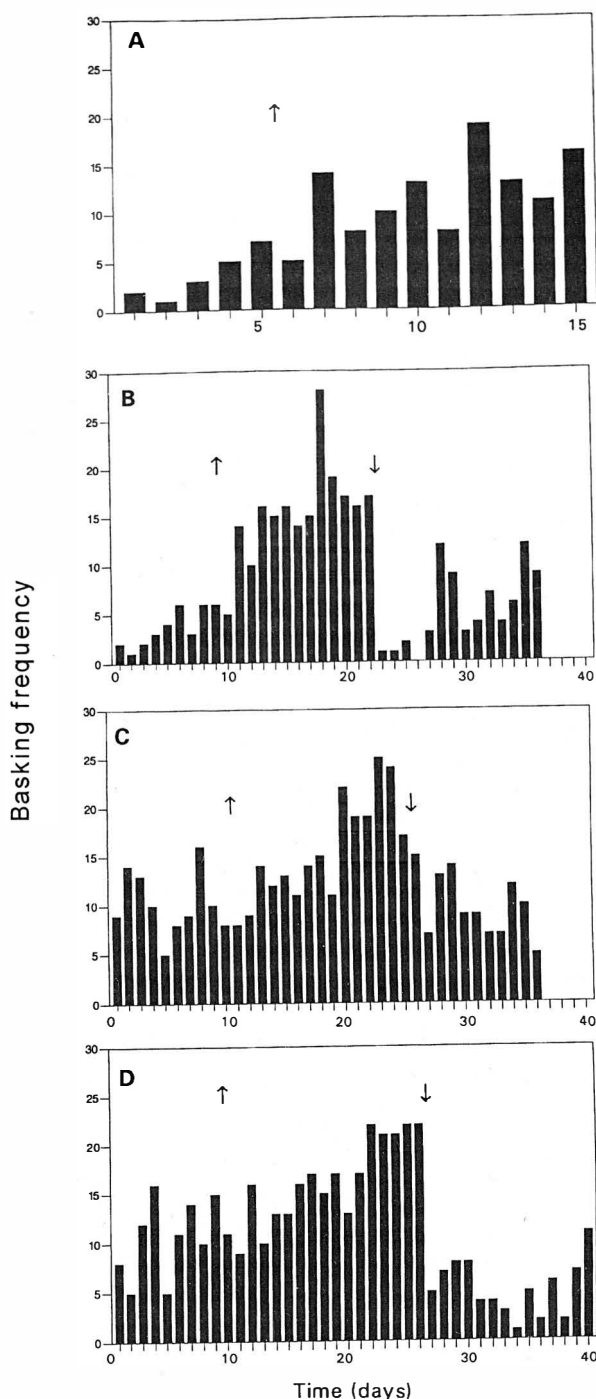


FIG. 1. A, basking frequency during preliminary trial. Fresh water was available on days 1-5 and absent on days 6-15. B, basking frequencies during experiment 1. Fresh water was available on days 1-9 and 23-36. It was absent on days 10-22. C, basking frequencies during experiment 3. Fresh water was available on days 1-10 and 26-36. It was absent on days 11-25. D, basking frequencies during experiment 3. Fresh water was available on days 1-9 and 27-40. It was absent on days 10-26. Up arrows indicate onset of fresh water deprivation; down arrows indicate restoration of fresh water availability.

mals, selected randomly from those available, were placed in an air-filled vessel in which a water tank and water-soaked absorbent paper (both inaccessible to the turtles) ensured a water-saturated atmosphere. They

were fasted for 12 days and weighed daily as described above.

Fig. 1A shows the results of the preliminary basking frequency trial. Terrapins deprived of fresh water spent more time out of water than they had previously in fresh water (on average 3.25 times the basking frequency), despite the lower temperature they encountered by doing so.

This is confirmed by the data shown in Figs 1B-1D. In each case a similar pattern of behaviour was seen. When fresh water deprivation started there was initially little change in basking frequency, but thereafter there was a progressive increase. When fresh water availability was restored there was an abrupt drop in basking frequency. Regression analysis confirmed that each period of water deprivation was associated with a rise in basking frequency (Table 1). Maximum basking frequency scores (22-28 out of a possible 30) indicated that terrapins deprived of fresh water were spending 73-93% of their time out of water.

During the period of the first mass change experiment, with terrapins held in fresh water, sea water and air, recorded relative humidities (RH) ranged from 61% to 85%. However, although there were differences in RH amongst the experiment vessels on each day, there was no significant pattern of difference, and no statistically significant difference between mean RH ($P > 0.05$). During the second experiment, with terrapins held in water-saturated air, RH values were always in the region of 98-100%.

All animals showed a similar pattern of rapid mass loss during the first four days of the experiments when they were defaecating. Thereafter, mass changes were much slower and very steady. Accordingly, regression analysis of mass changes was conducted from day 4 to day 12 of the experiment (Table 1). It is evident that rate of mass loss in air could be less or greater than the rate of loss in sea water, depending upon the RH.

Diamondback terrapins are vulnerable to avian and mammalian predation when on land (Seigel, 1984; Lovich & Gibbons, 1990). However, from the data collected it is evident that diamondbacks progressively spend more time on land when they lose access to fresh water. Under the experimental conditions employed in this study they consequently encountered reduced, not elevated temperature, so gained no thermal benefit. From the results of the mass change experiments it may be seen that they also experienced a heightened rate of water loss, when RH levels were in the range 61-85%, but a reduced rate of water loss at high RH (98-100%). Enhanced water loss in air of RH 61-85% presumably occurred across the skin and shell since respiratory water loss should have been similar for turtles held in fresh water, sea water or air. Dunson (1976, 1986) showed that diamondbacks lost mass in sea water at a rather lower rate ($0.32\% \text{ d}^{-1}$) than that recorded in this study ($0.56\% \text{ d}^{-1}$). This difference probably stemmed from the much smaller size (ca. 230 g) of our terrapins (and consequent higher surface area-to-volume ratio)

TABLE 1. (a) Rate of change of basking frequency during periods of water deprivation, where y = frequency of basking; x = length of period of water deprivation (days). (b) Rates of mass change in fasting diamondback turtles, where y = mean mass (g) and x = days of fasting. Regression equations are for the period between 4 and 12 days after initiation of fasting. From equations in Table 1 (b) it can be seen that the fasting diamondbacks lose little mass (0.15% d^{-1}) in fresh water, compared with 0.36% d^{-1} in water saturated air, 0.56% d^{-1} in sea water and 0.90% d^{-1} in air of 61-85% RH.

	Equation	r^2	P
(a)			
Experiment 1	$\log y = 0.028x + 0.29$	0.413	0.018
Experiment 2	$\log y = 0.023x + 0.73$	0.589	0.001
Experiment 3	$\log y = 0.021x + 1.02$	0.711	0.000
(b)			
In fresh water	$y = 232.5 - 0.36x$	0.66	0.007
In sea water	$y = 231.6 - 1.29x$	0.95	0.000
In air (61-85% RH)	$y = 224.6 - 2.02x$	0.97	0.000
In air (98-100% RH)	$y = 230.3 - 0.83x$	0.98	0.000

by comparison with those studied by Dunson (ca. 1000 g).

Cowan (1974) showed that blood concentration of terrapins rose from about 290 to 400 mOsmoles kg^{-1} during a four month exposure to full sea water. Taken with the flux studies of Robinson & Dunson (1976), it seems that all of the mass loss and rise in blood concentration that occurs in terrapins exposed to sea water may be accounted for by osmotic dehydration; salt influx and efflux are in balance. On the face of it therefore, terrapins would tend to suffer more osmoconcentration by leaving sea water and basking in air of 61-80% RH than they would if they remained immersed in sea water. However, when they do leave seawater salt influx will cease, but there would appear to be no reason for all salt efflux to cease during emersion. Minimal sodium efflux by the cloacal and lachrymal gland routes (65% of total efflux) should continue at around 4 - 7 μ moles Na 100 $g^{-1} h^{-1}$ (calculated from Robinson & Dunson, 1976). Given a total body Na content of 108.6 μ moles g^{-1} (Robinson & Dunson, 1976) this corresponds to a loss of 0.9-1.55% of body sodium per day. So, by moving from sea water into air of 61-85% RH a terrapin will incur an extra water loss cost of 0.34% body mass d^{-1} (i.e. 0.9% minus 0.56% d^{-1}), but lose sodium at 0.9-1.55% d^{-1} . This suggests that basking animals will lose more body water by basking, but suffer significantly less overall osmoconcentration of the body fluids. Obviously the balance between these two influences will depend upon RH. At high RH levels (98-100%), which are perhaps more likely close to the muddy substrata of salt marshes, emersed terrapins will lose less water than they would in sea water, as well as avoiding salt influx and continuing to excrete salt in tears and urine.

Diamondbacks can withstand considerable loss of body water, first because they have large extracellular subdermal spaces that act as water stores, and second

because they partition water loss so that the intracellular compartment is maintained (Robinson & Dunson, 1976). Avoiding osmoconcentration of the body fluids is probably a higher physiological priority than preventing water loss; 'basking' (i.e. emersion) in response to lack of fresh water would appear to accomplish this aim, even when RH levels are below saturation. Obviously diamondbacks will bask for thermoregulatory purposes, just as do other emydids (the best studied being *Trachemys scripta*; Spotila *et al.*, 1990). However, the evidence presented in this paper demonstrates that basking might have an osmotic control function too.

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**THE TAXONOMIC STATUS OF
TYPHLONECTES VENEZUELENSE
FUHRMANN (AMPHIBIA:
GYMNOPHIONA:
TYPHLONECTIDAE)**

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At the turn of the last century, the genus *Typhlonectes* comprised three distinctive species, *T. compressicaudus* (Duméril & Bibron), *T. natans* (Fischer) and *T. kaupii* (Berthold) (= *T. dorsalis* Peters) from Northern South America, all of which showed some degree of lateral compression of the body and development of a dorsal 'fin' that set them apart from all other caecilians and indicated adaptation to a distinctive aquatic existence. In a classic early monograph on the aquatic caecilians, Fuhrmann (1914) described a new variety, *Typhlonectes compressicaudus venezuelense*, for a form represented by two specimens from Caracas and Maracaibo, Venezuela, distinguished from the Amazonian and Guyanan form *T. c. compressicaudus* by minor and subtle differences in head shape. Dunn (1942), who examined many more specimens than were available to Fuhrmann, considered this form to be a junior synonym of *T. natans*, and he also considered *natans* to be no more than a variety of *compressicaudus*.

Taylor's (1968) treatment of *Typhlonectes* introduced radical changes. *T. kaupii* was transferred to a new genus, *T. natans* was resurrected to species status, and *T. c. venezuelense* was removed from the synonymy of *T. natans* and elevated to specific status. In addition, Taylor (1968) described three new species of *Typhlonectes*. One of these new species, *T. eiselti*, is a highly distinctive lungless caecilian that has been transferred to the genus *Atretochoana* (Nussbaum & Wilkinson, 1995). Taylor's other new species cannot be diagnosed on the basis of any features that reliably distinguish them from *T. compressicaudus* and are considered junior synonyms of that species (Wilkinson, 1991). Nussbaum & Wilkinson (1989) noted that *T. venezuelense* was of doubtful validity and did not include this species in their synopsis of the content of *Typhlonectes*. My aims here are to clarify the taxonomic status of *T. venezuelense*, describe simple distinguishing features for the species of *Typhlonectes*, and raise concerns over the taxonomic status of a recently described species.

Taylor's (1968: 255) diagnosis of *Typhlonectes venezuelense* indicates that it has a distinctly higher (less flattened) head than does *T. natans*, but includes no other features that might distinguish these forms [the diagnosis states "Head distinctly flatter than the head of *natans*." and "flatter" is corrected to "higher" in an Errata, that, unfortunately, is not included in all copies of the work]. Neither Taylor nor I have been able to locate the holotype of *T. venezuelense*, a specimen catalogued in the Berlin Museum and which is presumed lost, but I have examined available type material of both *T. venezuelense* (ZMH A00257,

TABLE I. Morphometric and meristic data for *Typhlonectes natans* and *T. venezuelense*.

	<i>Typhlonectes venezuelense</i>		<i>Typhlonectes natans</i>	
	ZMH A00257	ZMB 9523	LACM	
	Paratype	Cotype	67435	67436
Total length	350	500	345	343
Circumference at mid-body	43	43	41	39
Primary annuli	92	93	88	90
Head length	10.7	12.7	10.8	10.7
Head width at eye	9.3	9.7	8.8	8.5
Head depth at eye	5.5	5.5	5.3	5.2
Head width at occiput	11.1	11.9	10.8	10.7
Head depth at occiput	7.3	6.5	7.0	6.7
Interorbital distance	7.1	7.7	6.9	6.6
Internarial distance	4.6	4.4	4.6	4.5
Eye-narial distance	4.8	5.7	4.9	4.8
Eye-tentacle distance	4.3	4.9	4.5	4.4
Tentacle-narial distance	0.7	0.7	0.5	0.5
Premax-maxillary teeth	44	46	42	39
Vomeropalatine teeth	45	39	42	44
Dentary teeth	34	36	34	32
Splénial teeth	12	10	9	8

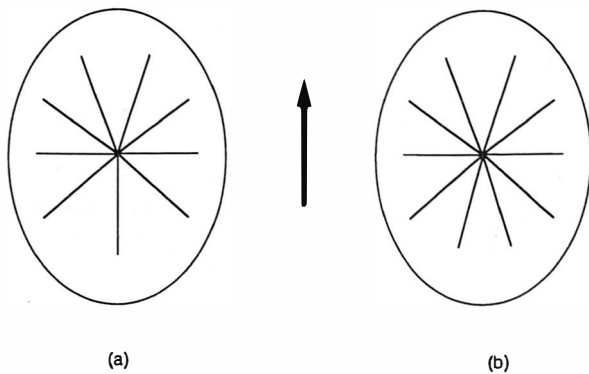


FIG. 1. Diagrammatic representation of the patterns of denticulations surrounding the vent that can be used to distinguish those species of *Typhlonectes* with low numbers of splenial teeth. (a) *T. natans* (b) *T. compressicaudus*. Arrow is directed posteriorly.

paratype) and *T. natans* (ZMB 9523 cotype) as well as several hundred specimens of *T. natans*. I can find no differences between the types that warrants their recognition as distinct species. Differences in the shape of the head exist, but the relatively flat skull of the cotype of *T. natans* is attributable to the fact that the skull and cranial musculature are extensively macerated. Certainly, other *Typhlonectes* from the vicinity of the type of *T. natans* in the Rio Magdalena-Rio Cauca drainage in Colombia, and which were readily assigned to *T. natans* by Taylor (1968, 1973), have less flattened heads than does the cotype and do not differ in this respect from the type material of *T. venezuelense*. Morphometric and meristic data for the type material, together with data for two specimens that were assigned by Taylor (1973) to *T. natans*, are summarised in Table 1. The latter specimens are from a single locality, close to the type locality of *T. natans*, and they are similar in total length to the paratype of *T. venezuelense*. As can be seen from Table 1, they agree closely with the paratype of *T. venezuelense* in their measures and counts, including those that reflect the shape (width and depth) of the head. Fuhrmann (1914) described some minor differences in the disposition of the lungs and urinary bladder of *T. venezuelense* and *T. natans* which are attributable to intraspecific variation.

These observations support Dunn's (1942) earlier conclusion that, in the absence of any significant differences, *Typhlonectes venezuelense* must be considered a junior synonym of *T. natans*. In contrast, there are several major morphological differences between *T. natans* and *T. compressicaudus*, (e.g. in the dentition, relative lengths of left and right lungs and the form of the cloacal disk [Taylor, 1968; Wilkinson, 1991]) that do not support Dunn's view that these forms are merely geographic races of the same species. For the purposes of identification, *T. natans* and *T. compressicaudus* can be distinguished most readily by the arrangements of the denticulations that radiate from the vent to form the cloacal disk (Fig. 1).

The type specimens of *Typhlonectes venezuelense* are reported to be from Caracas and from Maracaibo, Venezuela. Other specimens of *T. natans* have been collected in the region of Maracaibo as recently as 1981 (Wilkinson, submitted). In contrast, no other specimens of *T. natans* are known from Caracas, and whether the Caracas specimen originated in the vicinity of Caracas, or was collected elsewhere in the region, is uncertain.

Cascon *et al.* (1991) recently described a new species of *Typhlonectes*, *T. cunhai* from Manaus, Brazil, an area that has also yielded many specimens of *T. compressicaudus*. Unfortunately, the diagnosis of this new species, which, as in *T. compressicaudus*, has 10 denticulations about the vent, emphasises features of the body shape and fin that are notoriously variable in *T. compressicaudus*, and provide no compelling evidence that their new form is specifically distinct. The uncertain status of *T. cunhai* represents the major unresolved problem in the species level taxonomy of *Typhlonectes*.

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A NEW EXAMPLE OF FEMALE
PARENTAL BEHAVIOUR IN
LEPTODACTYLUS VALIDUS,
A FROG OF THE LEPTODACTYLID
'*MELANONOTUS*' SPECIES GROUP

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A common feature of the anuran sub-family Leptodactylinae is the deposition of eggs in a mass of foam, either on the surface of water, or in a burrow. There are few reports of post-depositional parental care in this group, but adults of two members of the 'ocellatus' species group (Heyer, 1969), *L. ocellatus* itself (Vaz-Ferreira & Gehrau, 1975) and *L. bolivianus* (Wells & Bard, 1988), have been observed attending nests and tadpoles. Here, I extend these observations to *L. validus* (sensu Heyer, 1994), a member of the 'melanonotus' species group (Heyer, 1969). The similarities in these behaviours may have some bearing on the relationships between these two species groups. Kenny's (1969) account of the frogs of Trinidad (where my observations were made) names a single species of the 'melanonotus' group, *L. podicipinus petersi* (Steindachner). The equivalent species in Heyer's (1994) most recent revision is *L. validus* Garman. Kenny found this species throughout Trinidad at lower elevations in heavily shaded areas. My field observations confirm this, but I also found this species in roadside ditches, as long as there was vegetation to provide cover. After heavy rains, males can be heard calling in chorus, more rarely as individuals, beside flooded areas, during day and night. Kenny found foam nests free-floating or, more commonly, covered with leaves or sticks. I have always found nests at the edges of small pools, usually well covered by dead vegetation. My observations of foam nests, tadpole and parental behaviour in *L. validus* were made in 1983, 1987, 1991 and 1994, from late June to mid August. Sites where frogs, nests and tadpoles were observed included rough woodland, close to the Commonwealth Agricultural Bureau in St Augustine; a small cocoa plantation 2 km west of Matura village; a small mango and citrus wood beside the main road just east of Valencia village; and the stream behind Mount St Benedict monastery in the Northern Range. All observations on parental behaviour were made during the day. In all cases except Mount St Benedict, *L. validus* reproduction occurred in temporarily flooded areas. In this latter case, quite exceptionally, *L. validus* nested in a small mountain stream. Table 1 summarises the

results on nest and tadpole shoal attendance: occasional sightings from the early years are supplemented by a more complete set from 1994. Single adult frogs were found beneath recently made nests on four occasions; where sex was confirmed, these were females. A pair in amplexus was once found beneath a nest and captured. On return to the vicinity of the nest, the male rapidly swam away, but the female stayed by the nest. Nests without attendant adults were frequently found, but since discovery of nests involves considerable disturbance of the covering vegetation, it is possible that attendant adults escaped. *Leptodactylus validus* are small cryptically-coloured frogs and are very difficult to locate when submerged in detritus-filled pools. Single adult frogs were observed close to tadpole shoals on six separate occasions: when it was possible to determine their sex, they were all females. In five cases, the shoals were of recently-hatched tadpoles and in two of these, adults were seen close to their shoals on two separate occasions, four days apart. In the sixth case, the adult was close to a shoal of large tadpoles.

Whenever found, recently-hatched *L. validus* tadpoles formed tight shoals: these occasionally dispersed, then reformed, or split into groups, then reformed. They spent much of the time near the surface, tadpoles milling over one another, but also occasionally descended to the bottom and browsed on the decaying leaves and twigs characteristic of the shaded pools where they live. It was not clear whether shoaling normally continued till metamorphosis. Shoals of late-stage tadpoles were found, but isolated individuals were found too. Adults attending tadpoles were observed over short (10 min.) and longer (45 min.) time periods. Over the longer time, the following behaviour was seen. The adult made frequent changes of position, with occasional dives into the pool, but spent most of the time at the edge of the pool, head out and pointing towards the edge, legs under the water. 'Pumping movements' with the hind legs occurred several times over a 45-min. period, always when the tadpole shoal was close to the adult, milling around, or clustered beside the hind limbs. 'Pumping movements' involved raising the back, then rapidly moving up and down in the water for a few seconds. On the occasions

TABLE 1. Summary of observations on nest and tadpole shoal attendance. a, sex not identified; b, sex identified as female by dissection; c, sex identified as female by size (50 mm SVL); d, pumping movements seen; e, no pumping movements.

Year	No. adults seen attending nests	No. adults seen attending tadpole shoals
1983	/	1a,d
1987	1b	/
1991	/	1a,e
1994	2a; 1c	1b,e; 1a,e; 1a,d; 1b,d

noted in Table 1 when pumping movements were not seen, observation periods were short. Tadpoles tended to stay close to attending adults, but did on occasion move away; they then either returned to the adult, or the adult followed them.

As part of a wider study on leptodactylid reproduction, eight *L. validus* foam nests were collected and returned to the laboratory to observe hatching. The earliest hatchlings appeared after 2.5 days at 26°C, but most took nearer three days to emerge from the foam. On hatching, tadpoles mostly remained in contact with the thick mucus material at the base of the nest, rather than moving away. This was in marked contrast to another floating-foam nesting leptodactylid, *Physalaemus pustulosus*, where hatchlings mainly attached themselves to the sides and bottom of their incubation container after leaving the foam (Downie, 1993). Taken together, these observations show that adult female *L. validus* stay with the foam nest after deposition, that tadpoles stay with the nest after hatching and form a shoal, and that the female then remains with the shoal, at least for some time. The occasional nature of the observations makes it impossible to tell whether long-term shoal attendance is normal. Given that time to metamorphosis is as long as eight weeks (Kenny, 1969) it would be surprising if females remained that long in attendance, especially if their feeding opportunities are restricted.

Observations like these have been made on two other leptodactylids. Vaz-Ferreira & Gehrau (1975) reported that *L. ocellatus* females remain with their nests, often staying in a hole in the middle of the nest, then close to their shoaling tadpoles up to metamorphosis. Females would behave aggressively towards potential predators, such as birds, during this time. They did not report 'pumping movements'. Wells & Bard (1988) reported female attendance on shoaling tadpoles in *L. bolivianus*. They studied the detailed interaction of females and tadpoles (developmental stages not reported) but did not follow the interaction of a particular female with tadpoles over more than a few days. They were not able to confirm that females attend their nests, but did once find an adult frog (sex not known) with a nest. They reported 'pumping movements' very similar to those I have seen in *L. validus*. *Leptodactylus bolivianus* tadpoles were found in shallow, narrow ditches, and the details of the female-tadpole interaction suggested that the pumping movements represent some form of communication (physical, chemical, or both) which allows the female to lead her tadpoles along the ditch. This leading behaviour was mostly apparent at night. During the day, tadpoles and females tended to hide, without moving much along the ditch, and though the pumping movements still occurred, they were less frequent than at night. My observations on *L. validus* do not support a leading function, but they were made only during the day. Vaz-Ferreira & Gehrau (1975) suggest that the obvious function of nest and tadpole attendance is pro-

tection. *L. ocellatus* and *L. bolivianus* are both large species (around 9 and 11 cm SVL respectively) for whom aggression against small birds and fish seems feasible. However, *L. validus* females are only 4-5 cm and are not aggressive in my experience. My observations are from a different leptodactylid species group to the previous ones. *L. ocellatus* and *L. bolivianus* belong to the 'ocellatus' group; *L. validus* to the 'melanonotus' group (Heyer, 1969). Rex Cocroft and Victor Morales have observed female attendance on tadpoles, with pumping movements, in another species of the 'melanonotus' group, *L. leptodactyloides* (personal communication). Field observations of more species in these groups are much needed. These observations on parental care are consistent with Heyer's (1969) view that the 'ocellatus' and 'melanonotus' groups are the most closely related of the five *Leptodactylus* groups he identified. In these examples of leptodactylid parental care the parent has been the female. In predominantly externally-fertilising vertebrate groups like fish and amphibians, parental care is biased toward males (fish - Gross & Sargent, 1985) or is approximately even (amphibians: Gross & Shine, 1981). In fish, Gross & Sargent (1985) have suggested that males more frequently look after the young because they have less to lose in future fecundity than females. No similarly detailed analysis has been performed on amphibians, but future fecundity depends on feeding: it would therefore be of considerable interest to discover how much foraging attendant female leptodactylids do, and how long it takes before they are able to breed again, compared to species where no attendance occurs.

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A PALAEOBATRACHID ANURAN ILIUM FROM THE BRITISH EOCENE

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The extinct anuran family Palaeobatrachidae Cope extends from the Late Jurassic to the Plio-Pleistocene (Meszoely *et al.*, 1984). The most abundant genus, *Palaeobatrachus*, occupied a broad adaptive zone in space and in time, occurring in both the Old and New World, and existing from Cretaceous through Miocene times. The ecological niche of *Palaeobatrachus* is thought to have been similar to that of the modern highly aquatic pipid frog *Xenopus*. Palaeobatrachids have been reported from the British Isles only from a single Late Eocene locality at Headon Hill on the Isle of Wight (Rage & Ford, 1980; Meszoely *et al.*, 1984), and from another Late Eocene locality on the sea at the nearby Hordle Cliff, Hampshire, (Milner *et al.*, 1982). These fossil remains did not include ilia.

British palaeobatrachid material in Rage & Ford (1980) and Milner *et al.* (1982) was referred only to the family Palaeobatrachidae. Meszoely *et al.* (1984), however, described a new genus and species of palaeobatrachid, *Albionbatrachus wightensis*, from Isle of Wight material collected at Headon Hill (Totland Bay Member of the Headon Hill Formation, Upper Eocene) [Insole and Daley, 1985]. Their new taxon was based on an almost complete frontoparietal (holotype), an atlas, a synsacrum, a few presacral vertebrae, and an angular.

Albionbatrachus wightensis was diagnosed on the basis of the frontoparietal as a palaeobatrachid frog that closely resembles *Palaeobatrachus* sp. from Oligo-Miocene deposits at Laugnac, France, discussed by Vergnaud-Grazzini & Hoffstetter (1972). The Isle of Wight frontoparietal differs from the French specimen only in having spur-like prootic processes (Meszoely *et al.*, 1984, Figs. 1-3). The referred atlas, synsacrum, vertebrae, and angular were described anatomically, but they were not compared with similar elements in other *Palaeobatrachus*. This is apparently because many palaeobatrachid fossils consist of skeletons embedded in matrix in such a way that details of individual bones are difficult to see.

The British Ilium. Estes & Sanchiz (1982) showed that ilia of palaeobatrachids are diagnostic to the generic and the specific level, and compared their new North American species, *Palaeobatrachus occidentalis*, with various European fossils of *Palaeobatrachus* on the basis of iliac structures and their muscle attachments.

The British left ilium (Michigan State University Museum Vertebrate Paleontology Number 1360, Fig.

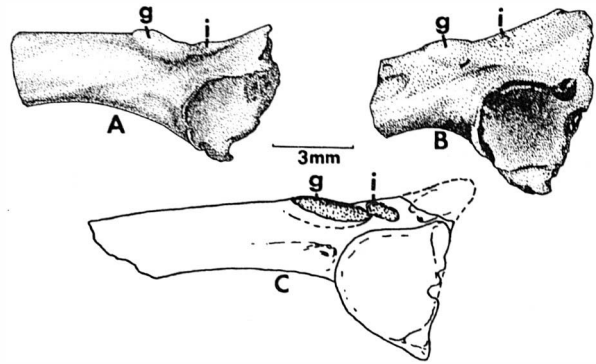


FIG. 1. *Palaeobatrachus* sp. ilia. A, left ilium (Michigan State University Museum Vertebrate Paleontology Number 1630) from the Totland Bay Locality, Totland Bay Member, Headon Hill Formation, Late Eocene, Isle of Wight, England. B, left ilium from the Late Paleocene of Cernay, France, drawn from a photograph in Vergnaud-Grazzini & Hoffstetter (1972). C, left ilium from the Rijksuniversiteit Utrecht Collection, Early Oligocene of Belgium, after Estes & Sanchiz (1982). Abbreviations are: g = gluteus tubercle, i = iliofibularis-iliofemoralis attachment. The 3 mm line applies to all three drawings.

1A) was collected by David Harrison in 1991 at the Isle of Wight Totland Bay Locality, a stratigraphic equivalent of the Headon Hill Locality. The fossil is so well-preserved that specific iliac features and muscle origins may be easily discerned.

Based on these features, MSUVP 1360 represents the genus *Palaeobatrachus*. It most specifically resembles a specimen referred to as *Palaeobatrachus* sp. from the Rijksuniversiteit Utrecht collection Early Oligocene of Belgium (Fig. 1C) figured by Estes & Sanchiz (1982). Unfortunately, more specific information is not available for this specimen. In the British and the Belgian specimens (Figs. 1A,C) the dorsal tubercle from which the gluteus muscle arises is elongate and a smaller tubercle from which the iliofibularis and iliofemoralis muscles arise is adjacent to it posteriorly.

In other *Palaeobatrachus* species the gluteus tubercle may be short and the iliofibularis and iliofemoralis attachment obscure (Fig. 1B) and/or the two tubercles may be separate (see iliac drawings in Estes & Sanchiz, 1982; Fig. 4).

There is a problem regarding the status of the Isle of Wight palaeobatrachid material. We have one genus, *Albionbatrachus*, described on the basis of a single frontoparietal bone that differs from *Paleobatrachus* in a character that could be specifically or even individually variable. Yet a well-preserved ilium appears to be almost identical to a lower Oligocene *Palaeobatrachus* sp. from Belgium. Both of these Isle of Wight bones were collected from stratigraphically equivalent horizons. Other British palaeobatrachid bones appear to be undiagnostic beyond the familial level. Obviously more complete palaeobatrachid skeletons are needed to clear up the taxonomic uncertainties.

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THE HERPETOLOGICAL JOURNAL

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