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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 233–236 (1982)

# GROWTH OF JAMAICAN HAWKSBILL TURTLES (*ERETMOCHELYS IMBRICATA*) REARED IN CAPTIVITY

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(*Received* 18 *December* 1981)

## SUMMARY

An investigation into the feasibility of rearing captive hawksbill turtle (*Eretmochelys imbricata*) hatchlings was conducted in 1980. One hundred and three individuals were collected from two nests near Kingston Harbour, Jamaica, and reared in a 3 m diameter tank for six months, after which they were released.

During this period they willingly fed on chopped offal and meat from a variety of fish species. Mortality was low. The turtles grew faster and were heavier than their wild counterparts. At the time of release the mean shell length was about 19 cm, though seven individuals retained for further studies grew slightly slower thereafter, reaching a mean length of 26 cm at the end of their first year. The relatively faster growth of shell length with respect to total weight could be explained by the faster growth of this parameter in relation to the other shell parameters.

## INTRODUCTION

Populations of the hawksbill turtle (*Eretmochelys imbricata*, L.) have been declining since the mid-seventeenth century, largely as a result of commercial exploitation for the fine shell. It is now designated as an endangered species (I.U.C.N. Red Data Book, 1970) and captive hawksbills have been reared for both commercial and conservation reasons. Little data exist on the survivorship to maturity of wild individuals, but it is probably similar to that of green turtles (*Chelonia mydas*, L.), which is about 1% (Hirth, 1971). Rearing of captive hatchlings offers a potentially viable method of avoiding the very high first year mortality. In spite of this, however, data on hawksbill growth seems somewhat sparse, particularly compared to that of the green turtle.

The discovery of hawksbill hatchlings emerging from two nests near Kingston, Jamaica, permitted an investigation into the feasibility of rearing captive hawksbill turtles with the aim of later release into the wild. This paper reports on the methods employed to rear these hatchlings and on their growth in captivity. The success of these methods is assessed by comparing the absolute and relative growth of different morphometric parameters in the captive hatchlings with the limited data available from wild populations.

## MATERIALS AND METHODS

Hatchling turtles were obtained from two nests at the Port Royal Cays near Kingston Harbour, Jamaica (lat. 17°, long. 76°). Of the 115 hatchlings emerging on 20 January 1980, 74 were collected, whilst all 29 individuals emerging from the second nest on 10 February were taken. On each occasion all the hatchlings crawled to the nearest water's edge immediately after emergence. During this period hatchlings may undergo some type of chemoreceptive imprinting with the locality of their nest site, either whilst crawling over the sand or in the first few minutes in the water (Carr, 1972). Accordingly, collection of the hatchlings was made by boat only after they had been swimming for some time.

Within a day of capture all the young hawksbill turtles were placed in a circular black fibre glass tank 3 m in diameter with a through-flow of fresh seawater. Wire mesh was placed over the tank to prevent attacks by birds. The tank was drained and refilled weekly. Possibly due to a build-up of waste organic matter, algal growth was quite rapid, both on the walls of the tank and on the turtles themselves. When the tank was drained, both it and the turtles were scrubbed clean.

Within 24 h of emergence most of the turtles were accepting food. They were offered a choice of turtle grass (*Thalassia testudinum*), flat oysters (*Isognomon alatus*), and chopped fish meat and offal from the following species: *Jenkinsia lamprotaenia, Sardinella aurita, Harengula jaguana, H. humeralis, Opisthonema oglinum, Cetengraulis edentulus* and *Anchoa lyolepis*. Almost invariably the fish meat was preferred. Initially they were fed once daily, but after a month this was doubled. Food was provided in excess of their demand, which, during the early stages, was about 5 g of meat/meal for each individual. During the first month food was taken immediately at the surface, but thereafter the turtles tended to forage more for pieces lying at the bottom of the tank.

Throughout the experiment mortality was very low. The only deaths occurred accidentally, when three hatchlings drowned in the outflow pipe. Many turtles were lost however, through theft, which was a constant

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problem throughout the experiment. Overt infections were rare, in spite of wounds caused as a result of aggressive behaviour. Individuals with such wounds were separated for several days, and invariably the skin lesions healed rapidly.

During the experiment growth was monitored. The hatchlings were first measured and weighed on emergence day, then numbered with white, non-toxic paint. For the first month shell and body dimensions (Fig. 1) were recorded weekly. Later the frequency of this was reduced to monthly measurements, and only shell length and weight were recorded. During this period several wild adults were obtained from fishing nets or by scuba diving. These provided useful size and weight data for comparison with the captive indviduals.

Six months after their emergence all the turtles were tagged with small numbered plastic discs and (excepting seven individuals retained for further studies) were released in sheltered water of 7 m depth on the inside of the coral reef at the hatching site. This site was selected because of the frequent occurrence of similarly sized wild hawksbills in the area. Upon release the young turtles immediately started foraging amongst coral heads and the roots of turtle grass.

## RESULTS

### ABSOLUTE GROWTH

Figure 1 shows the growth of the captive hawksbill turtles from January to July 1980. Initially growth in shell length was about 0·5 cm/week, but after three months this rate increased to about 0·7 cm/week. At an age of six months, when the majority of the turtles were released, the mean size was about 19 cm. The seven individuals retained to monitor further growth grew more slowly thereafter, and reached a size of 26 cm at the end of their first year.

### RELATIVE GROWTH

Differences in shell proportions have frequently been used to define species of turtles. Data were therefore collected on shell and body dimensions, as well as weight, as the young turtles grew.

The relationship between shell length ($L$) and total weight ($W$) was tested for its fit to the allometric equation;

$$W = a\,L^b$$

where $a$ and $b$ are constants. This equation can be rewritten in logarithmic form as

$$\log W = \log a + b \log L$$

so that if weight and length are allometrically related they plot rectilinearly on logarithmic axes. When two variables having the same units of measurement are related by a power function of this type, a value of unity for the exponent $b$ indicates an isometric relationship in which the two variables maintain geometric similarity with size increase. In weight/length relationships, however, when the co-ordinate is a weight (or volume), $b = 3$ corresponds to isometry (Gould, 1966). Values of $b$ greater than 3 indicate that weight is increasing relatively faster than length, whilst values less than 3 indicate the reverse.

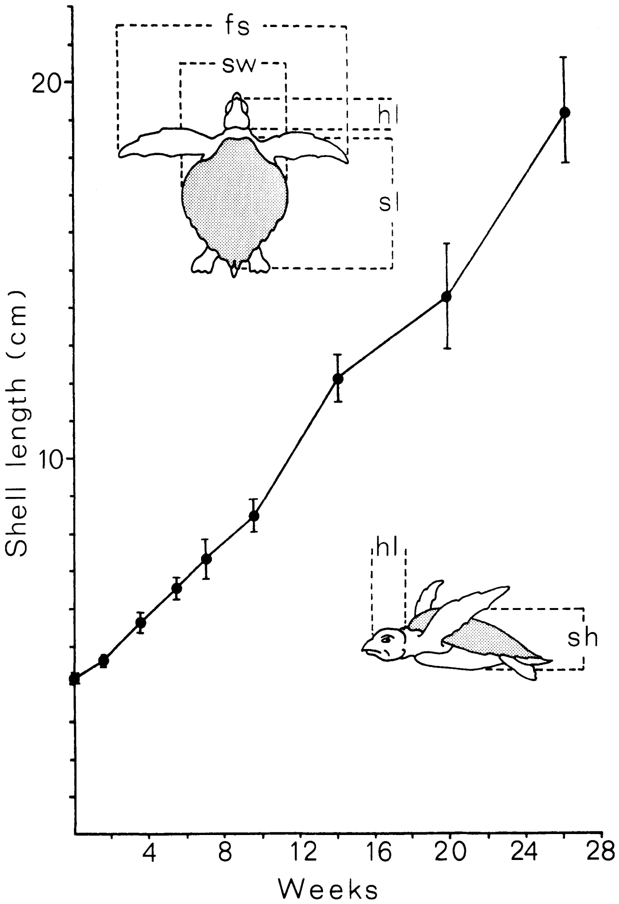

FIG. 1. Growth of captive hawksbill hatchlings; each point indicates the mean ± 1 SD. Size parameters measured: shell length (sl), shell width (sw), shell height (sh), flipper span (fs), and head length (hl).

The regressions between (logarithmically converted) shell length and total weight of the two batches of hatchlings were virtually identical, and can be expressed by the equations:

$$\log W = 2.59 \quad \log L - 2.56 \text{ (20 January nest)}$$

and

$$\log W = 2.59 \quad \log L - 2.48 \text{ (10 February nest).}$$

In both cases, therefore, shell length increased relatively faster than weight in the young hatchlings. Figure 2 compares this relationship with data from six of the captive hawksbills after their first year, and with data collected from wild individuals. The captive yearlings were signficantly heavier than similarly sized wild individuals ($t = 2.626$, $P < 0.05$). In spite of this, in both groups shell length continued to grow faster than weight ($b = 2.946$ and 2.552 respectively). Only when larger wild individuals (over 50 cms shell length) were included, did the effect shift to one of increased weight relative to length ($b = 3.434$).

Figure 3 shows the relationship between shell length and other body parameters in the hatchlings. Shell width, height, and head length all grew relatively slower

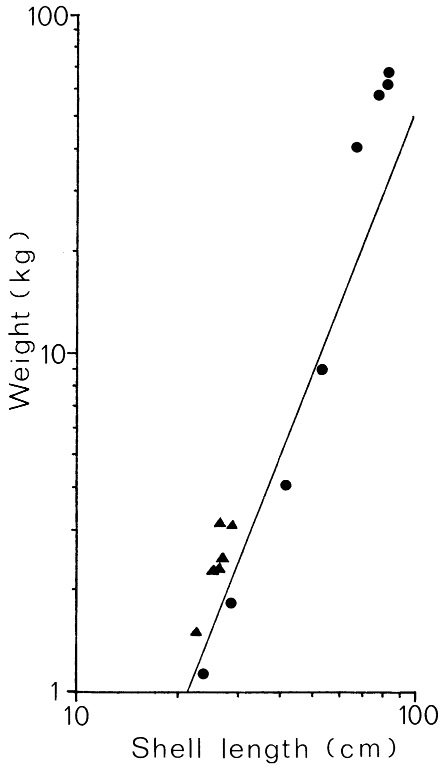

FIG. 2. Logarithmic plot of shell length/weight relationship in captive yearlings (▲) and wild individuals (●). Line indicates slope of relationship extrapolated from hatchlings in their first two months.

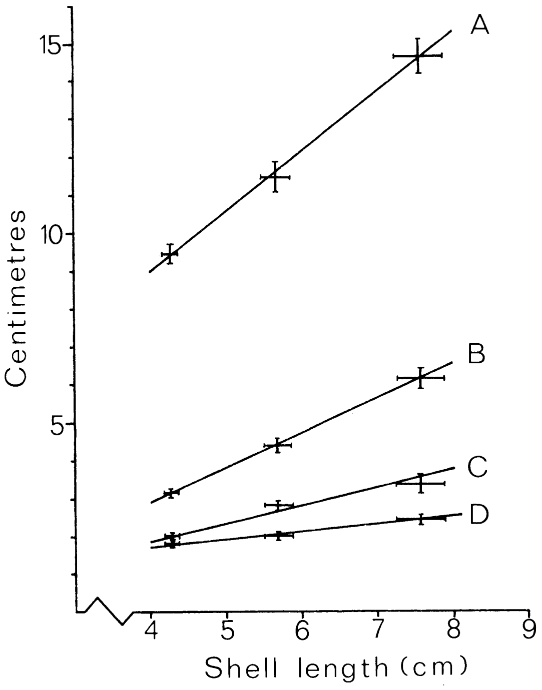

FIG. 3. Relationship between shell length and flipper span (A), shell width (B), shell height (C), and head length (D), in the first seven weeks of hatchling growth. Vertical and horizontal bars indicate 1 SD about the mean for each parameter.

than shell length. The young hawksbills tended, therefore, to become longer and flatter with relatively smaller heads. By contrast, the foreflippers became conspicuously longer relative to shell length, and the effect of this could be seen in greatly increased swimming efficiency after two months growth.

## DISCUSSION

A major consideration in the feasibility of rearing hawksbills on a large scale is the method of feeding the hatchlings. Reports on the dietary preferences of hawksbills vary considerably. Both Lewis (1940) and Ingle & Smith (1949) found that they took turtle grass and algae when young, but the latter noted that later they preferred bivalves, barnacles and fish. Carr & Stancyk (1975) found adult hawksbill stomachs to contain coral encrustations, sponges, ascidians and molluscs. It seems therefore, that hawksbill turtles are fairly omnivorous. The fish meat offered during the present experiment was obtained as a by-product from a fisheries investigation. The greater weight of the captive yearlings compared with their wild counterparts suggests that this diet would be suitable for a large scale attempt to rear captive hawksbills. It seems likely that similar waste products from fish processing plants would be readily accepted by the young turtles.

The growth achieved by the experimental hatchlings compares favourably with the limited data on wild hawksbill turtles. Hornell (1927) estimated an average growth of 16.5 cm/year in the Pacific, and Kowarsky & Capelle (1979) recorded growth rates of between 8 and 10 cm/year in the Torres Straits, whilst Schmidt (1916) estimated a growth rate of about 13 cm/year. In a study on eleven captive hatchlings, Diamond (1976) obtained a growth of 17.4 cm/year, although their poor survival limited the value of his results. The majority of the captive hatchlings featured in this study had achieved this size in under six months.

With the exception of the few large wild individuals featured in this study, shell length increased relatively faster than total weight. Carr & Caldwell (1956) found a similar trend in green turtles (*b* = 2.87) and in Atlantic Ridley Turtles (*b* = 2.49). An explanation for this situation may lie in the relatively faster growth of length with respect to the other shell parameters. Carr, Hirth & Ogren (1966) found that both green turtles and mature hawksbills became longer and flatter with increased size, although Atlantic Ridley turtles remain almost circular (Carr & Caldwell, loc. cit.).

From the limited information available in the literature, it appears that the experimental hatchlings compared favourably with their wild counterparts both in their growth rates and in length/weight relationships. It remains to be seen, however, what effect the release of such yearling turtles would have upon the fecundity of wild turtle stocks. Carr, Hirth & Ogren (1966) suggest that reproductive maturity may occur when hawksbill turtles are about 36 kg in weight—possibly about six years of age. Virtually nothing is known about the movements of hawksbills in the years between hatching and their return to the original nesting area, though considerable migration distances seem to be involved. It is, therefore, impossible at present to identify the best area for releasing such artificially reared individuals, though in the present investigation the turtles were released at a site where similarly sized turtles occurred.

## ACKNOWLEDGEMENTS

The authors are grateful to the University of the West Indies for provision of research facilities at Port Royal Marine Laboratory. We should also like to thank Charles Watson and Joslyn Campbell for their valuable assistance in maintaining and feeding the turtles, and Frances Brown who first drew our attention to the nests.

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# SYSTEMATICS OF *PLATYMANTIS PAPUENSIS* (AMPHIBIA: RANIDAE) AND RELATED SPECIES OF THE NEW GUINEA REGION

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## SUMMARY

*Platymantis papuensis papuensis* is restricted to New Guinea and nearby small islands, New Ireland, and probably to New Britain.

In parts of eastern Indonesia, *P. papuensis* is represented by a small subspecies, *occidentalis*, described herein as a new taxon.

*P. schmidti* of New Britain, New Ireland and, probably, of the Admiralty Islands is a distinct species, not a race of *papuenis*.

*P. weberi* of the Solomon Islands is also a distinct species, not a race of *papuensis*.

## INTRODUCTION

Currently, 24 species or subspecies of *Platymantis* are known from the New Guinea region. Most of these occur in the Bismarck Islands (9 taxa) and the Solomon Islands (10 taxa) while only 4 occur in New Guinea or on nearby islands. Many of the species have been described in the last 20 years, in fact more species have been described since 1960 than before that time. The most recent comprehensive accounts are those of Zweifel (1969) for mainland of New Guinea spp., Brown & Tyler (1968) for those of New Britain, and Brown (1952) for those of the Solomon Islands. Other recent papers included Brown (1965), a description of three additional species and a key to those occurring in

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the Solomon Islands; Zweifel (1975), two more New Britain species and Brown & Menzies (1979), a description of one more species and a summary of the situation on New Ireland. All species, except one, are said to be restricted to either the Solomon Islands or the Bismarck Islands or to New Guinea.

The exceptional species with a much wider distribution is *Platymantis papuensis* which is said to occur in islands of eastern Indonesia (the Moluccas), through New Guinea to the Bismarck and Solomon Islands. If this is correct, then *P. papuensis* has the widest distribution of any frog species in the region in question. However, populations in the Bismarcks and Solomons have been distinguished subspecifically as *schmidti* (Brown & Tyler, 1968) and *weberi* (Brown, 1952) respectively. Brown and Tyler give a key to distinguish the three races.

Despite the recent profusion of literature, much remains to be learnt about the taxonomy of *Platymantis*. Most species have been described from small samples (sometimes as small as one) and additional material may show variation which weakens the morphometric data on which the species are founded.

Work reported herein is part of my continuing study of the frogs of the Papuan region and, in particular, results from field work in eastern Indonesia, New Guinea and archipelagos further east. Results indicate that changes to the taxonomy of what is presently regarded as *Platymantis papuensis* are required.

## MATERIAL AND METHODS

Frogs collected by myself were generally preserved in the field in isotonic formalin but supplementary morphometric data were obtained from museum specimens indicated in the text as follows: AMNH—American Museum of Natural History, New York; BMNH—British Museum (Natural History), London; RMNL—Rijksmuseum van Natuurlijke Historie, Leiden; SMF—Senckenberg Museum, Frankfurt; UP—University of Papua New Guinea, Port Moresby. Thanks are due to the curators of those museums for their assistance.

Measurements are taken in the manner of Menzies & Zweifel (1974) and abbreviations in the text are: S-V, distance from the tip of the snout to the upper margin of the cloacal opening; TL, Tar, length of the tibial and tarsal sections of the hind limb with the joints held at right angles; T3, T4, lengths of the 3rd and 4th toes measured from the proximal end of the outer metatarsal tubercle; TD4, horizontal diameter of the terminal disk on the 4th toe; F3, FD3, length of the 3rd finger from the base of the central palmar tubercle and the horizontal diameter of its terminal disk; HL, head length from snout tip to posterior margin of the tympanic membrane; HW, head width at mid-tympanic level; E-N, distance between posterior margin of the nostril and anterior corner of the eye; IN, least distance between the nostrils; E, Ty, horizontal diameters of the eye and tympanic membrane; I-D, least interorbital distance.

## RESULTS

*Platymantis papuensis* Meyer 1874
*Platymantis corrugatus papuensis*, Meyer 1874

This frog, and its subspecies *schmidti* (Brown & Tyler, 1968) and *weberi* (Schmidt, 1932) are reported to occupy the whole of an extensive region stretching from (A) eastern Indonesia, Maluku Province, through (B) mainland of New Guinea and satellite islands, (C) Bismarck Archipelago, New Britain, New Ireland, Admiralty islands to (D) the Solomon Islands from Buka south to Malaita and Guadalcanal. The taxonomic status of *papuensis* in each of these regions will be discussed in turn.

### (*A*) *Eastern Indonesia*

Collections that I made on the south coast of Serum indicated that a small *Platymantis* was common there. Using Zweifel's 1969 key, these were identified as *P. papuensis* but morphological differences lead me to establish a new subspecies.

### *Platymantis papuensis occidentalis*, new subspecies

*Holotype*: UP5258, adult male collected in July 1975 in secondary forest near Piliana, south Seram (3° 15′ S, 129° 34′ E Indonesia, altitude approximately 700 m.

*Paratypes*: UP5259–63, all adult ♂♂ collected near Piliana village and UP5264–66 collected near Rohua village (3° 38′ S, 129° 20′ E) at sea level.

*Diagnosis*: a subspecies of *P. papuensis* distinguished by its small size.

*Dimensions of the holotype* : S-V, 35.3; TL, 20.2; HL, 13.7, HW, 13.6; E-N, 3.92; IN 5.07; T, 3.28; T4, 17.0; E, 5.07; Ty, 3.28.

*Description*: dorsum plain brown, strongly barred on fore and hind limbs; parts of the thighs concealed at rest, spotted; venter plain white, yellowish posteriorily; fingers and toes with well-developed though small disks; subarticular, inner and outer metatarsal tubercles well developed; a rudiment of webbing between the toes; vomerine teeth in two small groups internal and posterior to the internal nostrils.

*Variation*: Of the eight paratypes, five are dorsally plain, 2 have light dorso-lateral stripes and one has a light mid-dorsal band, the distribution of these three morphs is in the same proportion as in mainland *papuensis*.

Dimensions are summarized in Table I.

*Field note*: all specimens were collected in secondary forest or in overgrown plantations within a short distance of villages. All were detected by their calling, heard from mid-afternoon into the evening. Judging by the amount of calling heard between Amahai and Telluti Bay and into the hills around Piliana, this frog is very common.

*Discussion*: two points require comment, the difference between the new taxon and previously described taxa and the limits of its distribution.

Four species of *Platymantis* are known from the New Guinea mainland and nearby islands (Zweifel, 1969) and three of them (*batantae*, *papuensis* and

TABLE I. Selected dimensions and ratios of ♂ *Platymantis papuensis* subspecies

| | *P. p. occidentalis* (*n* = 9) | *P. p. papuensis* (*n* = 24) |
|---|---|---|
| S-V | 33.5 ± 1.80 (31.7–35.3) | 40.6 ± 1.99 (36.9–44.5) |
| TL | 19.8 ± 0.56 (19.0–20.4) | 20.1 ± 4.43 (20.6–27.0) |
| TL/S-V | 0.59 (0.56–0.63) | 0.56 (0.52–0.62) |
| E-N | 3.64 ± 0.22 (3.34–3.92) | 4.05 ± 1.09 (3.78–4.87) |
| IN | 3.19 ± 0.18 (2.92–3.50) | 3.65 ± 1.71 (3.35–3.98) |
| E-N/IN | 1.16 (1.07–1.24) | 1.20 (1.07–1.36) |
| HL | 12.9 ± 0.75 (12.1–14.0) | 15.8 ± 0.95 (14.4–17.9) |
| HW | 12.7 ± 0.61 (11.8–13.9) | 15.4 ± 1.34 (12.6–16.7) |
| HL/HW | 1.03 (1.00–1.08) | 1.03 (1.01–1.11) |

*punctata*) occur on islands to the west of New Guinea, some 230 km N of Seram. *Punctata* has partly webbed feet, a smooth dorsum and is considerably larger (♀♀ up to 78 mm). *P. batantae* is a small species (♂♂ to 31 mm, ♀♀ to 40 mm) and so within the size range of *occidentalis* but has widely spaced nostrils (E-N/IN 1.00 or less, more than 1.06 in *occidentalis*). *P. cheesmanae* is a very small species (maximum S-V 27 mm) and is known only from the Cyclops Mts. *P.p. occidentalis* is sufficiently different from all these to need no further comparison.

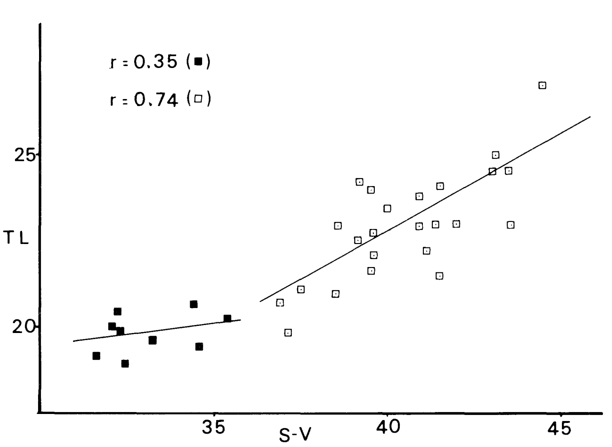

FIG. 1. Regression of tibial length on body length in male *Platymantis papuensis*. Solid squares: *P. p. occidentalis*, open squares: *P. p. papuensis*.

A random sample of 24 male *papuensis* from New Guinea (ranging from the Sepik River to the d'Entrecasteaux islands) has a mean S-V of 40.6 ± 1.99 (range 36.9 to 44.5). This is outside the range of the Seram specimens (mean 33.5 ± 1.8, range 31.7 to 35.3). A '*t*' test between samples gives a value of $t$ = 6.19, exceeding the 99% level of probability. In addition to overall size differences, *occidentalis* may also have longer hind limbs with a TL/S-V ratio ranging from 0.56 to 0.63, mean 0.59 (0.52 to 0.62, mean 0.56 in *papuensis*). These parameters are graphed in Fig. 1. However, in one case the degree of correlation is low and a larger sample would be needed to substantiate this difference.

Very little collecting has been done in eastern Indonesia and the postulated distribution of the new subspecies (Fig. 2) is based on only 26 specimens, including the 9 type specimens. Three specimens (RMNL 5322 and 5463) come from Sulabesi in the Sula group of islands, 220 km W of Seram. These are

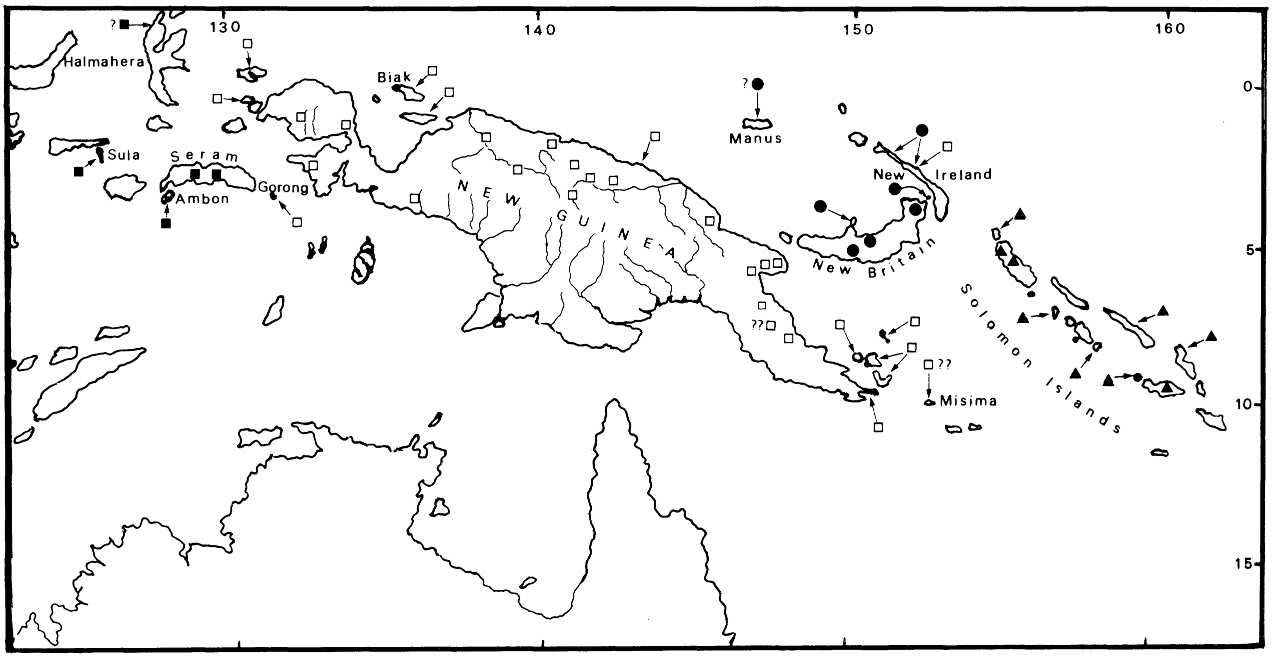

FIG. 2. Distribution of *Platymantis*. Solid squares: *P. p. occidentalis*, open squares: *P. p. papuensis*, spots: *P. schmidti*, triangles: *P. weberi*, ?: possible occurrence, ??: doubtful occurrence.

♀♀ so cannot be compared directly with the type series which are all ♂♂. Their S-V lengths are 42.0, 45.3 and 48.4 mm. Females from the mainland range from 43 to 64, mean 50 ± 4.1, so two of the Sula specimens are within the mainland range although below average. I refer these three specimens to *occidentalis*. Mertens (1930) records two specimens from Ambon but both are juvenile. There are two other specimens in Frankfurt (SMF 60521–2) and one in Leiden (RMNL 5318) from Ambon. Two are ♀♀, the other is an adult ♂, S-V 32.5. These are also *occidentalis*.

A ♂ (AMNH 6686) and two ♀♀ (BMNH 1910.4.26.70–71) from Gorong Island (= Goram Is.), 60 km SE of Seram are adult at 37.3, 53.0 and 50.6 mm. They are larger than any of the type series and well within the range for *p. papuensis*, so I refer them to the nominate subspecies. Boettger (1900) records specimens from north Halmahera (SMF 7061/65) but four of them are juvenile and less than 30 mm long. One female (S-V 29.3) has discernable ova. At this body length it is well below average for *p. papuensis*, suggesting that *p. occidentalis* occurs in Halmahera, but correct determination of the north Moluccan population must await the availability of more material.

### (*B*) *New Guinea mainland and associated islands*

The type locality of *papuensis* is Biak Island off the north west coast of New Guinea. I have heard, but not tape-recorded, the calls of *Papuensis* on that island and they sounded identical to those heard on the mainland. Zweifel (1969) has summarized distribution in this region and there are only a few points to add to his notes. Altitudinal range is from sea level to approximately 1000 m and the species is absent from the lowlands through most of southern New Guinea. However, there are two specimens (BMNH 1901.1127.151.–16), correctly identified, bearing the label "Albert Edward Ranges, New Guinea, not less than 6000′ ". This record is almost certainly erroneous, a view also expressed by Zweifel (1969). Typical *papuensis* occurs in islands of the d'Entrecasteaux group (Normanby, Fergusson, Goodenough) to the south-east of New Guinea and also in the nearby Trobriand islands but I failed to find them on Misima in the Louisiade group, further to the south-east. Occurrence in that group is based on a single juvenile specimen (BMNH 89.7.1) collected by Thomson in 1887. As, elsewhere in its range, *papuensis* is a common and noisy species and unlikely to be overlooked, the Misima record may also be erroneous. In his narrative, Thomson (1889) mentions "... a frog, *Cornufer corrugatus* (= *P. papuensis*) was met with in Sudest Island". There are, however, no specimens from that island in the British Museum or elsewhere, as far as I can determine. During the same voyage, Thomson visited Rossel, Fergusson, Normanby and Goodenough islands, in all of which, except Rossel, *papuensis* is common.

### (*C*) *The Bismarck Islands*

I have collected frogs on New Britain and on New Ireland which, using Brown & Tyler's 1968 key, I identified as *P. papuensis schmidti*. However, I have pointed out that gross differences in call structure between mainland *papuensis* and Bismarck *schmidti* justify their being considered as distinct species (Menzies, 1982). Brown & Tyler distinguish *schmidti* from *papuensis* by larger finger disks, probably a reflection of its more scansorial habitat, for I have found males climbing into vegetation one meter or more above ground level. The possibility of other morphological differences was considered worth investigating and are described in more detail in the next section. Results supported the elevation of *schmidti* to specific rank.

In central New Ireland, in relatively undisturbed forest above the coastal plain, I collected a single male *papuensis*, identified by its call (Menzies, 1982); many others were heard calling nearby. Thus *papuensis* and *schmidti* are sympatric in this part of New Ireland, at least. In much of northern New Ireland the soil is dry and derived from coral rubble and there is a lack of surface water. In the locality where the *papuensis* was collected, on a hillside above Lamerika plantation, the soil consisted of a wetter clay and the atmosphere near ground level noticeably more humid. It is tempting to suppose that *papuensis* prefers a moister habitat and so is absent from much of New Ireland unlike *schmidti* which appears to tolerate relatively dry conditions.

Distribution of the two species is shown in Fig. 2. It seems unlikely that *papuensis* is absent from New Britain, in view of its occurrence in New Ireland but this must await the availability of more field data.

### (*D*) *The Solomon Islands*

*Platymantis weberi* Schmidt was reduced to a subspecies of *papuensis* by Brown (1952) while Brown & Tyler (1968) distinguished it from *papuensis* by its slightly larger size (females are immature while less than 50 mm S-V) and more numerous, narrower and more elongate skin folds on the dorsum. To investigate the extent of morphological divergence between *papuensis*, *weberi* and *schmidti*, a small sample of females of each taxon were run through a discriminant analysis programme (Klecka & Tuccy, 1975) using 15 body parameters (S-V; TL; Tar; T3; T4; TD4; F3; FD3; HL; HW; E-N; IN; E; Ty; I-O). The stepwise analysis enabled rejection of variables which did not contribute to discrimination; in this way, 11 of the original 15 variables were included in the final analysis and four (S-V; TL, IN; E) rejected. The first discriminant function accounted for 88% of the between-groups variance and greatest weight in this axis was given by characters FD3, F3, HL and HW. TD4 contributed significantly to the second axis confirming that digital disk size is important in distinguishing these three species. Body size did not enter into the final analysis and the skin fold character used by Brown & Taylor was not amenable to quantification so could not be included.

Results of the analysis are shown in Fig. 3. In all cases, distances between group centroids are highly significant ($P < 0.01$). There is no longer any justification for regarding the three taxa as subspecies of *papuensis*. Additionally, *weberi* does not appear to

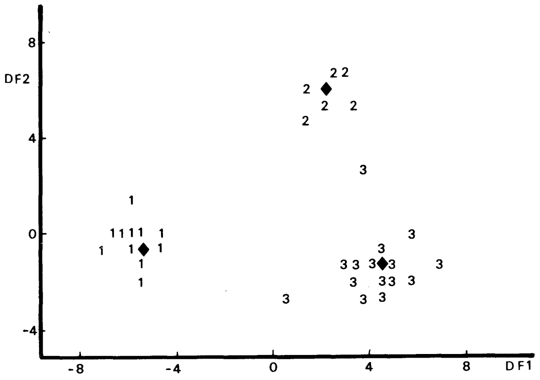

FIG. 3. Discriminant analysis. 1: *P. p. papuensis*, 2: *P. schmidti*, 3: *P. weberi*. Star symbols show group centroids.

be the ecological equivalent of *papuensis* or *schmidti*, which are abundant in plantations, gardens and similar lowland habitats. The common *Platymantis* in this type of habitat in the Solomon Islands is *solomonis* and I am told (Parker, personal communication) that *weberi* is restricted to higher altitude forests.

Removal of *weberi* and *papuensis* now means that only a single species of amphibian occurs in New Guinea *and* in the Bismarck Islands *and* in the Solomon Islands. This one is *Litoria thesaurensis*.

## ACKNOWLEDGEMENTS

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# THE VOICES OF SOME MALE *PLATYMANTIS* SPECIES OF THE NEW GUINEA REGION

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## INTRODUCTION

*Platymantis* species form an important component of the ranid fauna of islands to the east of New Guinea. Together with the common *Platymantis papuensis* of mainland New Guinea and islands to the west they have been the subject of a recent profusion of literature in which, in the last 20 years, some 13 new species or subspecies have been described. Despite this, relatively little is known about the natural history of these frogs and only in the case of mainland *papuensis* are any extensive ecological data recorded (Zweifel, 1969).

In the New Guinea situation, where sibling species are often difficult to distinguish on morphological features (Menzies & Zweifel, 1974), ecological and behavioural characters may be particularly important. The present paper records the male vocalization patterns of five species. As a result of this study, two taxa hitherto distinguished only at the subspecific level are shown to merit specific distinction.

## MATERIAL AND METHODS

This work is based on frogs collected by myself and recorded in the field with a Sony portable tape-recorder. Calls were subsequently analysed with a Kay Elemetrics Company sonagraph and, after reduction to 1/64th normal speed, on an oscilloscope. All specimens referred to are now in the museum of the Biology Department of the University of Papua New Guinea (UP), with the exception of specimens of *Platymantis papuensis* from Seram, Indonesia, which have been deposited in the Museum Zoologicum Bogorensis, in Java.

## RESULTS

The calls of five species of *Platymantis* are described here. They show some similarity in structure, suggesting their recent common origin. In each case the call consists of a series of phrases containing one to many notes. There is a tendency for the calling frog to commence with isolated notes at fairly long intervals, thereafter phrases increase in length and the call ends with a long series of notes. There is an inverse relationship between the number of notes in a phrase and the length of intervals between notes ($r = -0.59$ for *P. schmidti*). There is usually a relatively long pause between calls.

As far as is known, all *Platymantis* species are terrestrial or arboreal and have a direct life cycle without a larval stage. In common with other frogs showing this type of life cycle, they do not form breeding aggregations and the call of the male frog is probably as much territorial as a female-attractant (Zweifel, 1969). In four of the five species recorded, individual notes have a common structure, each consisting of three syllables. The first of these is pulsed and contains a number of different frequency bands which are not harmonically related and are best described as white noise. The second syllable is not pulsed but does have a well-marked harmonic structure, with the first harmonic dominant. Frequency rises through this syllable but amplitude is more or less constant. The third syllable is a mirror image of the second, with a descending frequency. This structure is best seen in *papuensis* (Figs. 1 and 3A) and *magnus* (Figs. 3D and 3C). Call parameters are summarized in Table I.

TABLE 1. Call parameters of *Platymantis* species. Times are in ms. Mean note length includes intervals, if any, within the note. Mean syllable lengths do not include intervals

| Species | Maximum notes/phrase | Mean note length | Interval length (mean and range) | Mean syllable length 1 | 2 | 3 |
|---|---|---|---|---|---|---|
| *papuensis* (New Guinea) | 48 | 76 | 130 (80–270) | 33 | 17 | 24 |
| *papuensis* (Seram) | 12 | 60 | 190 (150–250) | 14 | 26 | 19 |
| *schmidti* | 25 | 60 | 90 (30–120) | 55 | 11 | 7 |
| *magnus* | 12 | 170 | 360 (250–520) | 25 | 91 | 89 |
| *solomonis* | 5 | 230 | 700 (450–1100) | 178 | 66 | 90 |
| *neckeri* | 6 | 120 | 190 (150–230) | — | 92 | 87 |

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*Platymantis papuensis* (Figs. 1 and 3A)

The call has been described by Zweifel (1969) who divides individual notes into two "components". Zweifel's first "component" equates to the first "syllable" in my terminology while his second "component" equates to my second and third "syllables".

There is less variation throughout the extensive range of this species (from the Moluccas in eastern Indonesia to the d'Entrecasteaux islands to the east of New Guinea) than there is between individuals in any one area. However, the frogs in the Moluccas show a slightly higher dominant frequency (2.5 rising to 3.0 kHz) than those on the mainland or New Ireland (2.0 rising to 2.8 kHz). Within the limits of the sample available, the Moluccan frogs appear to have a more structured call with a steady increase in notes per phrase as the call progresses. Notes are comparatively short but the number of notes per phrase may be as high as 40 or more.

The first syllable of each note includes up to eight pulses of white noise without interval and merging without pause into the unpulsed second syllable. Commencement is explosive and amplitude more or less constant throughout. Sonagrams (Fig. 1) show the pulsed structure clearly but pulses are too close together to show in the oscillogram (Fig. 3A). The note is damped and ends quickly.

Acoustic impression of the call is like the word "quick" repeated rapidly. Frogs may call from the ground or may climb onto boulders, logs, etc. a little distance above ground level. Calling takes place mainly at night but, in dull weather, frogs start to call in mid-afternoon.

*Platymantis schmidti* (Figs. 2A, B and 3B)

Basic call structure is much as in *papuensis* but individual notes and intervals between notes may be very much shorter. The first syllable consists of a single pulse separated from the rest of the note by a distinct gap. In fact, this pulse may be more or less equidistant from the preceding note. Syllables two and three occupy no more than 10 ms and may (Fig. 2B) or may not (Fig. 2A) be distinguishable. Though frequency rises and falls as in *papuensis*, duration is so short that the note is little more than a succession of double clicks. The first harmonic carries most energy, around 3 kHz. Notes are damped and fade quickly and, as in *papuensis*, number of notes per phrase may be high.

Calling frogs are usually stationed on the ground but may climb onto rocks, or even into vegetation one metre or more above ground level. The call lacks any musical quality and merely sounds like a stick being rubbed along wooden railings.

This taxon was previously known as *Platymantis papuensis schmidti* Brown & Tyler (1968). Differences in call structure described above suggest an effective premating isolating mechanism and the possibility of interbreeding with *papuensis* (on New Ireland and probably New Britain where they are sympatric) seems unlikely. Therefore I propose the new combination *Platymantis schmidti* Brown & Tyler.

*Platymantis magnus* (Figs. 2D and 3C)

Individual notes are much longer than in the preceding species (up to 250 ms) and it is rare for a phrase to contain more than 12 notes. The first syllable may contain up to eight or ten pulses of increasing amplitude, clearly distinguishable from one another. Syllable 2 follows without pause but its unpulsed structure renders it distinct. However, this syllable is broken into a number of irregular segments; this irregular structure best shows in the oscillogram (Fig. 3C). Syllable three commences with increased amplitude but fades over a comparatively lengthy period.

Altogether, this is a more "ragged" call than that of *papuensis* or *schmidti*, individual notes being less clearly defined and crisp. The acoustic impression is rather like the yelping of a young puppy. Frogs usually

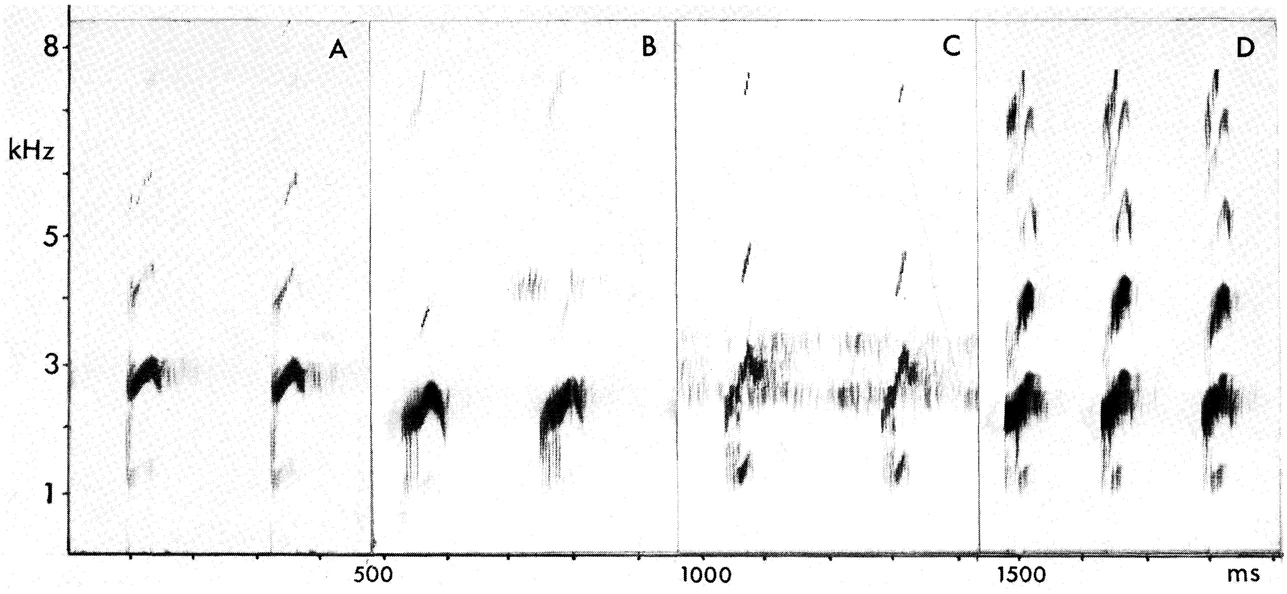

FIG. 1. Sonagrams of calls of *Platymantis papuensis*. A—frog UP5258, Piliana, Seram, no temperature data; B—frog UP3687, Lae, 25°C; C—frog UP5408, Goodenough Is, 27°C; D—frog UP5623, near Lamerika, New Ireland, 30.5°C.

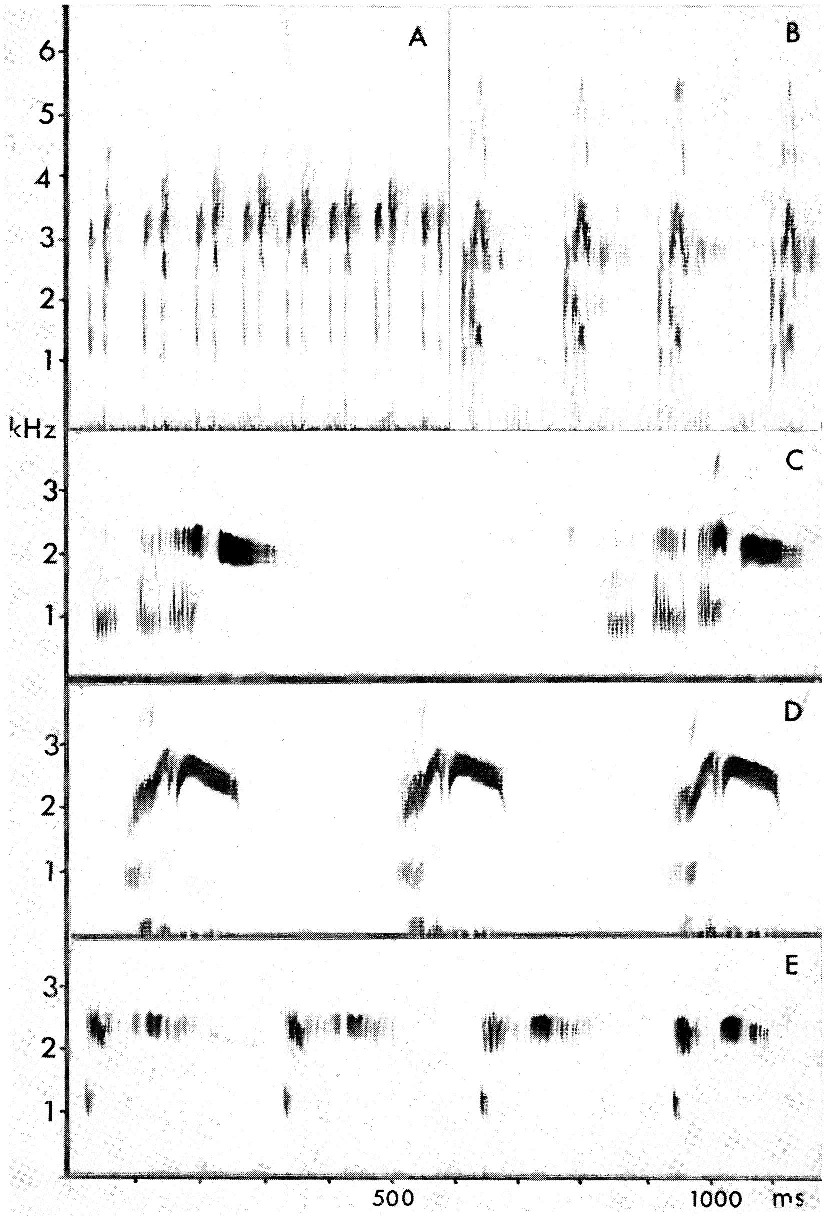

FIG. 2. Sonagrams of calls of *Platymantis* species. A—*P. schmidti*, frog UP1114, Kerevat, New Britain, no temperature data; B—*P. schmidti*, frog UP5648, Madina, New Ireland, 26.5°C; C—*P. solomonis*, frog UP5834, Panguna, Bougainville Is., 22.5°C; D—*P. magnus*, frog UP-, Madina, New Ireland, 25°C; E—*P. neckeri*, frog UP-, Panguna, Bougainville Is., no temperature data.

call from the ground, more rarely they climb onto rocks and tree stumps.

### *Platymantis solomonis* (Figs. 2C and 3D)

The tendency shown in *magnus* for individual notes to be elongated and disrupted is exaggerated in *solomonis* and it is now difficult to distinguish between syllables one and two. The pulsatile part, with pulses in groups of three to ten, lasts for nearly 200 ms, while the unpulsed syllable is only half as long. Syllable three is unchanged but amplitude fades over an extended period. Gaps within notes give them an overall length of nearly 400 ms, longer than in any other species recorded. Dominant frequency, the second harmonic, is about 2 kHz but because of the extended pulsatile component, the rise in frequency is not clear.

The call of *solomonis* is even more "ragged" than that of *magnus* but the acoustic impression is much the same, though with a wavering quality. Frogs usually call from the ground.

### *Platymantis neckeri* (Figs. 2E and 3E)

This species is arboreal and may call from a considerable height in forest trees, making accurate recording difficult. The structure of the notes graphed here is less clear than those of the previously described species and no part appears to be pulsatile, so that syllable one is absent. Syllable two consists of an

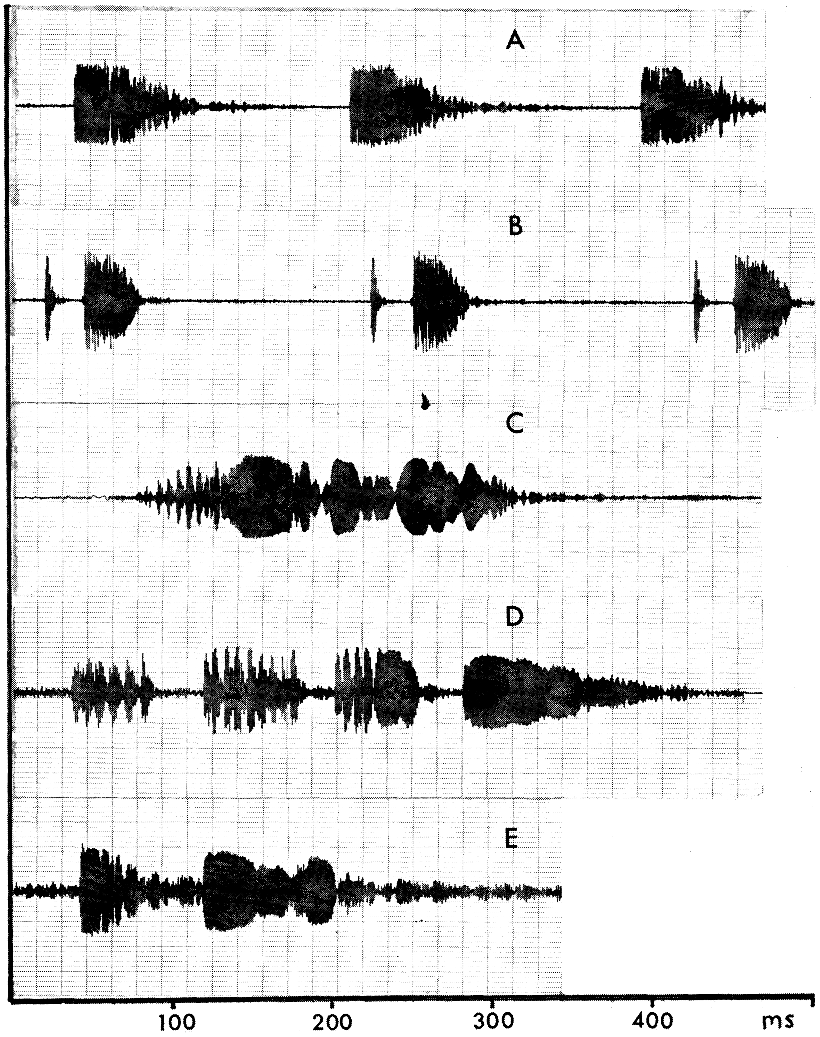

FIG. 3. Oscillograms of calls of *Platymantis* species. A—*P. papuensis* (data as ID); B—*P. schmidti*, frog UP5641, Madina, New Ireland, 25°C; C—*P. magnus* (data as 2E); D—*P. solomonis* (data as 2C); E—*P. neckeri* (data as 2E).

unpulsed segment about 100 ms long but includes a pause. Signals of low amplitude in this pause may be part of the call or, more probably, artifacts of recording. Syllable three has a similar duration and its wavering amplitudes may also be an artifact as it does not appear in the acoustic impression. The end of the note is effectively damped and note length and note interval are more or less equal.

The call has a ringing, metallic quality not heard in other species. Acoustic impression is of a small anvil being struck in regular rythm.

## DISCUSSION

If it is assumed that the most highly structured call is the most advanced, then clearly that of *solomonis* with its extended pulsatile component and lengthy fade is the most primitive. Based on this assumption it is postulated that the ancestral *Platymantis* call was fully pulsatile with the pulses in regular sequence. Clustering of pulses into discrete groups would permit some interspecific variation while further contraction would lead to loss of the pulsed structure through all or part of the note and result in the development of distinct syllables.

The call of *magnus* may be derived from that of *solomonis* by reduction of the first, pulsed syllable. As these two resemble one another morphologically (Brown & Menzies, 1979) it is suggested that *magnus* derived from *solomonis* after isolation in New Ireland. The two calls give a very similar acoustic impression but as the species are allopatric, no question of confusion could arise. The calls of the two terrestrial species, *papuensis* and *schmidti*, show further reduction of the pulsed syllable. These two species are sympatric in New Ireland (and probably in New Britain) and their calls are very similar in structure. However, comparatively small differences give them a totally different acoustic impression.

The call of *neckeri* is rather different from the other four species in that the first, pulsed, syllable has disappeared altogether. This may be connected with an arboreal, rather than terrestrial habitat or perhaps the call has been derived by a different evolutionary pathway. *P. neckeri* is one of the species formerly included in the genus *Cornufer* (see Zweifel (1969) for a discussion of the validity of the genera *Platymantis* and *Cornufer*) which includes arboreal, large disked species. In default of knowledge about the calls of other arboreal *Platymantis* it is impossible to speculate further about the evolution of this group of species.

Whether the male call is a female attractant or a territorial signal is immaterial as, in either case, it must give information as to species and location. Frequency differences are often determined by body size rather than species (Menzies & Tyler, 1977) so specific information may be given by modification of temporal call parameters (*i.e.* the shape of the "envelope" in an oscillogram). Orientation may be given by recognizing changes in phase, amplitude or time-of-arrival at left and right ears (Marler, 1967) but in the acoustically confused conditions of the forest floor it is possible that the first two methods are unsatisfactory. Time-of-arrival orientation requires short concise notes, rapidly repeated, somewhat contradicting the need for a lengthy species-identifying signal. Some frog species appear to have overcome this problem by uttering a two-part call, the first signal serving to alert conspecifics, the second to orientate them. *Platymantis* species may have achieved the same object by uttering single notes at fairly long intervals, for recognition, followed by rapidly repeated notes in lengthy series, for orientation. Clearly the calls of *papuensis* and *schmidti* would be superior in this respect to the less well defined notes of *magnus* and *solomonis*.

The call of *neckeri* does not appear to follow the same pattern as notes are uttered in consistent 6-note series rather than short series followed by long series. As its short concise notes offer satisfactory orientation, it is possible that recognition is less important in an arboreal habitat where few spp occur.

## ACKNOWLEDGEMENTS

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# RELOCATION OF THE LIZARD *LACERTA AGILIS*: AN EXERCISE IN CONSERVATION

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## SUMMARY

During August 1976, 30 sand lizards (*Lacerta agilis*) were removed from a heathland National Nature Reserve. A few days before this most of the Reserve had been destroyed by a fire and about 800 lizards were killed. A specially designed vivarium was later constructed on an unburnt part of the Reserve and lizards were released in the vivarium during 1978. The objective was to return the lizards to the Reserve, using a controlled method, and assist the natural recolonization process. Three years later (in 1981) the vivarium had a small breeding population of sand lizards.

## INTRODUCTION

In Britain, the sand lizard, *Lacerta agilis* L. is restricted to southern counties and an isolated population in the north-west of England. Although locally abundant in the south, it is limited, by ecological requirements, to relatively undisturbed areas of heathland and marginal land. A species which is on the edge of its geographical range in U.K., and threatened by many factors (Spellerberg, 1975), it is included in the list of endangered species in the 1981 Wildlife and Countryside Act.

The National Nature Reserves in southern England provide some of the few remaining habitats for the sand lizard. During August of 1976 an intense heathland fire destroyed more than 70% of a 258 ha National Nature Reserve in Dorset. This Reserve was known to contain suitable habitats for the sand lizard but sadly the fire completely destroyed all known sand lizard habitats—apart from a few small potential habitats near the perimeter of the Reserve. It had been established that prior to this fire, about 800 sand lizards were on the Reserve (Moore, 1976). A thorough search of the vast area of burnt heathland was undertaken during the two weeks following the fire and 30 live sand lizards were found and removed from the Reserve (Spellerberg, 1977). It seemed unwise to liberate these lizards in the small fragmented areas of heathland which had been untouched by the fire because it was not known at that time if these small areas were suitable for sand lizards. With most of the heathland vegetation destroyed, shelter was reduced, the difficulty in finding sufficient food increased and the lizards were at a greater risk from predators. During the following spring, an examination of the same area revealed a further five emaciated sand lizards that had died near burrows, suggesting that conditions for survival after the fire were not suitable for the lizards.

With the agreement of the Nature Conservancy Council, the lizards were kept in a temporary vivarium pending discussions on how to proceed. It was later decided that in order to preserve the inherent genetical characteristics of the population, the animals should all be returned to the Reserve when plant communities had become re-established and provided suitable habitats. Following a previous but less severe fire on the same Nature Reserve in 1959, the sand lizard had regained good populations by 1973. It was expected, therefore, that suitable vegetation would not be available for several years after the 1976 fire. If the lizards were to be kept in captivity for this length of time, any genetical advantages gained in keeping them and their progeny together, would be lost.

Acting within the accepted principle that each animal should be replaced as near as possible to the original site, it was originally suggested that the lizards be marked and released on the Reserve and subsequent movements noted. It would, however, have been difficult to make an adequate investigation of this sort and useful information about these animals may have been lost. Lizards placed in any of the isolated fragments of unburnt heathland would have no doubt dispersed and found difficulty in surviving without protective cover of the vegetation.

Instead, it was agreed with the Nature Conservancy Council that the lizards should be enclosed within one area of the Reserve and released at a later date when the surrounding habitat became more favourable. The enclosure, or vivarium, would act as an intermediate stage where lizards would be safeguarded and fed if necessary. This step-by-step procedure was an attempt to aid the re-colonization process and was the main objective.

A second objective was to investigate the ecological needs of the lizards, bearing in mind that an enclosed area might not enable the population to be entirely self-sufficient. The conditions provided in the vivarium were based on those outlined by Spellerberg (1975). The sand lizard's use of the vivarium was observed and this information contributed to a long-term analysis of sand lizard habitat (House & Spellerberg, 1980). The project was an exercise in experimental design for man-made habitats which could be employed in the practical conservation of the sand lizard and other wildlife species.

## METHODS AND MATERIALS

An investigation of possible sites for the vivarium took place in March 1978. Criteria used for the selection of the site included the following: an area of unburnt heath; diverse plant species composition and structure; suitable topography to maximize insolation; environs suitable for recolonization of the lizards if and when they were released. Four potential sites within the Reserve boundary were carefully examined and one of these was selected for the vivarium. The chosen site was in an area of over 3 ha of unburnt heathland and surveys had shown that there were a few sand lizards in the area.

The vivarium (18 × 30 m) was sited on a south-facing and free-draining slope of about 15°. Details of materials used and costs involved have been included in a detailed report to the Nature Conservancy Council. The area was enclosed with corrugated plastic sheets bolted firmly together so that the corrugations ran vertically. The plastic was placed 30 cm into the ground with about 100 cm above ground. Individual sheets of plastic (0.6 m wide), were bolted together. At every alternate join, the two sheets were nailed to a wooden stake driven firmly into the ground. The vivarium corners were re-inforced with larger posts.

Nine larger posts were placed inside the vivarium to support netting which covered the whole structure and protected lizards from predatory birds. The large posts (2–3 m high) supporting the netting enabled easy access to the central area of the vivarium. Aluminium strips were placed near the top of each supporting stake in order to prevent the lizards from climbing out.

In order to provide suitable conditions for the lizards during their period of winter dormancy, it was necessary to construct three "overwintering sites" (Fig. 1). Each "overwintering site" consisted of a shallow depression (2 m × 1.5 m × 30–40 cm deep) filled with peat, sand and gravel. A drainage channel was provided in each site. Peat, logs, straw and sand was then placed on each site, resulting in a mound of material about 40 cm high. A glass covering was then placed on each mound (to prevent too much water entry) and the whole structure was covered with turfs incorporating live plants, mainly *Calluna vulgaris*.

It had been noted during extensive field research that lizards readily bask on logs and stone surfaces. In addition, most basking sites appeared to be on the interface between vegetation types of low and high profiles (House & Spellerberg, 1982). To accommodate these apparent preferences, several large logs and concrete slabs were placed in the vivarium. These generally coincided with an interface between heather

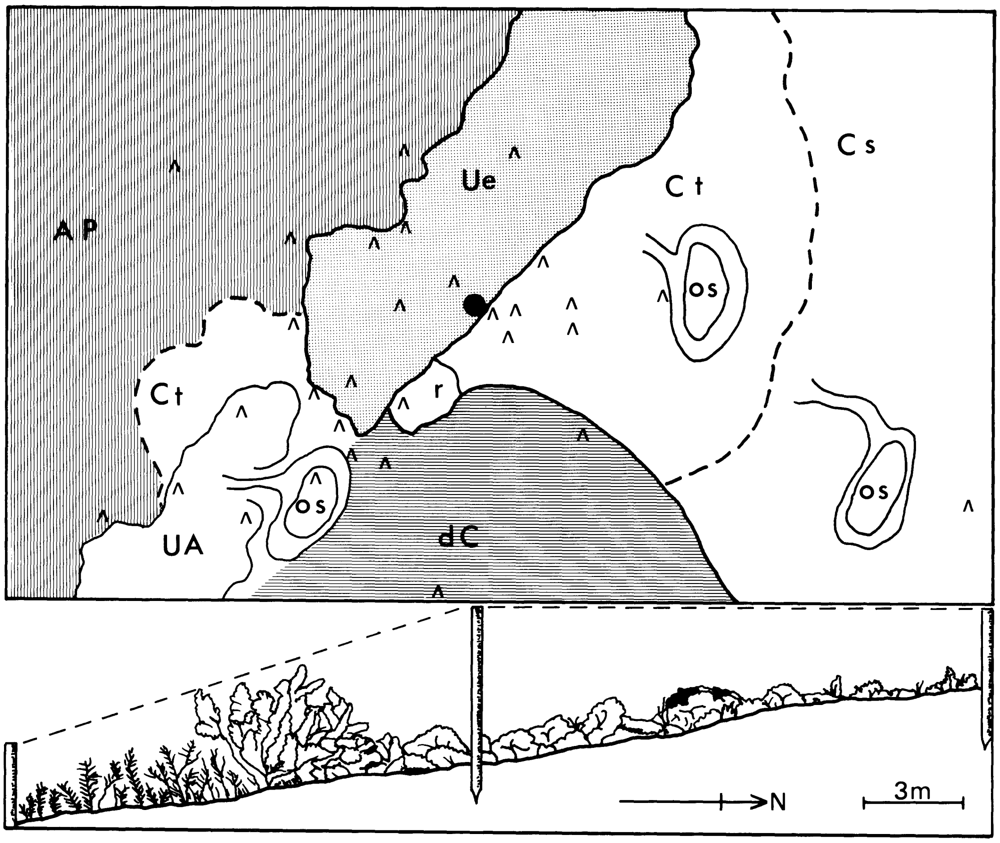

FIG. 1. Plan and cross section diagram of the vivarium. ● centre post. Λ position of a sand lizard when first seen (see text). OS overwintering site. Cs *Calluna* less than 30 cm tall. Ct *Calluna* more than 30 cm tall. Ue *Ulex europaeus*. AP *Agrostis* and *Pteridium*. UA *Ulex* and *Agrostis*. dC degenerate *Calluna*. r Rockery. The posts and vegetation in the cross section are not drawn to scale.

and gorse or heather and grass so that each basking site was associated with adequate cover.

The area enclosed by the vivarium contained a good variety of plant species, typical of the sand lizard habitat (House & Spellerberg, 1982). Five distinct vegetation zones were recognized (Fig. 1). *Calluna*-dominated vegetation; *Calluna* in a degenerate phase; gorse (*Ulex europaeus*); grass (*Agrostis* and *Festuca*); bracken (*Pteridium*).

## RESULTS AND DISCUSSION

The 30 lizards taken from the burnt areas of the reserve were initially kept in a small temporary enclosure. By 1978 there were 9 males and 7 females surviving. Some lizards had died, probably as result of burns received during the heathland fire. The male lizards were released in the vivarium during June of 1978, the females 4 weeks later. Each lizard could be individually recognized from skin colour patterns on its throat and dorsal region.

The vivarium was visited at least once every two weeks until September, then again during April and May of 1979. Eight males and five female lizards survived the 1978–79 winter and were first seen in the vicinity of the overwintering sites. Mating was observed during April 1979 and newly hatched lizards were seen in the vivarium during October of that year.

On each of five days during April and May of 1980, the location of each lizard, when first sighted, was recorded. The combined results indicated that the lizards were more often found (during April and May) in the central parts of the vivarium. Subsequent day-long observations showed that the lizards utilized all four vegetation zones in the vivarium. On each occasion when the vivarium was visited, there appeared to be an abundance of prey items. Lizards were frequently seen taking spiders, particularly *Pardosa* sp. (Lycosidae). During September of the same year, two further visits resulted in the sighting of nine newly-hatched lizards.

Five newly hatched lizards were seen during a visit to the vivarium in October 1981. On the same occasion five adult males and three adult females were recorded. It was evident by this time that the habitat in the vivarium supported a small breeding population of sand lizards. Consequently, a decision had to be taken, whether or not some lizards should be moved from the vivarium to suitable areas on the Reserve. Ideally it was important to first establish precisely how many lizards (adults and sub-adults) were in the vivarium, and also to evaluate the condition of the regenerating heathland on the Reserve. During October and November of 1981, efforts were made to determine the number of lizards in the vivarium. It proved impossible to survey the lizards without entering the vivarium and the exercise was eventually abandoned when trampling threatened to damage the vivarium vegetation. It was unfortunate that a precise count of the lizards could not be achieved but nevertheless a decision was taken to release immediately four sub-adult lizards, and a similar number in subsequent years.

By October 1981, five years after the fire, a general survey of the Reserve showed that recolonization and regeneration process by ericoid species was proceeding slowly. Recolonization is probably mainly from seed. An on-going survey (Roger Daniels personal communication) of the rate and extent of recovery after the fire has confirmed that recolonization by *Calluna* and other ericoid species has not been rapid. In the area where the original 30 sand lizards were found, the survey by Daniels has shown that by September 1980, percentage cover by *Calluna* ranged from zero to 71% (mean of 33% for 23 sampling sites, each of 1 m radius). To date (February 1982) there has been no noticeable change in the heather recolonization. A further setback in the recolonization process has been attributed to damage caused by the heather beetle (*Lochmaea saturalis*).

There are as yet few suitable areas on the Reserve which could confidently be used for the relocation of the sand lizard. By contrast, the 3 ha of unburnt heathland surrounding the vivarium, together with at least two further and adjacent hectares of rapidly regenerating heathland, seemed suitable for relocation. The vegetation on this area of the Reserve will continue to enlarge so therefore it seemed logical to adopt the policy of releasing each year a few sub-adult lizards in the vicinity of the vivarium. Within one or two years it may be considered safe to release all lizards in the vivarium. This being the case, then part of the vivarium wall would be removed so as to allow the lizards to disperse naturally.

It might well seem that unnecessary time and effort has been directed towards the conservation of so few lizards. Taken in isolation, this exercise in practical conservation may indeed seem trivial but when considered in relation to the number of lizards that perished in the fire, and also in relation to the apparent dwindling number of sand lizard colonies, then the value of this exercise becomes evident. Previous attempts to relocate the sand lizard or introduce it to areas outside its existing distribution, have met with little success. Since at least 1949, sand lizards have been taken from areas of southern England and relocated to what seemed suitable sites further north (Bunting, 1950; Allen, 1973; Arnold, 1973; Prestt *et al.*, 1974; Spellerberg, 1976). Vivaria were not used in these cases at the relocation site, and dispersal of the lizards would have occurred very quickly. There seems no doubt that relocation of these reptiles (and perhaps other species) should be attempted only if the dispersal of the relocated animals can be prevented. With the restricted movement of the animals, however, it is necessary that sufficient food, shelter, and other resources be provided.

The vivarium, together with an additional similar vivarium built by the Nature Conservancy Council, will be maintained for future occasions if and when relocation of sand lizards becomes necessary.

## ACKNOWLEDGEMENTS

The Nature Conservancy Council generously provided the finance and encouragement for this project. We would also like to thank Miss P. J. Taylor, Mr A. P. N. House and Mr N. D. Smith for their help during the construction of the vivarium.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 249–252 (1982)

# POPULATION AGE-STRUCTURE OF THE COMMON TOAD (*BUFO BUFO*) AT A LAKE IN MID-WALES DETERMINED FROM ANNUAL GROWTH RINGS IN THE PHALANGES

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## SUMMARY

The youngest age at which toads came to breed was two years for males and three years for females, but not all individuals of an age class may reach maturity at the same time.

The maximum age reached in the wild in the sample studied was five years for males and eight years for females.

There was no relationship between age and length, suggesting that linear growth is insignificant after a toad has reached sexual maturity.

## INTRODUCTION

One of the major obstacles to a fuller understanding of the population dynamics of the common toad (*Bufo bufo*) has been the lack of information on the age distribution within a population. Recently Hemelaar & van Gelder (1980) and Hemelaar (1981) have described a method for aging toads using the growth rings in bone that result from different rates of bone growth between the summer feeding periods and the winter hibernation periods. The growth rings consist of relatively broad layers of periosteal bone, separated by narrow resting lines which represent the hibernation period. Normally only one growth ring and one resting line are formed each year, the combination being termed a year ring, and the number of year rings represents the age of the toad.

The age of some individuals may be underestimated, however, as a result of resorption of some of the initial year rings. Smirna (1972) stated that commonly two lines were resorbed in the common frog (*Rana temporaria*) but, in a study specifically to determine the degree of resorption in the toad, Hemelaar (1981) found no resorption in 85% of specimens studied and partial resorption of the first ring in 9%, although these lines were still discernible. Thus, it was possible to age about 94% of the toads from the number of year rings, and this percentage could be raised to 98% by considering the pattern and width of year rings. The age of the remaining toads may be underestimated by not more than one year.

The present study utilized the method of Hemelaar & van Gelder to determine the age distribution within a population of the common toad at a lake in mid-Wales which has been studied for a number of years (Gittins, Parker & Slater, 1980; Wisniewski, Paull, Merry & Slater, 1980; Wisniewski, Paull & Slater, 1981; Paull, Wisniewski & Slater, 1981).

## MATERIALS AND METHODS

Toads were collected during the 1981 breeding migration to the lake, a description of which is given in Gittins *et al.* (1980). Toads were killed by traffic as they crossed the road surrounding the lake, resulting in 31 male and 20 female corpses being available for study. The corpses were collected each night and stored at −20°C for several months. Immediately before processing, each toad was thawed and placed in 70% alcohol. The snout-vent length of each specimen was measured along the spine.

The method used for determining the age of each toad was essentially the same as that described by Hemelaar & van Gelder (1980). A forelimb was removed, boiled in tap water for 30 mins to remove skin and muscle, and placed in Gooding and Steward's decalcifying fluid overnight (Carleton & Short, 1954). After decalcification, a single bone was selected from a phalange, freeze-mounted, and sectioned on a freezing microtome. Sections 20 $\mu$ thick were taken from the central region of the diaphysis, as growth rings were absent or incomplete in the epiphysis (Hemelaar & van Gelder, 1980). The sections were stained in Ehrlich's haematoxylin for 30 mins, washed in tap water, and mounted in D.P.X. (Phillip Harris Ltd). Sections were examined under a Zeiss light microscope at ×100 magnification, the haematoxylin staining the growth rings pink to light purple, and the resting lines dark purple (shown in monochrome in Fig. 1). The age of each toad was determined by counting the number of darkly-stained resting lines, and as these specimens were collected during the breeding season, before any current-year's growth had occurred, the outer margin of the bone was regarded as an additional resting line (Hemelaar & van Gelder, 1980).

## RESULTS

In all the sections of the phalanges prepared, the resting lines were distinct and easily counted. However, no attempt was made to allow for resorption, so the age

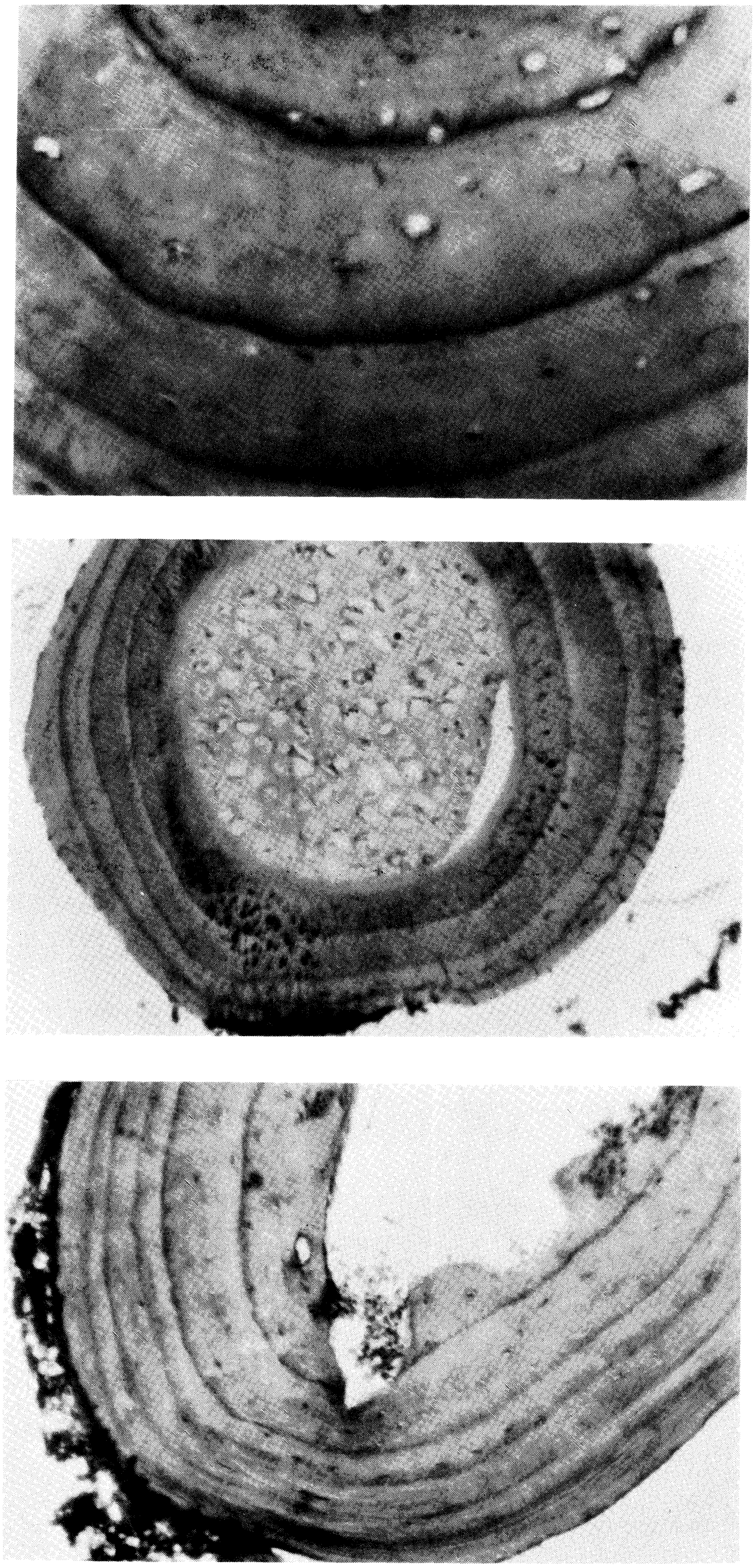

FIG. 1. Cross-sections of phalanges showing annual growth rings. *Top*—close-up showing details of growth rings and resting lines; *middle*—4 year old toad; *bottom*—6 year old toad.

of some of the individuals could be underestimated by one year (Hemelaar, 1981). As will be seen later, this level of inaccuracy in the data does not obscure the major findings of the study, although in future studies allowances should be made for resorption, as suggested by Hemelaar.

The corpses in this study can be taken to represent a random sample from the adult population breeding at the lake, allowing age-frequency distributions to be constructed for the population during 1981 (Fig. 2). As the population size at the lake has remained constant for at least the last four years, this distribution should approximate a stable age distribution for the adult breeding population (Odum, 1971). The youngest age at which males came to breed was two years, and for females three years. The oldest male found in the sample was five years old and the oldest female eight years. In a stable population it would be expected that the distribution for both males and females would show a fairly steady decline from maximum numbers at the first year of breeding until the oldest age group. Thus the increase in numbers between age two and three year old males and between three and four year old females is counter to expectation, and this point will be raised in the Discussion.

No significant regression was found between length as a function of age for males or females (Fig. 3). Even allowing for the under-estimation of the age of some individuals, there is clearly a poor relationship between length and age, and some of the smallest toads were, in fact, the oldest.

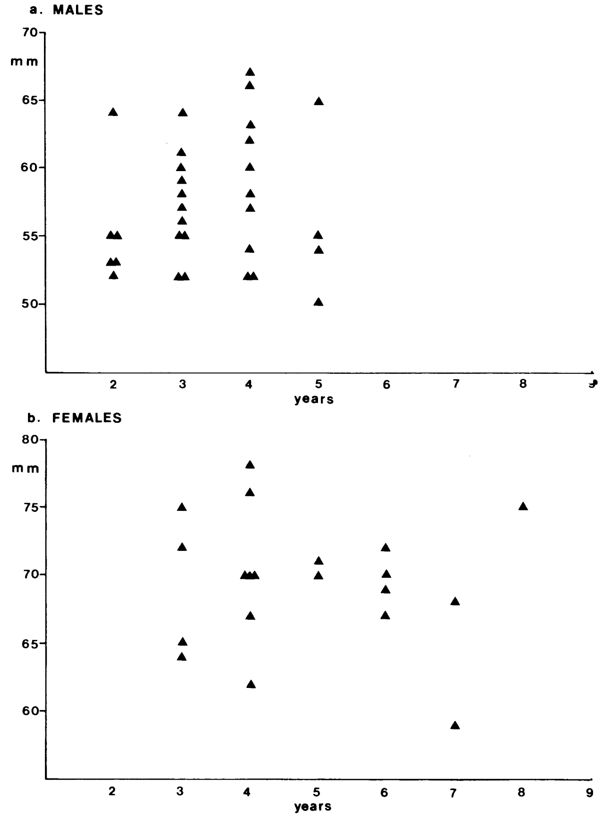

FIG. 3. Length as a function of age for male and female toads. No significant regression was found between length as a function of age for males (F = 0.6, $P > 0.05$) or females (F = 0.1, $P > 0.05$).

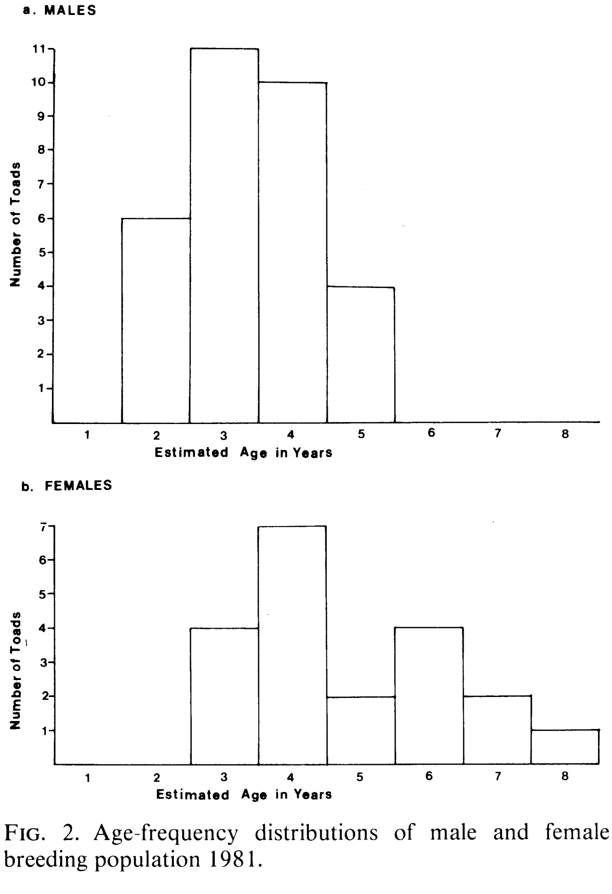

FIG. 2. Age-frequency distributions of male and female breeding population 1981.

## DISCUSSION

The oldest male found in this study was five years old, the oldest female was eight years. These findings are based on rather small sample sizes, and sampling the entire population would undoubtedly produce a few individuals older than these limits. The oldest individual found by Hemelaar & van Gelder (1981) in a sample 89 toads was ten years old. Thus, although toads can reach ages of 40 years or more in captivity (Smith, 1973) the implication of the above finding is that few toads survive beyond about ten years of age in the wild.

The youngest age at which males and females bred was two and three years respectively. In a stable adult population, it would be expected that the mximum number of individuals would be found in the first year of sexual maturity, with a steady decline until the oldest age group. The results of this study, however, show an increase in numbers between the two and three year old males, and the three and four year old females. This could be the results of sampling error as a result of the small sample sizes or of only part of the male year-class maturing at two and the females at three, the rest maturing one or more years later. Age distributions for subsequent years at the lake should go some way to confirming or refuting the first possibility. If the second proposition is correct, then it should be possible to calculate the proportion of males and females that reach sexual maturity at a given age from the stable age distribution. Further data are currently being analysed, employing larger samples from several years, and this should give a clearer picture of the actual age distribution.

The lack of any significant relationship between age and length in toads suggests that linear growth is insignificant once sexual maturity is reached. This agrees with the findings of Gittins *et al.* (1980), that the length-frequency distributions of male and female toads coming to breed were normal, implying that toads display determinate growth.

## ACKNOWLEDGEMENTS

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# THE SNOUT OF THE GHARIAL *GAVIALIS GANGETICUS* (GMELIN)

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## SUMMARY

Development, structure and biometrical relationships of the gharial snout are discussed. During the developmental stages within the egg, the snout is a papillated organ with margins of the jaws fitting closely together. Following growth of the teeth, the margins separate from each other to accommodate the teeth. The arrangement of the teeth on the premaxilla follows a definite pattern with respect to the mandibular teeth. The 1st, 3rd and 4th mandibular teeth are large. Tooth shedding is a regular feature. At hatching the snout is 29.76 ± 1.4 mm in length. At hatching the ratio between total length ($TL$) and snout length ($S$) is greater than 12; the relationship between these two variables is given by

$$S = 0.13TL - 12.09$$

Two months after hatching the ratio $TL:S$ is 8.0, later it becomes 7.5 ± 0.5. The ratio between $S$ and basal breadth ($BB$) is 2.9 at hatching, 4.9 at two months of age and 5.0–5.4 thereafter. Growth of the snout is extremely rapid during the first 2–3 weeks after hatching. No sexual dimorphism was noticed in the length of the snout.

## INTRODUCTION

Gharial have a sharply demarcated, long snout, which distinguishes them from other crocodilians, and is of considerable academic interest. The relationship between the length of the snout and its breadth at the base has been used as a character serparating the gharial from a superficially similar-looking crocodile, *Tomistoma schlegelii* (Lydekker, 1896; Smith, 1931; Guggisberg, 1972; Brazaitis, 1973 and Martin & Bellairs 1977). The development of a "ghari" ("narial excrescence") at the tip of the snout of males approaching sexual maturity forms the only marked example of sexual dimophism in the entire order Crocodilia (review by Martin & Bellairs 1977; Biswas, Acharjyo & Mohapatra, 1978). The structure of the snout is an adaptation to the gharial's piscivorous habit. In the present paper the development, structure, growth and biometrical relationships of the snout are discussed.

## MATERIALS AND METHODS

Data have been collected on dead embryos recovered after the end of the incubation period, and on captive-reared juveniles through various stages of growth. The measurements taken and the abbreviations used to indicate these are as follows (Fig. 1): $BB$, basal (at the point of origin) breadth of the snout; $BH$, basal thickness or height of the snout when both jaws are held together; $HB$, maximum breadth of the head; $HS1$, length between the snout-tip and the posterior margin of the occipital shield; $HS2$, length between the snout-tip and the posterior margin of the post-occipital scutes; $S$, length of the snout from its tip to the point of its demarcation from the head; $TL$, total length from the snout-tip to the tail-tip.

For determining the relationship between the snout and total length 24 observations were made for in-the-shell stage and 107 for stages from hatching to twentyfour months. For determining the relationship between $TL$ and $HS1$, $HS2$ and $BB$, mean values of a maximum of 55 observations were considered.

## RESULTS

### STRUCTURE

The snout comprises the upper and the lower jaws. During embryonic development up to about the 150 mm stage, the upper jaw is at least 2 mm longer than the lower jaw. Following this phase, until the 500 mm stage, the jaws meet at the tip, unless there is some deformity. Twelve kinds of deformities have been recorded in gharial hatchlings including crossed snout, one eyed juveniles and total blindness (Singh & Bustard, 1982). There are also instances of an elongated upper or lower jaw. In normal and completely blind gharial the jaws are in line with the body axis. In a one-eyed juvenile the upper jaw was arched in the middle of its length.

The teeth appear from the papillated jaws within seven days of hatching. The stage of development and the number of teeth at various stages are presented in Table I. Before the appearance of the teeth in the jaws the papillae of one jaw fit into the spaces between the papillae of the other jaw, thus giving a "sealed" appearance (Fig. 1B and Plate 1A). As the teeth develop over the papillae and the thickness of the jaws

TABLE I. Dental formulae of *Gavialis gangeticus* *TL* total body length (cm), *S* length of the snout (mm)

| *TL* | *S* | Formulae | Remarks |
|---|---|---|---|
| 9 | 6–8 | — | Almost smooth jaws, few indistinct papillae, two lateral grooves |
| 10 | 9–9.5 | $\frac{3 + 17}{20 - 21}$ | Papillated jaws, indistinct papillae, 3 premaxillary papillae large |
| 12–14 | 10–11 | $\frac{4 + 20 - 21}{23 - 25}$ | Papillae |
| 16 | 12 | $\frac{4 + 21 - 22}{23 - 25}$ | Papillae |
| 20 | 16–17 | $\frac{4 + 21 - 22}{25 - 26}$ | Papillae |
| 22 | 18–19 | $\frac{5 + 23}{25 - 26}$ | Papillae |
| 34–37 | 26–32 | $\frac{5 + 23 - 24}{25 - 26}$ | Just hatched juveniles. Papillae. Out of 39 examined one mandible with 27 on left and 26 on right |
| 35–220 | 26–290 | $\frac{5 + 23 - 24}{25 - 26}$ | Teeth (appeared within 7–10 days of hatching) |
| 540 | 670 | $\frac{5 + 22}{25}$ | Wild gharial, male, observed from left only |

along the middle increase, the lateral margins of the jaws separate from each other so that the teeth are more or less completely accommodated within the height of the snout. At later stages, therefore, the jaws touch each other only in the mid-region (Fig. 1C and Plate 1B). The location of the teeth in the premaxilla of the jaws is as follows (only one side of the jaw is shown).

Premaxilla : Maxilla

Left side of the snout

(1) 2 (3) (4) 5 : 1, 2, 3, etc. up to 23–24 upper jaw

(1) (2) 3 (4) 5, 6, 7 etc. up to 25–26 lower jaw

The parentheses indicate the serial number of the tooth that is large and is touching the outer surface of the other jaw. Therefore, the first, third and fourth premaxillary tooth and the first, second and fourth mandibular tooth are larger than others. In the maxilla there are 23–24 teeth an in the mandible there are 25–26 teeth. All teeth are socketed and so set on the

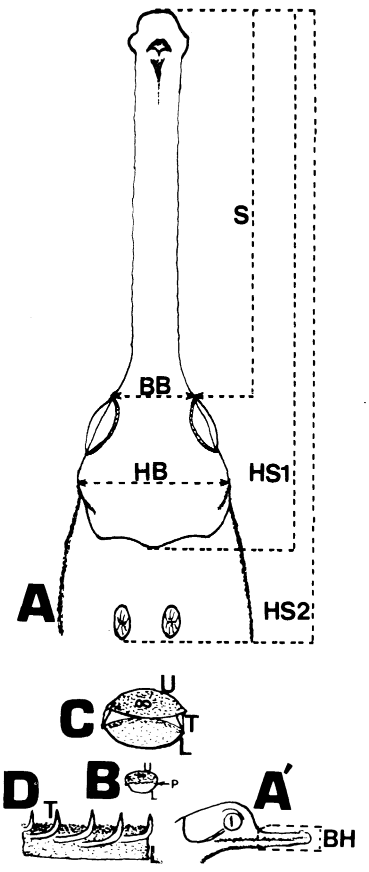

Fig. 1. A, A′: Head of the gharial showing locations where measurements were taken. A, dorsal view; A′, side view. (See text for description of symbols) B, C: Diagrammatic cross-section of the snout mid-way along its length. (B) in a hatchling, (C) in a one-year old individual. P, papilla; T, teeth; U, upper jaw; L, lower jaw. D: Diagrammatic L.S. of a portion of the lower jaw (L) showing teeth.

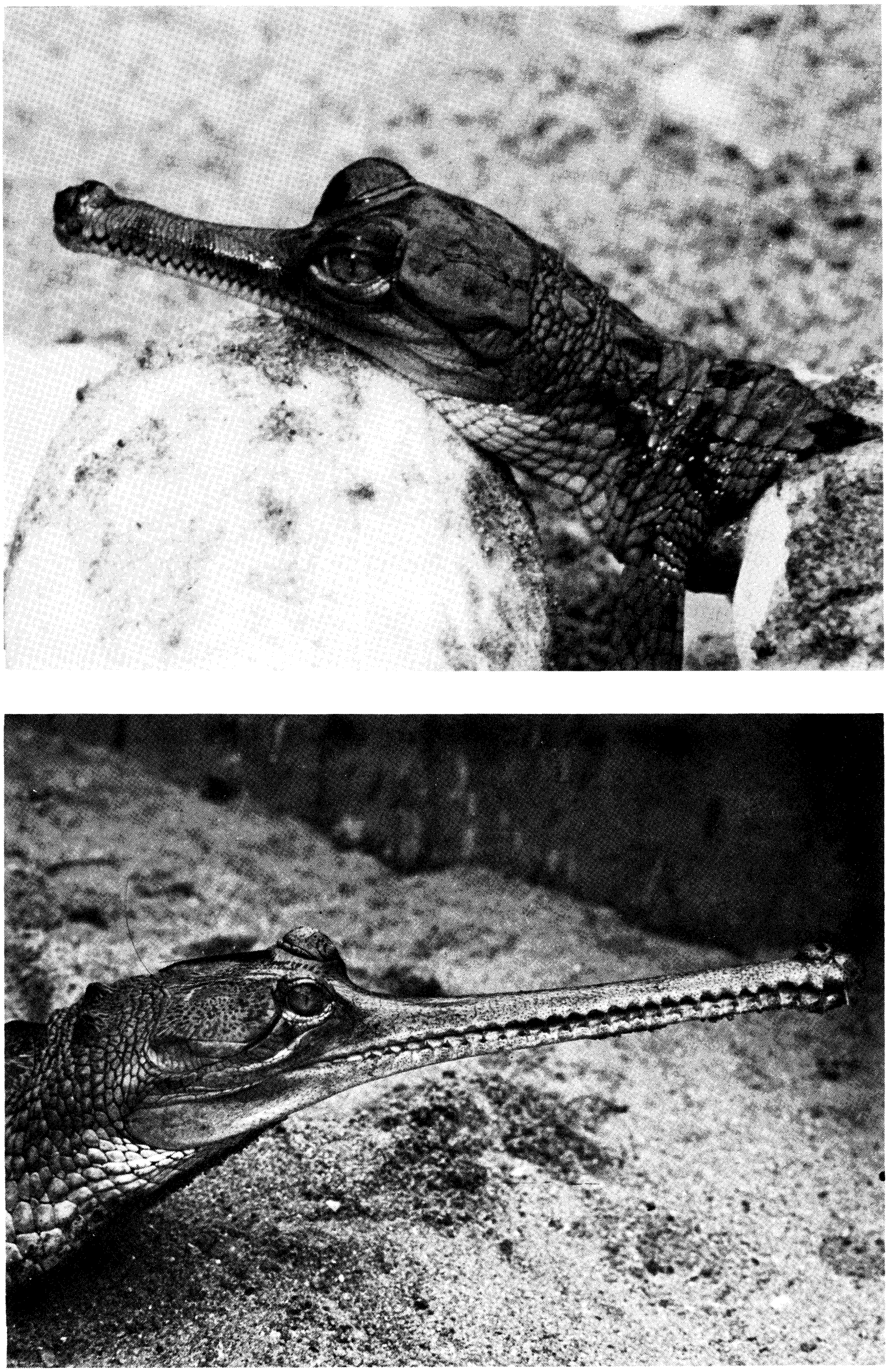

Plate 1. A. A gharial hatchling showing "sealed" appearance of the jaws. B. A yearling showing separated margins of the jaws.

jaws that the tips point backwards. Excepting a few in the most proximal region of the jaws, most of the teeth are curved below the surface of the jaws and are planted deep and backwards into the jaw (Fig. 1D). The free portion of the tooth bears two ridges along its height. The ridges of all teeth are aligned along a single plane on the margins of the jaws.

Twentyfive to thirtyfive days after hatching one or more teeth from either jaw may be missing, but they are replaced soon afterwards. Such tooth shedding and replacement appears to be a regular feature in the life of the gharial quite apart from teeth accidentally lost.

## GROWTH

In embryos 104.5–350 mm in *TL*, *S* varied from 8.0–31.0 mm. At the time of hatching the mean *S* for 39 hatchlings was 29.76 ± 1.4 mm. The growth of the snout during the first nine weeks is given in Table II. The percentage rate of increase was extremely high in the 2–3 weeks following hatching (20.2 and 12.8% respectively).

The mean lengths of the snout at the end of the 12th, 24th, 37th, 49th and 60th months after hatching were 107 mm (number of observations, $n = 80$), 167 mm ($n = 10$), 247 mm ($n = 6$), 302 mm ($n = 5$) respectively (Fig. 2B). On an average, monthly growth was 6.4 mm during the first year, 5.5 mm during the second, 6.1 mm during the third, 4.5 mm during the fourth, and 2 mm in the fifth. Following an early phase of rapid growth, the pattern of growth of the snout followed that of the animal as a whole. Hence, during winter, when growth of *TL* was slow, growth of *S* was also slow (Fig. 2).

The relationships between *TL* and *S* determined for embryos and juveniles up to 24 months of age were as given by the following (lengths in mm)

$$TL = 7.14S + 94.46 \qquad (1)$$

$$S = 0.13TL - 12.09 \qquad (2)$$

($P < 0.01$). The relation obtained in (1) was tested with measurements from 18 larger gharial ranging from 259 to 540 cm in *TL*. These individuals were from both the wild and captivity. The sexes were definitely known, and consisted of 7 males and 11 females. The deviation of the relationship from the regression (1) was not significant, indicating that there is no sex-linked variation in snout length (Fig. 3).

From actual measurements, the ratio *TL*/*S* was greater than 12.0 during the in-the-shell stage, and at hatching it was 12.0. It reduced to approximately 8.0 by the end of the second month after hatching. Thereafter the reduction was slow and the ratio remained constant around 7.5 ± 0.5.

TABLE II. Weekly growth of the snout (mm) during the first two months of post-hatching growth. $n = 39$

| Age in days | Length | Growth | Percentage growth |
|---|---|---|---|
| 1–2 | 29.7 | — | — |
| 10–12 | 35.7 | 6.0 | 20.2 |
| 17–19 | 40.3 | 4.6 | 12.8 |
| 25–26 | 44.0 | 3.7 | 9.1 |
| 32–33 | 46.7 | 2.7 | 6.1 |
| 38–41 | 49.4 | 2.7 | 5.7 |
| 47–48 | 52.5 | 3.1 | 6.2 |
| 52–54 | 53.9 | 1.4 | 2.6 |
| 62–67 | 56.6 | 2.7 | 5.0 |

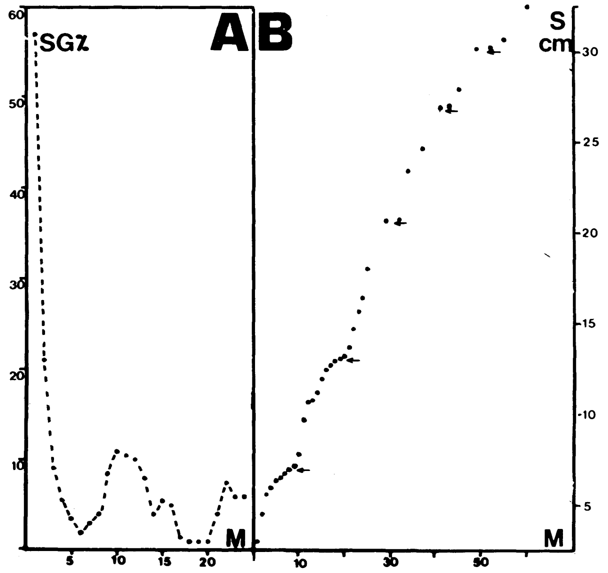

Fig. 2. Monthly (*M*) snout lengths (*S*) (Fig. B) and snout growth percentage (*SG*%) (Fig. A) in the gharial. Note the fall in growth rate during the winter (arrows in B).

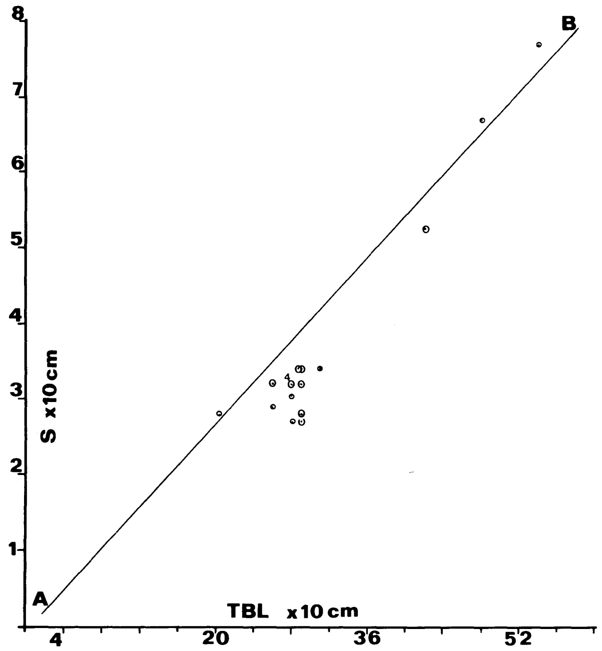

Fig. 3. Regression line (AB) showing a relationship between total length (*TL*) and snout length (*S*). Superimposed on the line are the actual measurements of 7 male (small circles) and 11 female (larger circles) gharial whose sexes were known. "4" indicate that four measurements are represented by that single circle.

## BIOMETRICAL RATIOS AND REGRESSIONS

The relations between *S*, *BH*, *BB* and *HB* are set out in Table III. The ratios *S*/*BB* and *S*/*BH* show a

TABLE III. The snout (mm) and various biometrical ratios

| $S$ Range | $S$ Mean | $BB$ | $BH$ | $HB$ | $S/BB$ | $S/BH$ | $BB/BH$ | $HB/BB$ |
|---|---|---|---|---|---|---|---|---|
| 25–35 | 30 | 10.1 | 8.8 | 21.9 | 2.9 | 3.4 | 1.14 | 2.16 |
| 36–45 | 40 | 10.8 | 9.8 | 22.2 | 3.7 | 4.0 | 1.10 | 2.05 |
| 46–55 | 50 | 11.6 | 10.5 | 21.5 | 4.1 | 4.7 | 1.10 | 1.85 |
| 56–65 | 60 | 13.0 | 12.2 | 28.6 | 4.6 | 4.9 | 1.06 | 2.20 |
| 66–75 | 70 | 13.6 | 13.6 | 28.0 | 5.1 | 5.1 | 1.00 | 2.00 |
| 76–85 | 80 | 14.8 | 14.4 | 30.9 | 5.4 | 5.5 | 1.02 | 2.08 |
| 86–95 | 90 | 16.5 | 15.5 | 34.5 | 5.4 | 5.8 | 1.06 | 2.09 |
| 96–105 | 100 | 19.1 | 17.2 | 36.7 | 5.2 | 5.8 | 1.11 | 1.92 |
| 106–115 | 110 | 20.8 | 19.0 | 40.5 | 5.2 | 5.7 | 1.09 | 1.94 |
| 116–125 | 120 | 23.6 | 20.0 | 43.9 | 5.0 | 6.0 | 1.18 | 1.86 |
| 126–135 | 130 | 25.3 | 22.0 | 47.8 | 5.1 | 5.9 | 1.15 | 1.88 |
| 136–145 | 140 | 26.8 | 23.4 | 52.1 | 5.2 | 5.9 | 1.14 | 1.94 |
| 146–155 | 150 | 27.6 | 24.9 | 56.8 | 5.4 | 6.0 | 1.10 | 2.05 |
| 156–165 | 160 | 30.6 | 26.4 | 60.8 | 5.2 | 6.0 | 1.15 | 1.98 |
| 166–175 | 170 | 32.1 | 27.5 | 62.5 | 5.2 | 6.1 | 1.16 | 1.94 |
| 176–185 | 180 | 35.5 | 29.2 | 69.4 | 5.0 | 6.1 | 1.21 | 1.95 |
| 186–195 | 190 | 37.5 | 30.8 | 73.1 | 5.0 | 6.1 | 1.21 | 1.94 |
| 196–205 | 200 | 37.5 | 30.0 | 73.0 | 5.3 | 6.6 | 1.25 | 1.94 |
| 288–292 | 290 | 58.0 | 45.0 | 110.0 | 5.0 | 6.4 | 1.28 | 1.94 |

gradual increase up to a stage when $S$ is between 56 mm and 65 mm ($TL = 480$ mm at two months of age). Thereafter the ratios remain constant. The ratios $BB/BH$ and $HB/BB$ are constant at all stages.

Relationships between $TL$, with $HS1$, $HS2$ and $BB$ are as follows

$$HS1 = 0.160TL + 10.065 \tag{3}$$

$$TL = 6.159\,HS1 - 51.456 \tag{4}$$

$$TL = 5.198HS2 + 2.749 \tag{5}$$

$$TL = 41.1BB + 0.38 \tag{6}$$

($P < 0.01$ in all cases).

## DISCUSSION

In the first year, the length of the snout shows an absolute increase of 3.5 times over its length at hatching; in two years it increases six times. Growth of the snout is low during winter.

There is a gradual increase in the proportion of $S$ in $TL$ as the growth shifts from "in-the-shell" stage to "hatching to 2 months" age and thereafter. This change in the proportion at the three successive stages is explicable according to the hypotheses "egg space economy during embryonic development" and "post-hatching growth priority" (Singh 1978). According to the former hypothesis, since the snout functions only after hatching, its growth is restricted during in-the-shell stage (egg space economy), and hence the proportion of $S$ in $TL$ is less. Following hatching, with no spatial limitations, and the requirement to obtain a snout length suitable to manoeuvre in catching and swallowing fish, growth of the snout is extremely rapid in the early stages after hatching (post-hatching growth priority), and hence the proportion of $S$ in $TL$ becomes relatively more than during in-the-shell stage. Later, $TL$ and $S$ maintain a constant relationship, but the proportion of $S$ in $TL$ now is further more than in the two previous stages. This proportion remained the same irrespective of the sex of the animal. However, this aspect of the study, sex-related variation in snout proportion, needs further investigation, where the specimens should be from the same habitat and reared under similar conditions.

The development of the teeth, their structure and arrangement on the jaws are also related to the piscivorous habit of the gharial. The orientation of the ridges of the teeth along the jaws helps in holding the fish and preventing escape.

It is interesting to note the larger size of the 1st, 3rd and 4th premaxillary and the 1st, 2nd and 4th mandibular teeth. They add to the efficiency in holding fish. The enlarged 4th mandibular tooth conforms to the basic condition found in all crocodilians. Members of the families Crocodilidae and Alligatoridae are characterized by the presence of a large 4th mandibular tooth. About the Nile crocodile, *Crocodylus niloticus*, Cott (1961) wrote "... according to Major W. E. Poles (1951), who watched crocodiles feeding on a hippopotamus in the Luangwa, the initial penetration is effected with an upward and sidewise slash delivered with the lower jaw, the 4th tooth of which is admirably adapted for a spear thrust. Once the jaws are locked, the crocodile executes a slow roll right round half a dozen times in succession to detach a piece of meat. Smaller animals are speedily dismembered in this fashion".

Like all the recent forms of crocodilians, the gharial also possesses a spear-like large 4th mandibular tooth. It appears, therefore, that this tooth together with the enlarged ones on the premaxilla and the corresponding region of the mandible were (and perhaps still are) of use to the animal in a fashion similar to other crocodilians. There is some evidence of gharial feeding upon carcases (Pitman, 1925; Smith, 1931; Singh, 1977). Perhaps, the gharial, like other crocodilians, also uses its enlarged tooth in dismembering portions of a decomposing carcase.

The remarkable elongation of the snout has attracted the attention of a number of authorities who examined the relationship between its length and the basal breadth. Lydekker (1896) reported that the length is more than 5 times the basal breadth in the young, and more than 3 times in the adult. The same observations are reported in the literature by Smith (1931) and Brazaitis (1973). Guggisberg (1972) mentions that the length is 4 times the basal breadth in adults and 5 times in juveniles. The observations reported in the present study do not confirm these findings. At hatching $S/BB$ is 2.9; it increases to 4.6 when the hatchlings are about 2 months old ($TL = 480$ mm approx.) but later the ratio remains between 5.0 and 5.4. These ratios were calculated up to 42 months of age, and tested with the data obtained for a 5.4 m wild gharial. From clear impressions where it had rested in the sand, the length of the snout and the $BB$ were precisely measured from this gharial and found to be 670 mm and 12 mm respectively, giving a $S/BB$ ratio of 5.5. The $S/BB$ ratio for a 4.236 m stuffed female gharial on display at the Crocodile Bank, Madras is $52.3/11.0 = 4.8$. It is not known if the ratio is different for male and female gharial, but it appears that 5.0 is a fairly correct figure for $S/BB$ in adults.

For *Tomistoma* the ratio $S/BB$ is stated to be 3.0–3.5 (Brazaitis, 1973). Should this prove correct, *Tomistoma* and gharial can be distinguished easily from this ratio alone, quite apart from other distinguishing features (Brazaitis 1973, Hecht & Melone 1972).

Martin & Bellairs (1977), discussing the relationship between head length (snout to the back of occiput) and total length, state, "In the gharial there is a tendency for these proportions to change with age; in young animals 55–135 cm long the ratio of head or skull length to total length is $1:\pm 5$, whereas in large specimens it is usually $1:6$–$1:6.8$. Wermuth's (1964) data are in accordance with our observations on mounted or recorded specimens...".

The relationships in equations (3), (4) and (5) of the present paper consider two different lengths of the head-snout, the $HS1$ and $HS2$. The head-snout length discussed by Martin & Bellairs is the $HS1$ in the present paper. By using (3) the $TL/HS1$ ratio was found to increase from 5.1 at hatching to 6.1 at 5 m total body length. This, therefore, supports the earlier work on this aspect.

Since the proportion of $S$ in $TL$ increases from $\frac{1}{12}$th to $\frac{1}{8}$ approx. while $HS1$ in $TL$ is less changing ($\frac{1}{5}$th–$\frac{1}{6}$th), it is deducible that the portion of the head without the snout (*i.e.*, $HS1$-$S$) is proportionately more at hatching and gets reduced as growth proceeds. It is expected that any animal will have a relatively higher cranial capacity at hatching or birth.

The relationship between head-snout and total length is apparently similar in *Tomistoma* (Martin & Bellairs 1977) but is different from other short-snouted crocodilians where the ratio is about 1:7.5. Such a similarity between gharial and *Tomisoma* are obviously because of their adaptive convergence towards a piscivorous habit.

The regressions given in (1), (4) and (5) could form valuable adjunct to survey and census work. When the animal is at the water's surface, any of the length from $S$, $HS1$ and $HS2$ could be seen and eye-estimated for subsequent calculation of the $TL$. Similarly, by using (6), the $TL$ can be calculated from the $BB$ data obtained on the sand, or when dead, from the skull or even a proximal piece of any of the jaws.

## ACKNOWLEDGEMENTS

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 259–260 (1982)

# GEOGRAPHICAL DISTRIBUTION OF THE GHARIAL *GAVIALIS GANGETICUS* (GMELIN) IN ORISSA, INDIA

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The State of Orissa in eastern India, situated between 17–20° N, 81–88° E, is at the southern distribution of the known range of the gharial. Literature accounts of the occurrence of the gharial in Orissa refer only to its presence in the Mahanadi river (Gadow, 1901; Smith, 1931; Brazaitis, 1973; Jayaram, 1974; Mukherjee, 1974) with the sole exception of Annadale (1915) who stated that it occurred in (the unlikely habitat of) Chilka Lake, a shallow, brackish-water "sea" and one of the largest lakes in Asia. A number of authors (see above) have been puzzled by this apparently anomalous distribution.

Since the initiation of the Gharial Conservation Project by the State Government of Orissa, through the State Forest Department, in 1975, we have collected extensive data on the present and former distribution of the gharial. In addition to the Mahanadi River, it occurred until recently in the two other major river systems of Orissa, the Brahmani and the Baitarani (Fig. 1), in both of which it is now extinct. It also occurred in the Sileru river.

## BRAHMANI RIVER

Along the main river some of the important places where gharial were formerly common are Banaigarh, Talcher, Kamakshyanagar and lower Brahmani. Near Talcher there is a village called Katarapada where the river is called Kumbhirakhai (which literally means the feeding place of crocodiles in Oriya) because a large number of gharial used to occur in this area.

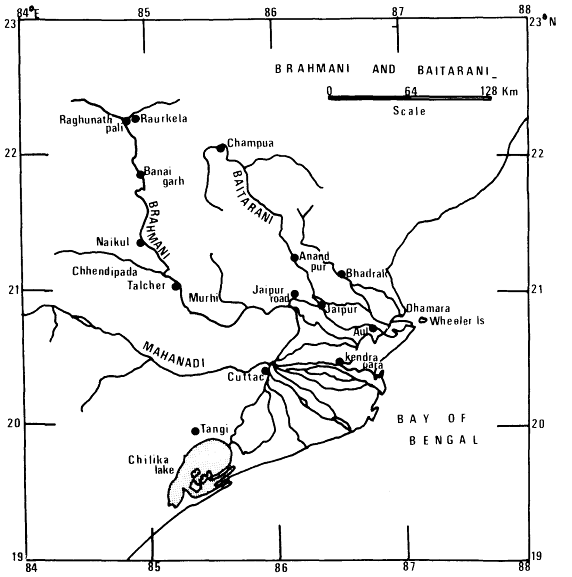

FIG. 1. The three main river systems of Orissa with place names given in the text.

The tributaries of the Brahmani formerly holding gharial were the rivers Kharasuma and Ramiyalu. Many gharial formerly inhabited the Sundarmundi Gorge of the Ramiyalu River.

## BAITARANI RIVER

Information indicates that gharial were formerly present in the lower Baitarani and near Anandpur and Jajpur areas.

## SILERU RIVER

This river joins the Godavari. There are reports of the occurrence of gharial in the Sileru up to 1971.

Hence the gharial is shown to have been present in all the major river systems of Orissa and its occurrence in the Mahanadi river reflects a distributional range extending down eastern India rather than an isolated population occurring there.

## ACKNOWLEDGEMENTS

We wish to express our thanks to the Orissa Forest Department, the Government of India, FAO and UNDP for assistance during this study.

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# EDITORIAL NOTE

The following five papers were read at an "International Herpetological Congress" held in the Zoology Department, Oxford University from 1–9 October 1981. The Congress was organized by Mr J. Coborn and the Dudley & West Midlands Zoological Society Ltd, with assistance from ASRA and the British Herpetological Society. The manuscripts have been extensively edited for publication by RAA, but not subjected to the normal refereeing process.

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# LIFESTYLE AND THERMAL ECOLOGY OF NATRICINE SNAKES

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## SUMMARY

*Natrix maura* and *N. natrix* have been regarded as Spain in September, with a mean active body temperature of 22°C. *Natrix natrix* was only seen active in daytime, at a mean body temperature of 26.6°C.

*Natrix natrix* was an active forager in summer, *N. maura* mostly a sentinel (sit-and-wait) predator. In spring, both species were seen basking and moving actively to a greater extent than in summer.

Differences in lifestyle (foraging mode) between these species in sympatry are extrapolated to cool temperate *N. natrix*, and the differences in thermophysiology between this species and *N. maura* examined from the standpoint of both lifestyle and climate.

## INTRODUCTION

This paper presents preliminary results of work on the ecology and behaviour of *Natrix maura* and *N. natrix* in eastern Spain. The main emphasis of the work is on the comparative energetics of the two species, to try to resolve the question of differential penetration into high latitudes.

Latitude is known to influence the metabolic rate-temperature relations of reptiles (Aleksiuk, 1971; Davies & Bennett, 1981) and lifestyle also has an influence on these relationships independently of latitude (Davies, Patterson & Bennett, 1981). Both influences may therefore underlie observed differences in the thermobiology of latitudinally separated species and populations.

*Natrix maura* and *N. matrix* have been regarded as ecologically similar in previous studies of latitudinal trends in reptiles (Spellerberg, 1976; Davies & Bennett, 1981; Davies *et al.*, 1981): here, differences of ecology are stressed. In particular, we examine how differences in lifestyle might help to explain some of the observed differences in thermobiology between *N. maura* and high latitutde *N. natrix*.

## METHODS

### FIELD OBSERVATIONS

*Natrix maura* and *N. natrix* were studied in a river near Calpe, on the east coast of Spain. The river runs over limestone rocks, and the extent of surface water normally fluctuates with season, from winter floods to summer dry season. 1980 and 1981 were drought years and during the study period surface water in the river was exceptionally restricted, to 6 km in spring and the 1.2 km study area in summer, 1981. Underground flow occurred along part of the river, surface flow along the whole river took place only in winter according to local residents.

Three periods of fieldwork are reported here, 30 March to 9 April (two observers), 9–19 August (two observers) and 6–23 September (one observer), 1981. The former period is regarded as spring, the latter two as summer (see macroclimate pattern, Fig. 4). Sampling in spring and in August was restricted to normal working hours, in September the whole diel cycle was examined.

Sampling was by walking slowly along the 1.2 km study length of river, noting all snakes seen; the time, their size, position and behaviour, and air and water temperatures. At night, a powerful torch was used to find snakes, which could be seen 2–3 m away. Snakes were assigned to one of five classes; "tiny", "small", "medium", "large" and "very large". They refer (approximately) to snakes <4 g, 4–12 g, 12–35 g, 35–80 g and >80 g respectively.

Body temperatures were measured within 30 s of capture with a Schultheis thermometer or a themistor and 1.5 mm diameter quick reading probe, inserted cloacally. Shade air and water temperatures were also taken routinely throughout the sampling period. Time spent actively searching was noted, that spent handling animals was subtracted from total time spent in the field. All fieldwork took place during Spanish summer time (GMT + 2), but results are shown against GMT. This centralizes the light phase at midday (the site is on the Greenwich Meridian), and facilitates comparison with times of year not covered by summer time.

### PREY ODOUR PREFERENCE IN THE LABORATORY

Eight tiny and 8 small/medium *N. maura* collected three weeks previously were used, these had experience of *Rana temporaria* tadpoles and the worm *Eisenia foetida* while in captivity. The set of odours were presented on fresh cotton swabs, in a random sequence, to each snake on four consecutive days, with 30 min between successive presentations to an individual snake. Live prey animals were left in tapwater for 2 hr before testing, and the swab dipped in this water and then rubbed over the surface of the prey item.

Tests were performed in 45 × 20 cm plastic aquaria (in which snakes were housed individually during the course of the experiment, unfed but with a dish of water) at the snakes' acclimation temperature, 26°C, just before the dark phase of a 12L:12D cycle. Scores were calculated as: total number of tongue flicks in the

120 s presentation period, plus (120-latency to attack in s) for trials in which the snake attacked the swab (after Mushinsky & Lotz, 1980).

## RESULTS

### ACTIVITY

The patterns of *N. maura* and *N. natrix* sightings over the diel cycle in September 1981 are shown in Fig. 1. Three hundred and four *N. maura* were seen in active searching periods, at a rate of 4.8 per hr; only 12 *N. natrix* were seen during this time. Frequency of sighting *N. maura* in August and in spring was similar, though exact figures cannot be given due to the complicating presence of more than one observer.

Types of activity of *N. maura* are shown in Fig. 2. Four main categories of behaviour are shown, as described below.

#### *1. Sentinel Predation*

This characteristic feeding behaviour took place only in water, and involved a sedentary snake striking at passing fish (Davies *et al.*, 1980; Patterson & Davies, 1982). Snakes in shallow water, 20 cm deep or less, were usually on the bottom, sometimes partly under rocks or debris. In water over 20 cm deep they were usually on submerged sticks or vegetation, raised from the bottom into midwater. This association between water depth and relative snake depth was highly significant ($\chi^2 = 30.16$, 1 d.f., $P < 0.001$). There was no significant association between water depth and snake position at the side or in midstream ($\chi^2 = 0.012$, 1 d.f., $0.95 > P > 0.05$). A few snakes were on the bank or on floating vegetation, with their rear dry and front in the water.

Sentinel snakes had their rear halves coiled around irregularities in the substrate, and their front halves free, and were seen to lunge at passing fish. Most sentinel predation was in still water, in which schools of roach, *Rutilus rutilus*, moved slowly near the bottom in shallow water and at the surface or around the edge or among submerged vegetation in deeper water. Encounters with fish and captures appeared infrequent, and few snakes were seen handling fish. All sizes of snakes except tiny ones were seen engaging in sentinel predation.

#### *2. Active in Water*

Other snakes in water were classed as active, this category containing the following activity types.

(*a*) *Breathing*. Sentinel predation must be punctuated with periods of movement to the surface and breathing. One snake, in water at 23°C, was observed for three periods of sentinel predation, mean $11.07 \pm 2.02$ min (± 1 SD) and three movements to the surface, mean $2.75 \pm 0.25$ min. This snake thus spent 20% of its time in movement when engaged in a period of sentinel predation.

(*b*) *Chasing fish*. Active pursuit of particular fish or groups of fish was rarely observed. This took place only in shallow water where the fish were confined and their range and speed of movement restricted. However, intense opportunistic feeding in drying pools full of trapped fish was common during reduction of the area of standing water in August.

(*c*) *Nocturnal foraging*. Another characteristic foraging behaviour, seen on two occasions at night, was similar to that described by Evans (1942). The snakes were swimming at the water surface in large still pools 30 to 50 cm deep. This was an exaggerated form of swimming, the body describing a series of figure 8s, and the snakes moved forwards only slowly. Their mouths were open, but they were not pursuing particular fish. Fish schools were present in these pools, and were at the surface in midstream during the night.

(*d*) *General movement*. Some snakes were moving about and not returning to the same place. Some of these may have been disturbed while breathing at the surface, sentinel snakes were hard to disturb even when closely approached. Others may have been moving to locate alternative foraging areas.

#### *3. Active on Land*

This was mostly attributed to exploratory movement or disturbance during basking. No active pursuit of amphibians on land was observed, though invertebrate prey may have been taken on land. A few snakes brought large fish to the bank for handling. The only other active behaviour on land was mating, which was seen twice in April. One of these pairings was observed for 30 minutes before the pair broke apart, undisturbed.

#### *4. Basking on Land*

Basking snakes were usually within 2 m of water, sometimes overhanging it. A variety of coiling patterns were seen but they showed no apparent correlation with thermal conditions, and seemed more related to the topography of the basking site. Individual bamboo stems, mats of plant debris and flattened reeds were commonly used. No body flattening or posturing orientation was seen, but the site chosen was often inclined towards the sun. After disturbance, snakes had sometimes reappeared in the same place when next passed, three or four hours later.

*Natrix natrix* observations were of basking (2, in spring), or activity (17, in summer). No sentinel predation or nocturnal activity was observed. Active snakes were at the waters' edge in marshy areas, or crossing at the surface of pools. Disturbed *N. natrix* swam across water to escape, *N. maura* usually dived.

### THERMAL RELATIONS

The daily march of air and water temperatures at the study site on sunny days in September is shown in Fig. 1c, together with means for the daylight hours in spring. Mean air temperature over the diel cycle, 21.8°C, was similar to that for the water, 21.6°C.

The relationship between body and ambient temperature for *N. maura* in water and on land is shown in Fig. 3. Dotted lines show body temperature = ambient temperature, the definition of a perfect thermoconformer (Huey & Slatkin, 1976). In water, snakes

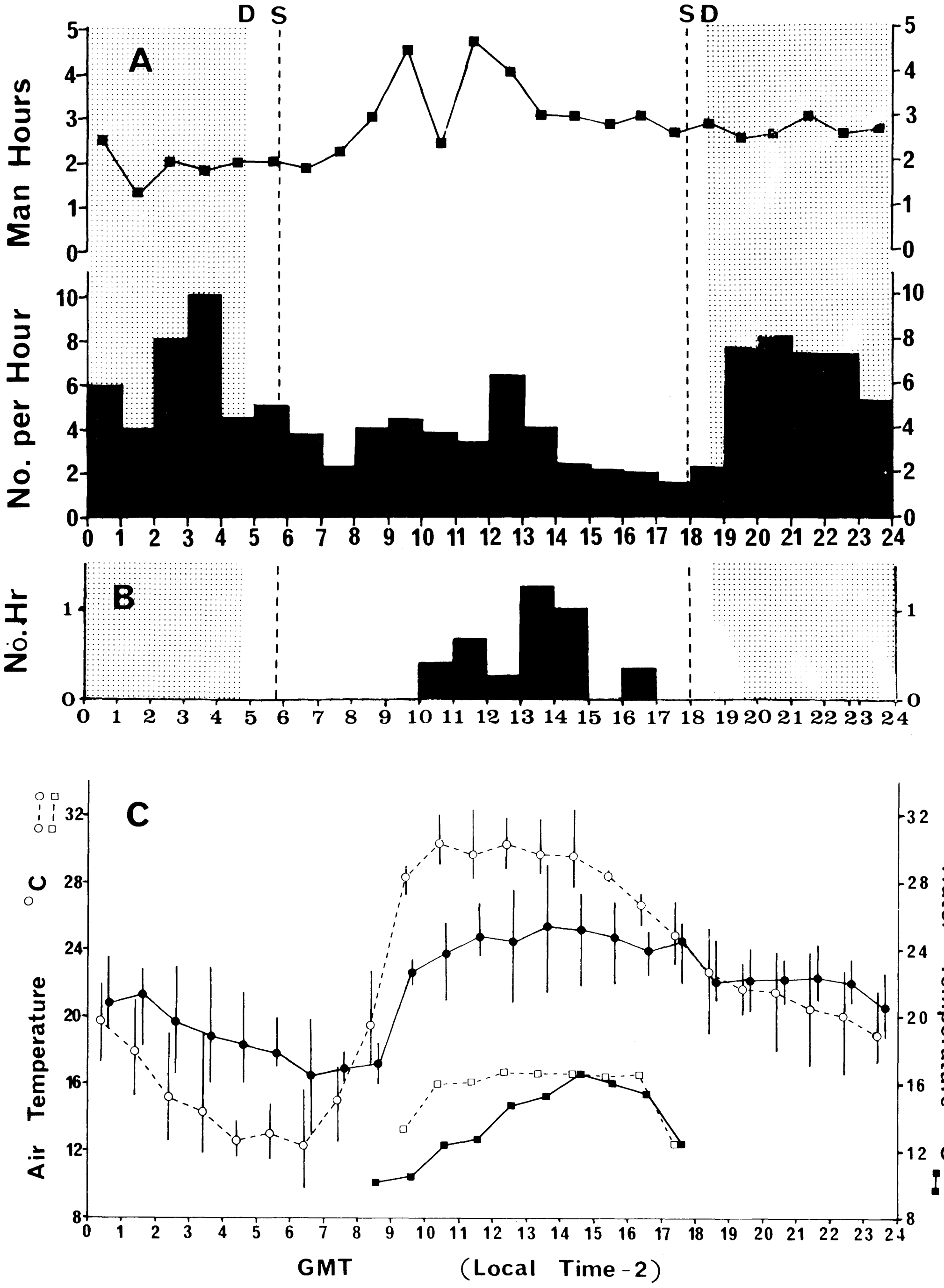

FIG. 1. Activity levels and thermal conditions, September 1981. (a) Search effort, and sighting frequency of *N. maura*, D = dawn and dusk, period of darkness is shaded. S = sunrise and sunset. (b) Sighting frequency of *N. natrix*. (c) Daily pattern of air and water temperatures on sunny days. Mean hourly air (○) and water (●) temperature, with range. Means for daytime in spring also shown (squares).

approximate to this condition, departures from the line being due to warming in the hand, or evaporative cooling at high temperatures. At equilibrium, snakes in water, both at rest and after a bout of activity, are perfect thermoconformers, and snakes above or below water temperature rapidly equilibrate to it after immersion. Snakes on land were often considerably above ambient temperature, as a result of basking.

Seasonal distributions of body temperature are shown in Fig. 4 as frequency histograms of body temperature in 2°C intervals. With the exception of the August results (see below), these appear approximately normal, and do not depart significantly from normality ($\chi^2$ comparison to normal distributions generated from sample mean and standard deviation — Sokal & Rohlf, 1969). Large and small sample *t*-tests have therefore been used to compare them, after variance-ratio testing for comparability of variances (Bailey, 1959).

In spring during daytime, *N. maura* in water were significantly cooler than those on land (means 19.1°C

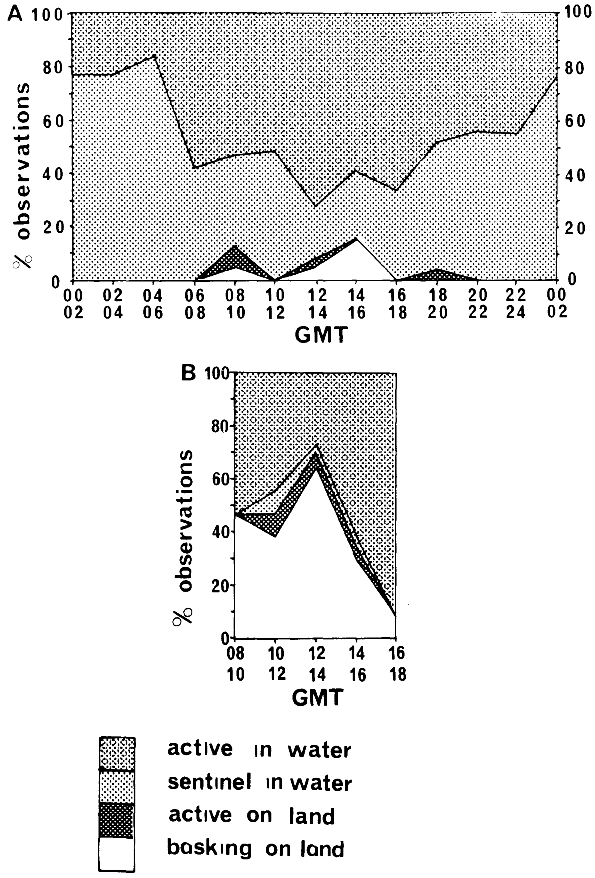

FIG. 2. Types of *N. maura* activity through the diel cycle. (a) September 1981 ($n = 332$). (b) Spring 1981 ($n = 192$). Data grouped into two-hour periods.

and 24.4°C respectively, $d = 6.586$, $P < 0.001$). In the daytime *N. maura* were warmer in August than in September, (means 27.3°C and 25.8°C respectively) though the August sample was not a conscious attempt at a representative proportion of the population, but was biased to snakes opportunistically feeding in warm shallow pools. Daytime September body temperatures were significantly higher than daytime spring ones (mean 21.4°C), ($d = 7.628$, $P < 0.001$), and daytime September body temperatures on land were significantly higher than those on land in spring (means 24.4°C and 29.2°C, $t = 2.344$, 34 d.f., $P < 0.05$).

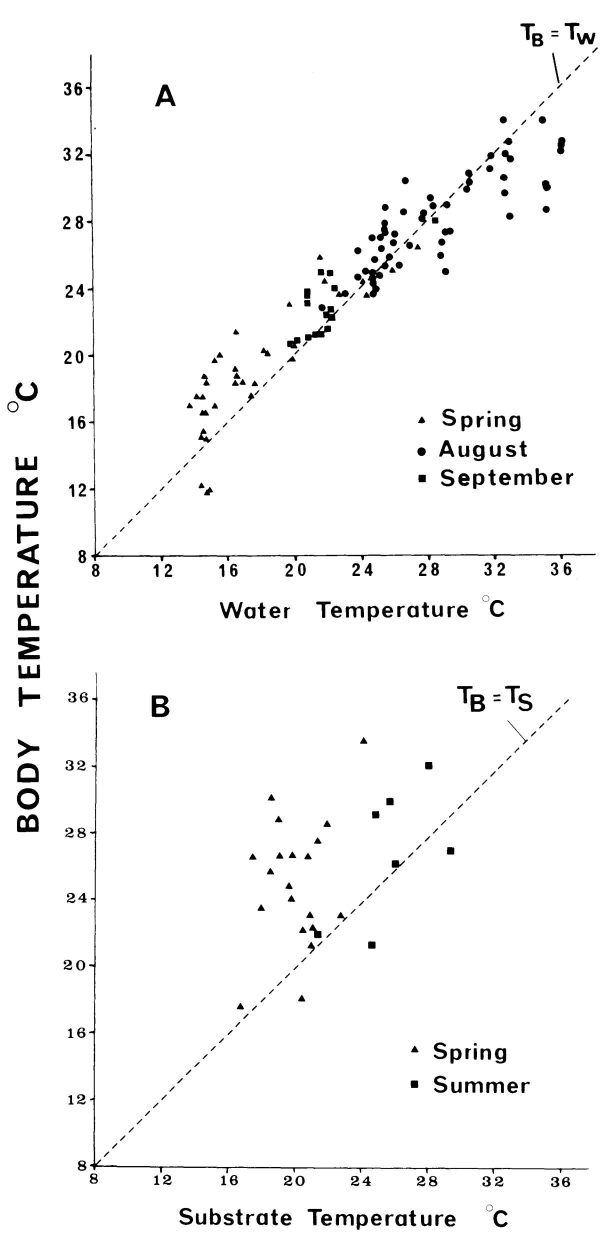

FIG. 3. Relationship between body and ambient temperature for *N. maura* (a) in water and (b) on land. Dotted line is definition of a perfect thermoconformer.

TABLE I. Values of the $U$ statistic comparing tongue flick scores to different prey odours. upper values in each pair relate to tiny snakes, lower values to small/medium snakes. Odours have a significantly different effect ($P < 0.05$) if $U$ is $>715$

| Odour | Mean score | Water | Frog | Fish | Tadpole |
|---|---|---|---|---|---|
| Water | 17.4 | | | | |
| | 27.7 | — | — | — | — |
| Frog | 29.7 | 644 | | | |
| | 53.1 | 671 | — | — | — |
| Fish | 33.8 | 677 | 550 | | |
| | 51.1 | 652 | 518 | — | — |
| Tadpole | 47.1 | 737 | 626 | 588 | |
| | 66.6 | 731.5 | 574.5 | 565.5 | — |
| Worm | 60.0 | 802 | 709 | 677.5 | 573.5 |
| | 75.9 | 767 | 626.5 | 628.5 | 555.5 |

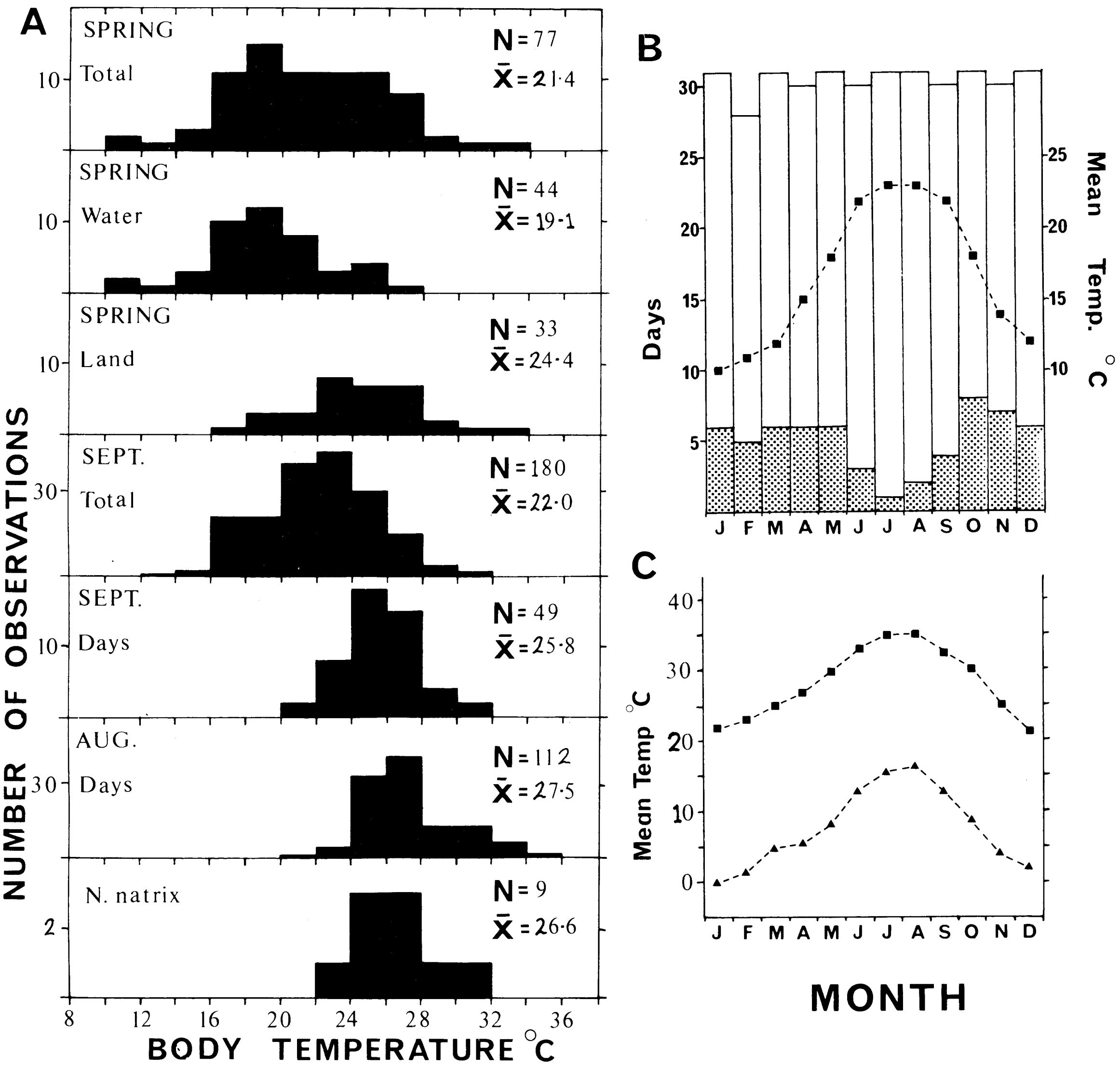

FIG. 4. Thermal relations. (a) Frequency of observation of body temperatures in 2°C intervals. (*N. maura* unless otherwise stated.) (b) Climate of Costa Blanca (i). Histogram shows mean number of sunny (unshaded) and cloudy (shaded) days per month. Curve shows mean daily air temperature for each month. Source: Firestone Costa Blanca tourist map. (c) Climate of Costa Blanca (ii). Mean maximum (squares) and mean minimum (triangles) monthly air temperatures. Source: Meteorological Office publications.

*N. natrix* body temperatures in summer were not significantly different from those of *N. maura* during the daytime (means 26.6°C and 26.8°C respectively, $t = 0.6885$ with 168 d.f., $P < 0.5$).

### PREY ODOUR SELECTION

Figure 5 shows the numbers of tongue flicks given by the snakes in the presence of different odours. These distributions are not normal or easily normalized, and treatments have been compared by nonparametric means, the simultaneous test procedure of the Wilcoxon–Mann–Whitney U statistic (Table I) (Sokal & Rohlf, 1969). For both tiny and small/medium snakes, fish and frog odours produced a similar, non-significant increase in response over the water control, and tadpole and worm odours produced larger, significant increases. Tongue flicking rates were generally higher in small/medium snakes than tiny snakes.

## DISCUSSION

### ACTIVITY

*N. maura* were nocturnally active in summer, as reported from the Sahara by Gauthier (cited by Cloudsley Thompson, 1971). Significantly more were seen in the hours of darkness (19.00–04.00, 149 in 21 hr, 7.1 $hr^{-1}$) than in the daylight hours (05.00–18.00, 140 in 38 hrs, 3.7 $hr^{-1}$, $\chi^2 = 32.09$, 1 d.f., $P < 0.001$). Differences between sampling in daylight and by torchlight, such as in conspicuousness of snakes or observer, or flight distances, mean that greater nocturnal than diurnal activity in this population cannot be

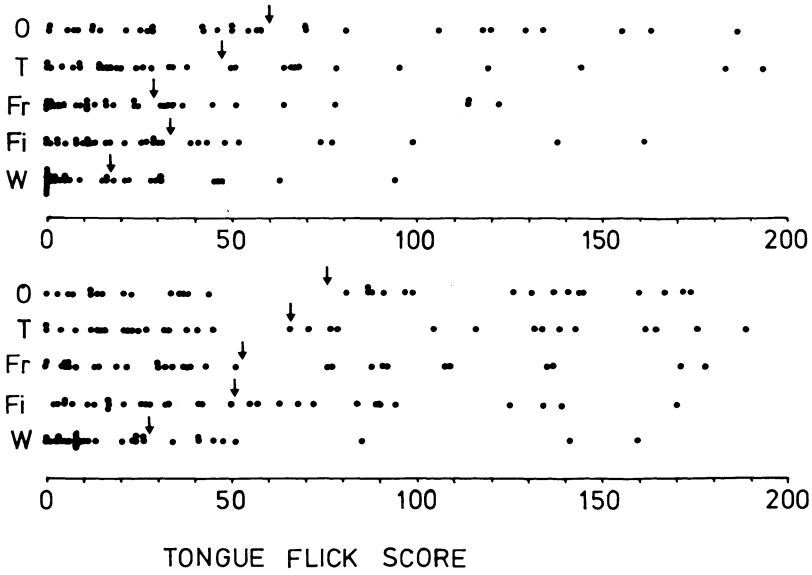

FIG. 5. Tongue-flick scores of individual *N. maura* to prey odours. Tiny (upper) and small/medium (lower) snakes. Arrow: mean score. Odours are: tapwater (W), frog, adult *Rana temporaria* (Fr), a cyprinid fish, *Carassius auratus* (Fi), a tadpole, *Rana temporaria* (T) and an oligochaete, *Eisenia foetida* (O).

assumed, though nocturnal activity is clearly important. Though often overlooked in European natricines, nocturnal activity is well documented in North American species (e.g. Conant, 1975, Mushinsky & Hebrard, 1977).

In September there appeared to be a change in activity type of snakes in water over the diel cycle, from activity in daytime to sentinel predation at night (Fig. 2). There was a significant association between activity type and time of diel cycle, as day or night ($\chi^2 = 18.74$, 1 d.f., $P < 0.001$), in this direction. This result may also be affected by sampling differences.

There was a clear difference between spring and summer in numbers of snakes seen basking. As some snakes active on land were probably disturbed while basking, snakes on land have been grouped together, and a significant association found between season and proportion on land ($\chi^2 = 62.81$, 1 d.f., $P < 0.001$). This is in the direction of more than expected on land in spring and in water in September.

The functional significance of the high body temperatures attained during spring basking by *N. maura* is not at present fully understood, though many physiological optima are known to coincide with preferred temperatures in reptiles (Dawson, 1975). It is possible to recognize two extreme patterns of basking, which accompany different types of benefit of high temperature. Alternating basking and other types of activity over a short time scale is usually associated with foraging, and the benefit of high temperature is probably that of increased capacity for movement (*e.g.* Greenwald, 1974). Sustained basking is probably related to physiological processes over a longer time scale, such as digestion (Goodman, 1970, Skoczylas, 1970) or maturation of reproduction products (Prestt, 1971; Nilson, 1981). Intermediate patterns are most likely where basking and sentinel predation can be combined.

In spring some *N. maura* had conspicuous food bulges, and some others had cloudy spectacles and were approaching ecdysis. Most, however, were not visibly in any special condition, and many were some distance from or above water, in such positions that it was unlikely that they could see the water to enter after specific prey. The combination of basking sites blind to the water and the short-lived nature of the thermal advantage once a snake enters water suggest that basking was not primarily to increase foraging success and that longer term benefits are more important. Studies of basking patterns of individuals of European reptiles are rare and should be more widely employed, since they can provide evidence for the functions of basking which studies of the population as a whole cannot (Hailey, 1982).

There was no significant association between time of the diel cycle, taken in four-hour periods, and relative frequency of sighting of different size groups of *N. maura* ($\chi^2 = 13.41$, 10 d.f., $P > 0.05$). For this analysis, the five size groups were reduced to three (tiny and small, medium, and large and very large) to meet the requirement that no expected value was below five. An important difference in behaviour was noted, however, between tiny snakes and other sizes. Tiny snakes, <150 mm snout vent length and <4.0 g, formed a characteristic group in both spring and late summer, and were believed to be animals in their first year after hatching. They were not seen engaging in sentinel predation, but were usually moving actively in areas of shallow water or marshy vegetation, often where no fish were present. They were seen investigating leeches, planarians and water snails, and to have regurgitated worms; tadpoles may be important prey items when abundant (Patterson & Davies, 1977). In our study area, they seemed to be largely invertebrate feeders, whereas larger snakes fed mostly on fish.

In the tongue flick experiment both tiny and larger snakes responded to all prey odours more than to the tapwater control. Both groups responded most to worm, and this was greater relative to the other prey odours in tiny than in other snakes. Snakes can distinguish between different species of prey of the same type (*i.e.* frogs, fish, worms), both as reflecting geographical distributions (Burghardt, 1970) and as a result of learning (Fuchs & Burghardt, 1971). Sympatric prey species were not available in the present study, and easily obtainable types were used, so the relative responses to the different prey types cannot be used as evidence of prey-selection in the field.

It is, however, apparent that *N. maura* does not possess an ontogenetic switch in responsiveness to different prey types, such as that found in *Nerodia erythrogaster* by Mushinsky & Lotz (1980), to parallel the observed change in diet and foraging behaviour in the field. Snakes of all sizes were found to eat worms, tadpoles and fish in captivity, and prey selection in the field is probably related to availability and instantaneous cost-benefit relations rather than long-term genetically fixed patterns. *N. maura* appears to be a rather opportunistic feeder, and will take dead and dying fish in the wild. Most individuals would eat the worm *Eisenia foetida*, though many other animals find it distasteful, and there was evidence that it was toxic to the snakes.

## THERMAL RELATIONS

The thermal ecology of *Natrix maura* has previously been considered in terms of diurnal activity only, and agreement found between field and laboratory observations. Spellerberg (1976) found an activity range of 20–38°C, mean 29°C, in a thermal gradient, and Davies *et al.* (1980) a range of 20–28.5°C, mean 25.7°C. These values were comparable to those found in daytime in the field—mean body temperatures 25.5°C in spring and 27°C in summer (Davies *et al.*, 1980; Patterson & Davies, 1982)—and encourage the view that *N. maura* is active with an eccritic temperature about the same as its preferred temperature, 26–27°C.

The present study shows *N. maura* to be less thermophilic than the observations above suggest. In spring they were active in water down to 13.8°C in daytime, possibly even lower if nocturnal activity occurs at that time of year. Daytime eccritic temperatures in summer—27.5°C in August and 25.8°C in September—were comparable to those found by Patterson & Davies (1982). The occurrence of nocturnal activity reduces the daily activity eccritic temperature to 22°C. Although there is some bias from a relatively greater number of animals caught at night, at a time of year when most active snakes are in, and at the same temperature as the water, mean daily water temperature will be a good guide to mean body temperatures. This was 21.6°C on sunny days in September. Thus in summer the mean activity body temperature of *N. maura* is lower than previously thought, and the range much wider. It is probably less thermophilic, and more of a thermal generalist, than previously supposed.

## COMPARISONS BETWEEN *NATRIX MAURA* AND *N. NATRIX*

*Natrix natrix* extends north into Finland, *N. maura* only to France (Steward, 1971; Arnold & Burton, 1978). Spellerberg (1976) and, in more detail, Davies & Bennett (1981) and Davies *et al.* (1981), have compared these species using *N. natrix* from the northern part of its range, in terms of thermal ecology and thermophysiology, and interpreted their results in terms of genotypic adaptation to latitude and cold climates. They therefore treated the species pair as being ecologically equivalent but thermally distinct, based on macroclimatic considerations.

The present work suggests another difference between the species, that of lifestyle, both as an effect in itself and one with an effect on thermal relations. The limited number of encounters show *N. natrix* as an active forager, spending much of its time searching for and pursuing its anuran prey on land. It showed a tendency towards thermal specialism, with a relatively narrow range of activity body temperatures. It may be expected to have physiological adaptations to this lifestyle, as well as morphological adaptations such as elegant shape.

*N. maura* at the study site was largely a sentinel predator, and more of a thermal generalist. This lifestyle, too, may be accompanied by physiological and morphological adaptations, such as stout shape.

In summer at least, activity of *N. natrix* away from the river or hidden in vegetation is unlikely to change this pattern as daytime shade air temperatures are high, indeed body temperatures may be higher away from water (several *N. natrix* fled from land into water just before capture, and were probably cooled by this). Daytime activity temperatures of the two species in summer in Spain were similar, the main difference in their thermal relations being the nocturnal activity of *N. maura*. Nocturnal activity in *N. natrix* is possible, though perhaps unlikely due to difficulty of finding and pursuing prey in darkness; this is at present under investigation under controlled laboratory conditions.

There are thus at least three possible influences on metabolism which may be involved in differences between rate-temperature curves of cool temperate *N. natrix* and warm temperate *N. maura* demonstrated by Davies & Bennett (1981): (a) differences in their thermal relations due to latitudinal, climatic effects; (b) differences in their thermal relations due to thermal generalism/specialism, the thermal effects of lifestyle. These may be less likely in juvenile snakes. A tendency towards thermal generalism will have a similar effect on body temperatures as increasing latitude (Davies *et al.*, 1981). Influences (a) and (b) will act to cancel each other out in this case; (c) differences in lifestyle may have a direct effect on metabolic relations (Davies *et al.*, 1981), with resting metabolism perhaps related to frequency, duration or level of activity.

Davies & Bennett (1981) interpreted the difference in metabolism in terms of the first influence, climate. We point out that it is not the only possible one, indeed all three may be involved.

Differences of lifestyle in snakes along an active foraging-sentinal predation axis are widely recognized (*e.g.* Pianka, 1978), though often considered at a rather gross level, *i.e.* the colubrid-elapid type versus the boid-viperid type. Shine (1980) demonstrated a lifestyle effect among elapids, but little work has been done at lower taxonomic groupings. A comparison of *N. maura* and *N. natrix* in sympatry is in progress to evaluate the possible effects of lifestyle in closely related forms. Comparative work on cool temperate *N. natrix* will show how climate affects one of these species, and may indicate why the other does not extend as far north.

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# A PRELIMINARY NOTE ON THE CARE AND BREEDING OF *BOMBINA MAXIMA* (BOULENGER, 1905) IN CAPTIVITY

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## SUMMARY

Notes are given on the behaviour of *Bombina maxima* as observed in captivity. The males, and to a lesser extent also the females, display a behaviour pattern which has been provisionally described as territorial. Clasping, making sideways jerking movements and the emitting of the excitement-call, are here explained as serving to maintain or to establish a certain distance between individuals. The toads have been bred in captivity. The development of tadpoles is described and compared to that of the other known species of *Bombina*.

## INTRODUCTION

Very few specimens of *Bombina maxima* (Boulenger, 1905) had been seen alive in Europe until fairly recently, and even major museums failed to have it in their collections. The species was collected for museums in Britain, Germany, Austria and the U.S.A. during the early part of this century (Boulenger, 1905; Mell, 1922; Werner, 1924; Schmidt, 1927; Pope, 1931). Stadtmüller (1931) reports on a specimen examined by him which he bought from a dealer and which originated from Yunnan. Reports that the species has been kept and bred in Hungary cannot be corroborated for lack of further information. Liu (1936, 1945, 1950) was the first to deal with the species in detail and describes its life history.

During the latter part of 1980 hundreds of *B. maxima* suddenly turned up on the European market. They were shipped via Hong Kong to two major herptile dealers, Van Mourik (Netherlands) and Hoch (Germany). After a short boom the number of specimens kept alive in captivity dwindled rapidly for various reasons, but mainly because of an epidemic caused by a bacterial infection (Diesener, 1981). It is now once more rare in amateur terraria.

The collecting locality of the specimens is unknown. Marked differences occur in dorsal and ventral colouration patterns (Kühnel & Epperlein, 1981).

The aim of this paper is to present information on the care and breeding of the species under captive conditions. All observations are made on captive specimens.

## CARE

Eighteen specimens were kept in glass aquaria. Most bell-toads measure *c.* 60 mm but some attain at least 75 mm. Six specimens were housed in a 60 × 30 × 30 cm tank, furnished with a ground soil of coarse sand, with stones and pieces of corkbark placed on it. The waterlevel was 7 cm. The toads could find hiding places both under and above the watersurface. Twelve specimens were housed in two full-glass aquaria of 60 × 40 × 40 cm, furnished with 10 cm high density foam, stones and pieces of masonite sheeting to afford hiding. In both instances the toads were bred.

In order first to increase the animals' condition, the water temperature was raised until it reached approximately 20°C, and the toads were fed several times weekly on naked mice and big earthworms. In the beginning of February 1981 the temperature was lowered again. The aquarium was standing in an unheated room, where temperatures could sink to about 7°C in winter. Food was still accepted at temperatures of 10°C. In spring the males developed large black nuptial pads on the first three fingers and the forearms, but hardly on the chest.

One of the observation tanks will be dealt with here. Although the aquarium was too small for the six toads, they were left in it for the time being. At that time other keepers of *B. maxima* lost many specimens due to sudden diseases. Our own toads were apparently healthy, so it was decided to maintain the *status quo* for some time. The average temperature of the water rose according to the season; during summer, temperatures sometimes exceeded 25°C. Food was now offered once a week. There was however little mating activity and the mating call was not heard.

In August 1981 the toads were moved to a larger aquarium of 110 × 55 × 50 cm, furnished with big stones, sand on the bottom, a waterlevel of 8 cm and some floating waterplants (*Fontinalis, Elodea, Ceratophyllum, Hydrocotyle*). During the day the tank was illuminated by a 25 W neon light. The waterpart was not filtered or aerated. In this aquarium most observations on the toads' behaviour were done. Although the thickness and the black colour of the males' nuptial pads clearly decreased in July and August, calling and amplexus were still observed. The toads appeared to be much more active now than earlier in the season in the small aquarium and from now the six toads were observed in the larger aquarium.

Although the toads were often visible and active at daytime, especially when they were fed, they led a mainly nocturnal life. At night they moved about most and could also be seen sitting on land. During the day they sat in the water, hiding under it but also squatting at the water's edge.

Like the other *Bombina* species, these toads actively jump or swim towards prey. Then the tongue is protruded first, but if the prey cannot be caught in that way it is snapped up. Even big prey like naked mice and the biggest worms are eaten. Prey can also be captured under water. *B. maxima* appears to be very voracious but less impetuous in swallowing prey and fighting for it, than the other species of *Bombina*. A few days after feeding the faeces are found in the water; they are of elongate shape and approximately 1.5 cm long.

## REPRODUCTIVE BEHAVIOUR

Any sudden movement in the aquarium by objects approximately the size of a toad immediately provokes two kinds of behaviour. If, for instance, food is offered and one or more toads start moving towards the prey, this frequently induces the males to clasp. If the clasped animal is a male, it usually frees itself with some rapid movements, at the same time uttering the release-call. If the clasped animal is a non-receptive female, she also gives a release-call (at present not distinguished from the male's release-call). She keeps her hindlegs stretched or flabby, flattens her body and keeps the eye membrane closed over the eye. By slow crawling movements of the forelegs she tries to slither away out of the male's grip. These movements look like those on a slow-motion picture. This phenomenon has also been described in *B. variegata* and named "Chamäleonreaktion" by Birkenmeier (1954; see also Savage, 1932). By making too sudden movements the female would possibly stimulate the male to strengthen its grip. While escaping from a male, the female of *B. orientalis* often hammers on the clasping male's forelegs with her forelegs. This behaviour has not been observed in *B. maxima*. The male attempts to prevent the female from climbing ashore and thereby from breaking away from his grip by making rowing movements with his hindlegs and so staying in open water. Other males, attracted to these movements, are knocked off by the amplecting male by fierce thrusts of the hindlegs.

During the amplexus the clasping male makes some remarkable movements. It moves its body to the left, to the right or alternating left and right, with short jerks, quickly succeeding each other. First, these movements appeared to be only connected with the strengthening of the grip but that was not necessarily always the case. The actual grip is often very loose, the male hardly touching the female's back with thorax and throat. The movements were, furthermore, also made without clasping. This behaviour is often provoked when two or more animals come into each other's proximity. In such a case, the toads sit opposite or next to each other for some minutes, constantly making these jerking movements with intervals of approximately one or a few seconds. It is noteworthy that the females show this "jerking" behaviour too. Moreover, the females also execute claspings, although not so frequently and persistently as the males. Since the males can from a distance easily be distinguished from the females by the observer, this observation is not open to doubt. It is apparently a wilful amplexus during which the female tightly clasps the flanks of another toad. It is often elicited during feeding when one animal seizes prey and a female has to wait till another prey item comes in reach. It thus seems to be an aggressive behaviour and could indicate ranking in the hierarchy. Clasping females were also observed by another keeper of *B. maxima* (Houwaart, personal communication 1981). It is not yet known in the other species of *Bombina*.

During periods of intense activity the toads often swim up to each other and a sort of wrestling ensues during which the toads clasp randomly. The jerking movements are made constantly and both the release-call and the excitement-call are emitted.

This behavioural repertoire: jumping on each other, making jerking movements, clasping and emitting the release- and excitement-calls, is displayed all summer and autumn. Only the "real" mating call, the 'Unkenruf', was not heard any more after August. From July onwards the males gradually lost the big black nuptial pads, but retained the thickened forearms. Even when the temperature dropped to 10°C in winter, the above-mentioned behaviour hardly changed. For this reason, it is most likely not exclusively associated with mating during the mating period but also has a social function which, moreover, is maintained after the reproductive period and could be territorial.

Some sort of territorial behaviour is known in different anuran families (Heusser, 1969) and in a number of species it is assumed that they "carry" their territory with them, *i.e.* they do not occupy a territory in the sense of a small marked-off area of which the boundaries are defended against potential rivals, but they maintain a certain individual distance ("Individualdistanz", Heusser, 1961), a critical distance between one individual and the others, that may not be transgressed. This has, for instance, been observed in the European *Bombina* species (Heusser, 1961, 1969; Lörcher, 1969). Investigations have shown that male fire-bellied toads (*B. bombina*) occupy more or less circular territories with a radial distance of 1–1.5 m, whereas the territories of the yellow-bellied toad (*B. variegata*) have a radius of only 0.5–0.75 m. The mating call in both species has been interpreted as serving to maintain the individual distance and therefore having a territorial function (Lörcher, 1969). In our opinion, amplexus may partly have the same territorial function. The behaviour of *B. variegata* which has received the somewhat inadequate name "Scheinpaarung" (sham-mating, Birkenmeier, 1954) could point to this.

Antiphonal calling is known in *Bombina* but the males do not necessarily form choruses when calling. Probably *B. maxima* is not an exclusive chorister either. The possibility may, however, be mentioned that the calling may serve to synchronize mating activity and to keep the males clustered, as it is known of certain typical chorus-forming species (cf. van Gelder *et al.*, 1978). The vocal repertoire of *B. maxima* is described by Van den Elzen & Sparreboom (in prep.) where the necessary equations for the regressions of Fig. 1 may also be found.

Observations on captive specimens of *B. maxima* during one year cannot give a definite answer to the question of the meaning of the behaviour described here. In our opinion, however, it has to do with establishing a certain distance between the individual

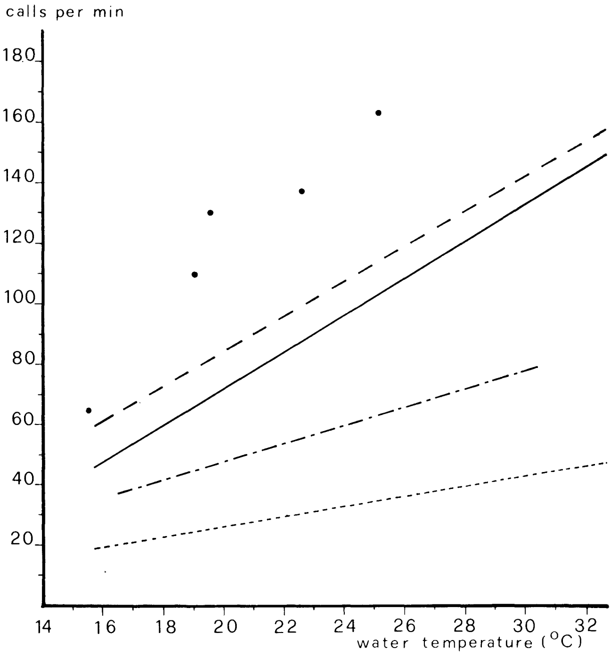

FIG. 1. Relationships between water temperature and calling rate (calls per min). The equations for the regressions will be published elsewhere (Van den Elzen & Sparreboom, in preparation). – – – –, *Bombina bombina*, 40 mm (Lörcher, 1969, Fig. 15). ——, *B. variegata*, 31–47 mm (Lörcher, 1969). –·–·–·–·–, *B. variegata* × *B. bombina*, 28–32 mm (Schneider & Eichelberg, 1974). ------, *B. orientalis*, 47 mm (Van den Elzen, 1979). ● ● ●, *B. maxima*, two males 55.0 and 64.4 mm.

toads during the whole period of activity. If this is correct, not only the mating call serves to maintain the distance as in the European species of *Bombina* (Lörcher, 1969), but the clasping behaviour, the jerking movements and the excitement-call do so as well.

## BREEDING

While the toads were still housed in the smaller aquarium, spawn was produced on 20 June 1981. The spawning itself was not observed. The eggs were deposited in small clusters among the vegetation (*Fontinalis*) and loose on the bottom.

According to Liu (1950), the eggs are laid in masses, which mostly sink to the bottom of the pools. If there is any vegetation floating on the surface, the egg-mass is attached to it and suspended from it. It has also been recorded (Anon, 1977) that the eggs are laid in small clusters that can also be deposited in marshy areas in stagnant water, between grasses and reeds.

The larvae were hatching on 25 June. There were about 40 hatching larvae. The eggs could not be counted. Half the number of larvae were kept in an aquarium of 70 × 40 × 40 cm, which had previously accommodated newts. The aquarium was furnished with sand, stones and some floating waterplants, moreover it contained much debris and algae. The rest of the larvae was put in a small aquarium (30 × 20 × 20 cm) containing waterplants. Anuran larvae, when kept in larger tanks, generally grow bigger than in smaller containers, but this was not the case here. In both aquaria the tadpoles grew alike and completed metamorphosis at the same time, having reached about equal size. Rearing the tadpoles presented no difficulties. Water temperature varied from 17–23°C. They were fed on bruised lettuce, algae, Tetramin and now and then a tablet of beer yeast. Development until the completion of metamorphosis took 5–6 weeks and proceeded as follows:

25 June: hatching. 28 June: larvae hanging at glass and plants. 6 July: ± 20 mm, grazing algae and lettuce leaves. 16 July: ± 35 mm, beginning of hindlegs. 29 July: first forelegs broke through. Dorsum became rough and warty and showed vague light spots on shoulder region. 3 August: biggest tadpole 42 mm. 5 August: first metamorphosis, all the other tadpoles underwent metamorphosis during the following week. Young toads measured 14 mm. They were fed on *Tubifex, Cironomus* larvae and *Drosophila.* A few months later, dewworms and flies were taken.

Twenty-three of the tadpoles grew up well and 22 reached metamorphosis. The young toads resembled their parents in colour and appearance. Some had light-green spots, distributed irregularly over the back and hindlegs. The green colour was somewhat lighter than in the adults. One juvenile had a completely green back. Unlike the other *Bombina* species, the yellow coloured vent becomes apparent before metamorphosis. Before the forelegs break through, two light spots can be distinguished: the yellow palms of the hands. On the hindlegs too, the yellow colour of the footsoles is already visible when the legs are still very small. The development of the larvae was found to agree with the account of Liu (1950). It can finally be noted that tadpoles of *B. maxima* do not grow as big as those of other *Bombina* species and accordingly reach metamorphosis at a smaller size. The following maxima have been measured of larvae bred and reared in captivity:

| | | |
|---|---|---|
| *B. maxima* | larva 42 mm | juv. 14 mm |
| *B. variegata* | larva 50 mm | juv. 19 mm |
| *B. orientalis* | larva 47 mm | juv. 17 mm |

The young toads were reared in small plastic aquaria (30 × 20 × 20 cm) filled with a shallow layer of water and a piece of corkbark serving as hiding place and

FIG. 2. *Bombina maxima*, adult male.

terrestrial part. In this way the animals could easily pick up food from the water. Almost one year old, the young toads now measure ± 4 cm and grow well on a diet consisting mainly of earthworms.

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# THE HERPETOFAUNA OF GIBRALTAR—STATUS, RECENT HISTORY AND CURRENT RESEARCH

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## INTRODUCTION

The acceptance of the International Strategy for the Conservation of European Herpetofauna in 1980 has served to highlight two major problems: (a) the increasing pressure on all species of European herpetofauna; (b) the lack of information available on the herpetofauna of some European regions.

The south of Iberia is rich in amphibians and reptiles, is little studied, and is an area where species are threatened by man's activities and ignorance. Gibraltar (36° 7′ N, 5° 21′ W), although politically distinct from the rest of the Iberian Peninsula, is an example of a site in which man has greatly altered habitats causing generally detrimental changes in the fauna. Being limited in extent and having a considerable recorded history, Gibraltar is a conveniently delimited area of southern Iberia in which a study of recent changes in vegetation and fauna has been possible.

The history of the herpetofauna of Gibraltar can be extrapolated from a knowledge of the present distribution and preferred habitats of the species and from the known history of the development of the vegetation of the area. A similar study of the history of the avifauna of Gibraltar has recently been attempted. (Cortés, Finlayson, Garcia & Mosquera, 1980).

## GIBRALTAR

Gibraltar is situated at the eastern end of the Strait of Gibraltar, and together with the southern coast of the Spanish Province of Cadiz forms the northern shore of the Strait. The Rock is a mass of Lower Jurassic limestone running approximately north-to-south along the greater part of a peninsula about 6.0 km long and 1.2 km across at its widest point. The northern end of the peninsula is a flat, sandy isthmus by which the Rock is connected to the Spanish mainland.

The northern and eastern faces of the Rock consist of steep cliffs rising to 426 m. The eastern cliffs are ascended to 290 m along the northern half by accumulated sand slopes. The western slopes of the Rock are less steep and largely vegetated, although the Town lies on the lower parts. On the south of the peninsula a series of flat, stony terraces descend from the highest point to the sea.

The terms "Gibraltar" and "the Rock" are locally synonymous, but in this paper "the Rock" will refer specifically to the limestone mass, in order to distinguish this from " the isthmus", which is of different geology and vegetation.

## CLIMATE

The climate of Gibraltar is Mediterranean. Mean temperatures of the coldest and warmest months are 13°C and 24°C for January and August. Mean annual rainfall is 797 mm although there are considerable yearly variations. Most rain falls between October and April. Due to its geographical positions, Gibraltar experiences less extreme temperatures and more rainfall than much of the surrounding area.

Predominating winds are from the east and west sectors (88% of the days per year). About 40% of days have winds from the east sector. The easterlies, forced up the sheer cliff, cause condensation and produce the "Levanter" cloud. Usually—particularly during the summer—the cloud covers the Rock while the isthmus and the extreme south remain clear. At other times the cloud will stretch several kilometres north and west from Gibraltar.

## THE HERPETOFAUNA

### METHODS

Current herpetological research concerns the ecology of *Psammodromus algirus* and *Podarcis hispanica*. Numerous other incidental observations have been made during the course of field work, particularly in relation to the habitats of the species observed. In addition, colleagues resident in various areas of the Rock have been invaluable in passing on to me records of their own observations of herpetofauna. Older residents of Gibraltar with an interest in natural history have been interviewed. By extrapolation from the present situation it has been possible to speculate broadly and qualitatively on the changes the herpetofauna of Gibraltar have undergone.

### HISTORICAL

The first known reference to the herpetofauna of Gibraltar is by Ayala (1782). Only a passing reference is made to snakes. There are somewhat confusing descriptions of lizards, although a fair one of *Acanthodactylus erythrurus* which is mentioned as occurring on the "white soils" (either the east sand slopes on, more likely, the isthmus) and of *Podarcis* and *Tarentola* on roofs. A vivid description is given of *Lacerta lepida*, which is considered "abundant on this hill".

## PRESENT STATUS AND RECENT HISTORY

The Western Spadefoot Toad *Pelobates cultripes* was formerly common and widespread on the isthmus and was frequently heard and observed up to the winter of 1979/80. Breeding must be doubtful since no pools persisted either in that year or in 1980/81. It is not known whether there is any breeding in two artificial duck ponds in the garden on the Spanish side. In past years individuals have been known to cross the airfield to the south (where there is no suitable habitat), but recolonization from further north must be virtually ruled out considering the urban belt of La Linea. The Natterjack *Bufo calamita* has been recorded (J. Bensusan, personal communication), but there are no recent records.

Busack (1977) uses old records in giving Gibraltar as a location for a number of reptiles. Caution is necessary when considering the records of Chameleon *Chamaeleo chamaeleon* and Spanish Psammodromus *Psammodromus hispanicus* in particular. Experience of old botanical and ornithological collections and records has shown that in most cases the locality "Gibraltar" does not refer specifically to the Rock, but to an indistinct area comprising the Rock, its hinterland in Spain (the "Campo de Gibraltar"), and even Cadiz Province as a whole (Wolley-Dodd 1914; Cortés *et al.*, 1980). There are no other records of *P. hispanicus* at Gibraltar, although it may have occurred on the isthmus. Observations of *C. chamaeleon* have occasionally been claimed (often due to confusion with *Tarentola*!) and one was captured in June 1979. Proximity to human habitation suggests captive origin and a subsequent thorough search of adjacent vegetated areas yielded none. If it did occur formerly it is likely to have disappeared at a time when the vegetation of the Rock was cleared.

The Moorish Gecko *Tarentola mauritanica* occurs on walls, buildings, cliffs and rocky clearings in vegetation.

The Spiny-footed Lizard *Acanthodactylus erythrurus* is common around La Linea on sandy ground and on the east end of the remaining vegetated strip of isthmus where plant cover is more open. It is likely to have been more widespread there and on the east sand slopes where it does not now occur. The species is not observed south of the airfield. It would appear that the airfields, roads and housing of the area impede colonization of suitable areas of the Rock.

The Three-toed and Bedriaga's Skinks (*Chalcides chalcides* and *C. bedriagai*) are present on the isthmus (including the Cemetery) and *C. bedriagai* has been confirmed on the sand slopes.

*Psammodromus algirus* in common in the Maquis, especially high Maquis with leaf litter, and on the edges of the Maquis. It is regularly encountered in firebreaks and open areas with scattered bushes, but avoids entirely open areas. It is not found in the Steppe vegetation of Windmill Hill Flats, the sand slopes or the isthmus. The present habitat of the Cemetery is similar in structure to areas on the Upper Rock where this species occurs. However *P. algirus* is not found there. The open vegetation present there until recently was probably unsuitable (and perhaps occupied by *A. erythrurus*) and recent colonization by *P. algirus* impeded by the roads and urbanization that has isolated the Cemetery.

The Iberian Wall Lizard *Podarcis hispanica* is more widespread, but is not found over most of the Town and is rare in the scrub away from stony clearings. It forages in low ground vegetation and in leaf litter, and spends longer than the last species basking. Both species climb in vegetation (*Psammodromus* more than *Podarcis*), but only *Podarcis* regularly scales walls and cliffs. The Wall Lizard is never encountered far from cover, and is rare in large flat areas of low continuous vegetation, probably due to lack of basking sites. It was hence probably rare over most of the isthmus, although it is now extremely abundant in the parts of the Cemetery where the vegetation has been broken up by tombstones which provide cover and basking sites. Colonization by this species has therefore not been impeded.

The Ocellated Lizard *Lacerta lepida* still occurs as an isolated population on the Cemetery. It is now rare, although older gravediggers recall times when it was regularly encountered (about 30 years ago). Increased human activity, allowing little undisturbed basking could be a contributory factor to the decrease. It is still found on the Spanish side of the isthmus. On the Rock itself there have been no confirmed records for about ten years. Disturbance and seral succession may have been causes for a decrease in numbers. The species is certainly no longer "abundant on the hill" (Ayala, 1782) and may well be absent from much of the western slopes.

Snakes on Gibraltar are known from relatively few observations, so that the state of their populations are even harder to determine. The Horseshoe Whip Snake *Coluber hippocrepis* is the most frequently observed. It occurs in dense and open scrub, firebreaks, the isthmus (including the Cemetery) and gardens, often venturing into households. The Southern Smooth Snake *Coronella girondica* is also widespread but not encountered as frequently. The Ladder Snake *Elaphe scalaris* and Montpellier Snake *Malpolon monspessulanus* have only been recorded from the Maquis, the latter a single dead individual. The Grass Snake *Natrix natrix* has been recorded on the Upper Rock and isthmus, while the Viperine Snake *Natrix maura*, formerly found on the isthmus (J. Bensusan, personal communication) has not recently been found.

## DISCUSSION

By simple consideration of the reduction in areas available to the herpetofauna their corresponding decrease becomes evident. Populations of most species have been reduced, some have disappeared from certain areas, and others are in danger of doing so. On the Upper Rock the herpetofauna has also been subjected to changes in habitat type. The habitat changes have caused changes in breeding species of birds (Cortés *et al.*, 1980). Colonization by reptile species is obviously much more difficult and necessarily a long term process. The result of habitat change will often be a drop in numbers and ultimate local extinction. This appears to be happening in the case of

*Lacerta lepida* on the Upper Rock. *Podarcis hispanica* will have been more common when the vegetation was more open, while *Psammodromus algirus* was possibly less so. The position as regards snakes is more difficult to determine.

## CONCLUSIONS

The problems faced by the herpetofauna of Gibraltar over the last few centuries, and today, are similar to those in other parts of Europe: fragmentation of habitats; seral successions; lack of breeding sites (especially for amphibians); predation by feral cats and children; disturbance; inadequate habitat protection and lack of law enforcement. (All wildlife is protected in Gibraltar under the 1964 Animals and Birds Ordinance. Enforcement is however difficult, especially in the case of reptiles which are generally viewed with disgust and contempt.) The measures needed to combat these threats are similarly common to other countries. Public education in particular is essential, particularly in those Mediterranean countries where herpetofauna is held in low public esteem. Some of this is now being carried out by the Gibraltar Ornithological Society on the Rock itself. The I.S.C.E.H. has been given wide coverage in the local media, and a Television programme on the loss of the isthmus has been produced and screened.

There is no protection in law against habitat loss, a matter which is now being reviewed by the legal authorities in relation to birds. There will however be a consequent benefit to reptiles. The difficulty lies in that there can only ever be small amounts of habitat available in a place of such a high density of population (30 000 inhabitants). Nevertheless, because of the political separation from the mainland, species of "local" importance have "national" status. In this way species that are common elsewhere in the region could receive protection and public support if a deliberate campaign is organized. This could reverse the situation and make the Rock an important refuge for some species.

Threats similar to those experienced in Gibraltar are currently increasing in the surrounding area of neighbouring Spain. Species which may not yet be in danger in the region may suffer local reductions as they have done in Gibraltar. More specifically, the "Campo de Gibraltar", already largely industrialized around the Bay of Gibraltar at the expense of coastal habitats, is earmarked for further development once the Spanish frontier is opened. In this case the herpetofauna of the whole area would be even more seriously threatened.

The problems of local extinction and difficulty of recolonization of isolated patches of habitat have been made clear in the case of Gibraltar (whose history is better documented than that of most equivalent areas in the region), and worsens the outlook for the future. Short term solutions—such as the digging of breeding ponds for amphibians—can only meet with limited success, especially when viewed against this background. The virtually total loss of the sensitive and rich coastal habitat on the isthmus occurred at a time when conservationists in the area were few. It need not have happened at all had political expediency not transcended environmental planning. Both these dangers remain.

The Province of Cadiz and the Rock of Gibraltar form the southernmost extreme of southwestern Europe. As such, the region's importance in determining the origins of the European herpetofauna have been recognized (*e.g.* Bons, 1974; Busack, 1977). However, even though Spain is one of the Mediterranean countries whose herpetofauna is best known (Lambert, 1981) there is scant knowledge of the distribution of most species in the region, away from Gibraltar. Busack's maps (Busack, 1977), although contributing much to a knowledge of the distributions, are incomplete and, in the case of the Rock, outdated. The distribution even of those well-studied vertebrates, the birds, is little known in the Province.

There is therefore a need to ensure full protection of species and habitats such as on the Rock itself; to achieve regional co-operation between Gibraltar and the local Spanish administrations once the frontier opens to prevent economic development being at the expense of conservation; to foster the mapping of the herpetofauna of this area—the part of Europe nearest Africa and with such a rich diversity of amphibians and reptiles; and to ensure, by education, the co-operation of the public in their protection.

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# WINTER HABITAT SELECTION BY SOME NORTH EUROPEAN AMPHIBIANS

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In Sweden today fourteen amphibian species are known to occur (introduced ones included). Nine of these, however, are concentrated in the southern part of the country; only five occur in the far north. These are the common frog (*Rana temporaria*), the moor frog (*R. arvalis*), the common toad (*Bufo bufo*), the crested newt (*Triturus cristatus*) and the smooth newt (*T. vulgaris*).

The border zone in which the central European plants and animals meet the more arctic (or high boreal) species is referred to as "limes norrlandicus" (Norrland is the name used for the nine northernmost provinces of Sweden; most of the country belongs to this area). The border (Fig. 1) is often defined as the northern limit of the pedunculate oak (*Quercus robur*). It is also defined by the northern limit of the field wood-rush (*Luzula campestris*) and the southern limit of the willow *Salix lapponum* and the sedge *Carex juncella.* This border is well to the south of Sweden; it can be reached within 150 km north of Göteborg.

North of "limes norrlandicus" climatic conditions are severe in winter. The first night frost normally occurs in August, and the first snow in October, or even September in the far north. Ice begins to cover the smaller lakes in November. Snow may remain on slopes facing north until May or even June. The snow does, however, offer excellent protection for plants and animals against extreme cold; temperatures beneath it are seldom below 0°C.

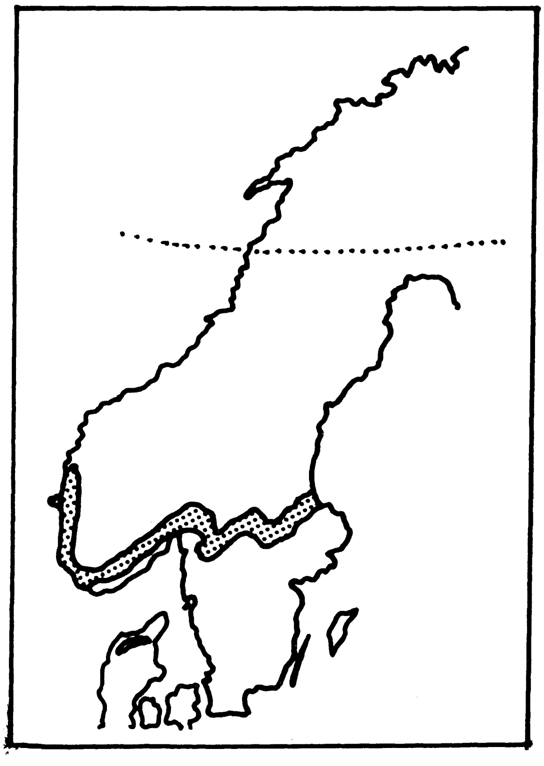

FIG. 1. Map of Scandinavia, showing the "limes norrlandicus" and the Arctic Circle.

The winter ecology of amphibians at such latititudes must be rather different from the ecology of amphibians in the British Isles or central Europe. This paper surveys what is known of the winter ecology of the five species which covers the "limes norrlandicus"; it is notable that they all probably occur north of the Arctic Circle.

The *common frog.* This is known to be able to spend the period of winter inactivity in water as well as on land. Details of the habitat preferences of males and females have, until recently, been incorrectly described in most Scandinavian textbooks of biology. It has been said that most males remain in the water, but that females spend the winter on land. Originally all male frogs were regarded as aquatic in winter—this was postulated by the famous Danish zoologist Japetus Steenstrup at a meeting of the Royal Danish Society of Sciences in 1846. Steenstrup was later criticized by other Danish zoologists for his conclusions, but the statement survived the polemics that followed; Steenstrup's authority was very strong.

Today, however, we know that in winter time both males and females of the common frog may remain on land *or* in the water. It seems likely, however, that if a good overwintering site is available in water, this will be preferred. A good site is one where the water is little polluted, but is rich in oxygen and where there is some protection against predation. Favourable sites include wells, especially those built in springs where clean water runs in slowly from underneath; parts of streams; and some stream mouths can be favourable, too.

The *moor frog.* Less is known about the winter ecology of this species, although it is commoner than the so-called common frog in many areas. The sight of moor frogs migrating in spring time from their winter quarters in piles of old leaves is familiar in many places, so many must overwinter on land. There seems no reason, however, why the frogs should not spend the cold season in water, and recently this has been observed at the Umeå area in northern Sweden; the frogs remain in a small river (J. Elmberg, personal communication).

The *common toad* is said by almost all authors to overwinter on land. It is remarkable, therefore, that in Sweden it is found in water during winter at least as often as the common frog. In many areas it is surprisingly easy to find in wells and small streams. The overwintering sites are sometimes the same as those of the common frog, but there are also sites where the water is running too fast for the latter. If one attempts to capture the toads at these sites they move away very quickly, even though the water may be very cold (1–4°C).

The *smooth newt* and the *crested newt* have been said, even in modern literature, to spend the winter in frostless places under the soil surface after digging themselves down. Newts are also, however, found in old stubs and logs or under piles of old leaves. The smooth newt has even been found in seaweed-covered walls on the seashore. This means that the newts do not necessarily have to dig, rather that they have tried to find places where some heat is produced by decomposing plant material. It seems most probable that such places are their normal winter habitat.

Overwintering in water by non-neotenic newts also occurs in Sweden, but it seems to be rare. The first, and still the largest, collection of such animals, was found in the early spring of 1969 at Hunneberg, close to the southern part of Lake Vänern. A fish pond, with slowly running water, was emptied, and 84 specimens of the two species were collected by digging amongst the horsetail (*Equisetum*) roots in the pond floor. The newts were almost inactive when captured—compare this with the situation in frogs and toads discussed above. Non-metamorphosed larvae of both species may also overwinter in water; this was first reported in Denmark in 1922 and in Sweden in 1972, but it seems to be rather common, especially in south-west Sweden. It can be observed in deeper ponds which are overshadowed by trees, where temperatures are too low to permit full development and metamorphosis of the tadpoles in one season.

In conclusion: the five amphibian species which cross "limes norrlandicus" may overwinter in water as well as on land; the preferred habitat depends on local conditions.

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# THE DISTRIBUTION AND POPULATION STATUS OF THE AMPHIBIANS AND REPTILES OF FINLAND FROM 1960 TO 1979 (ABSTRACT)

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Up-to-date dot maps were drawn for all the Finnish amphibian and reptile species, based on comprehensive enquiries carried out among amateur and professional biologists from 1974–1979. The species covered were: great crested newt (*Triturus cristatus*), smooth newt (*T. vulgaris*), common toad (*Bufo bufo*), common frog (*Rana temporaria*), moor frog (*Rana arvalis*), marsh frog (*R. ridibunda*), common lizard (*Lacerta vivipara*), slow-worm (*Anguis fragilis*), grass snake (*Natrix natrix*), smooth snake (*Coronella austriaca*) and adder (*Vipera berus*).

The marsh frog died out from two recorded localities in the 1960s, and slow-worms seem to have disappeared from the mainland of Åland at the beginning of this century, but no other changes in the ranges of the Finnish species could be detected. Some old, probably dubious records of the grass snake and the slow-worm from the vicinity of the Arctic Circle, inland records of the smooth snake, and records of the great crested newt from the southern and southwestern coastal area of the Finnish mainland, should be excluded from the herpetological literature referring to up-to-date ranges of these species in Finland.

Provisional abundance of eight Finnish species was worked out. Many local populations of the adder and the common toad seem to have been declining in southern Finland. More detailed data on both the methods and the results of the survey are given in the following paper: Terhivuo, J. (1981). Provisional atlas and population status of the Finnish amphibian and reptile species with reference to their ranges in northern Europe. *Annales Zoologici Fennici* **18,** 139–164.

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volumes are a collection of essays about various aspects of reptilian diseases; they are *not* a handbook to diagnosis and treatment, although both of these subjects are dealt with. The essays are clearly aimed at professional biologists and veterinarians, although others will find much of interest within them. The subjects range from "Pathology and histopathological techniques", "Viruses" and "Bacteria" to "Nutritional diseases" and "Clinical aspects of diagnosis and treatment". Most of the chapters are excellent, and I learnt a great deal from them. Some are less successful, and the chapters on "Protozoa", "Endoparasites" and "Ectoparasites" are rather boring and uncritical lists of some of the species which have been found in various kinds of (mostly unspecified) association with reptiles. Reptilian pathology may be one of the cinderellas of the sciences, but it can do better than this.

R. A. AVERY

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 278–280 (1982)

# BOOK REVIEWS

HANDBUCH DER REPTILIEN UND AMPHIBIEN EUROPAS. BAND 1. ECHSEN 1. Edited by Wolfgang Böhme (1981). 520 pp. Wiesbaden: Akademische Verlagsgesellschaft, DM 216 (DM 184 for advance subscribers to all five volumes).

A major gap in the herpetological literature was filled with the publication of the superb Arnold/Burton/Ovenden *Field Guide to the Reptiles and Amphibians of Britain and Europe*. The logical next step is a comprehensive and scholarly compendium—not a book to read, or an identification guide, but a work of reference. This now being supplied, under the able editorship of Dr Wolfgang Böhme. A major undertaking of this kind is inevitably a long time in completion, and so far only volume 1 has appeared. It covers all the lizards except for the genus *Lacerta* sensu lato. I find very little to fault, and much to admire, in this volume. The accounts of each species are dealt with under a standard series of subheadings, but for some there are gaps, which reflect our imperfect knowledge. There is also an imbalance of treatment. Taxonomy and systematics are emphasized; behaviour and ecology are dealt with, although in less detail; physiology is scarcely covered at all. In general, however, this reflects the current state of European herpetology; the situation will have changed by the time a second edition is published.

The book is not cheap, but will be so indispensable that I have bought my own copy. If the remaining volumes maintain the same high standard, then I cannot imagine a serious herpetologist in Europe being able to function effectively without them. He will need to be able to read German, although the book would be useful even for the References and the Figures (for which no linguistic skill are needed) alone.

Editor, contributors (sixteen for this volume, including four from the U.S.S.R.), and publishers are to be congratulated on this excellent book.

R. A. AVERY

THREATENED AMPHIBIANS AND REPTILES IN EUROPE. By Rene E. Honegger (1981). 158 pp. Wiesbaden: Akademische Verlagsgesellschaft, DM 68.

There are three particularly important parts to this book, which is a Supplementary Volume to the *Handbuch* reviewed above, and is produced in the same format. The first is a list, country by country, of legislation relating to the conservation of Reptiles and Amphibians in Europe (pp. 40–45). It is already out of date, but this is not a criticism, rather a reflection of the logistics of publication. The second is a "Comparative list of threatened Reptiles and Amphibians", in which species considered to be at some risk are listed under the headings Extinct, Endangered, Vulnerable, Rare and Indeterminate (pp. 48–56). The third is "Individual data sheets for threatened Amphibian and Reptile species" (pp. 72–139). In addition to it's immense value to the conservation effort, this section has a great deal of data on distribution, some of which is otherwise unobtainable. The author is to be congratulated on achieving the herculean task of compiling this material.

I have one criticism. This book, like so much of contemporary conservation literature, falls into the trap of "crying wolf". Thus *Lacerta agilis agilis* is included as "considered to be under some threat" because "... those taxa which are generally considered to be 'common' species, are included to demonstrate that even such taxa seem seriously threatened throughout Europe". *Lacerta viridis viridis* is included in the individual data sheets for threatened species. Both of these lizards are, of course, declining in parts of their range, but to include them in the categories above is quite absurd. If this were merely an intellectual debating point, no harm would be done. Unfortunately there are many influential members of the scientific community—and it is these in turn who influence governments and legislators—who read such wild statements and conclude that all conservationist opinion is consequently worthless.

So much for my personal hobbyhorse. Overall this is a commendable and very useful book. I fully endorse the sentiments expressed in the Dedication "For Katrin and her children's children, with the hope that they may enjoy many more warm summer nights full of Hyla-holler".

R. A. AVERY

BIOLOGY OF REPTILES: *An Ecological Approach*. By Ian F. Spellerberg (1982). viii + 158 pp. (Tertiary Level Biology). Glasgow and London: Blackie. £8.95 (paperback).

Although this has been written primarily for advanced undergraduates, herpetologists generally will welcome Ian Spellerberg's new, wide-ranging book, which integrates established knowledge with the latest findings in reptile ecology and behaviour. The final chapter reviews problems related to the exploitation and conservation of reptile species and populations. Dr Spellerberg begins, appropriately, with an account of the origins, radiation, and classification of reptiles in which he points out that Synapsida are inappropriately named because it was thought at one time that the single fossa was formed by fusion of the two fossae present in diapsid reptiles. The section on Euryapsida is enlivened by mention of the Loch Ness Monster *Nessiteras rhombopteryx*. Although believers are spared disclosure of its notorious synonym, Spellerberg does point out that a much-publicized picture of what appears to be a plesiosaur-like neck and head emerging from the waters of the lock is, in fact, just the enlarged part of a photograph of an otter's tail taken as the animal dived. Subsequent chapters are devoted to morphology, distribution and abundance, reproduction and development, the physical and biotic environment, and reptile behaviour.

Support is given to T. Swain's ingenious hypothesis that the archosaurs may have been poisoned by toxic alkaloids present in angiosperms: but the most serious flaw in this argument is not cited—that flowering plants first appeared 50 million years before the end of the Cretaceous, while the dinosaurs reached their peak of diversity some 30 million years later, almost certainly in response to the availability of this new food material! Reference is made to the author's own observations on the lizard fauna of the Australian deserts, to the absence of copulatory organs in *Sphenodon*, to the correlation between size dimorphism and sexual behaviour in Chelonia, to viviparity and placentation, excretion and water conservation, to thermoregulation, respiration, and other aspects of reptilian physiology. Indeed, there can be few readers who will not discover some new, interesting facts or ideas in Spellerberg's concise, refreshing, and informative account of reptile biology.

J. L. CLOUDSLEY-THOMPSON

POISONOUS SNAKES. By Tony Phelps (1981). 237 pp. Poole, Dorset; Blandford Press Ltd. £10.95.

This book (according to the author) is essentially a practical guide to the field study, husbandry and handling of poisonous snakes. Unfortunately these subjects are covered, somewhat inadequately, in something less than half the book's 237 pages. I found the book difficult to read and, at best, rather dull and humourless; at worst, clumsy and inconsistent. The author's pledge, "to state the facts as they really are ... by exposing some of the myths that surround these creatures" is largely unfulfilled. Malapropisms, anthropomorphisms and even spelling mistakes find their way between the covers of this volume.

The book's ten chapters include considerations on Classification and Distribution, Colubrids, Elapids, Vipers, Habits and Behaviour, Venom and Snakebite, Snakes and Man, Captivity and Field Study, together with two useful appendices on Antivenine Sources and Emergency Procedure in the case of snakebite. These, however, necessitate access to a medical dictionary for full comprehension as the jargon is not covered by the book's brief glossary.

The Introduction is very short and contributes little towards furthering the understanding of anyone with more than an elementary knowledge of reptiles.

Chapter 2, entitled Classification and Distribution, is difficult to follow and in parts confused. Mr Phelps appears to get quickly out of his depth when considering the more abstract arguments for taxonomic relationships. He even infers a taxonomic link between two monitor lizards (*Varanus* and *Tupinambis*) and snakes as they "are very serpentlike in their manner". The majority of this chapter is taken up by species and distribution lists, based on genera for the Colubrinae and species for Elapinae, Hydrophiinae, Laticaudinae, Viperinae and Crotalinae. There are distribution maps for families; one appears to be a treasure map, the crosses on which we are left to assume are spot records for marine elapids. I found it disappointing that there are no distribution maps at the species level for at least some of the more important species. If your geographical knowledge is poor (as is mine), distribution presented verbally becomes rather meaningless.

The three chapters that follow consider the rear-fanged Colubrids, the Elapids and Vipers, respectively. In each chapter, snakes are treated under taxonomic and/or descriptive headings (which I personally found annoying) and each section contains information on distribution, identification, ecology and prey species. It is a pity that at least some information on venom was not included here, as this would have added interest to what becomes little more than tedious catalogues of snakes. The chapter on Colubrids ends with a rather inconclusive summary which for some reason has been omitted from both the Elapid and Viper chapters. The thirty-three good colour plates occur in this section of the book.

The opening to the chapter on Habits and Behaviour lacks clarity and is accompanied by a great deal of conservationist drum-banging with little advice as to what might be done. There are some nice diagrams used to illustrate basking "modes" (?), but two out of the three attitudes shown appear to be the same, merely presented from different angles. Much of the information in this chapter is anecdotal and often unsupported by data, the author relies heavily on the use of "usually" to cover these insufficiencies. Where data are presented in figure form they provide valuable information but are seldom backed up by adequate interpretation.

It is difficult to ascertain quite why the author has chosen to further alienate those people who, for whatever reasons, are prejudiced against snakes at the start of his next chapter on Venom and Snakebite. It is even less easy to understand why he flatly refuses to enlighten such people with his statement, "a snake is a snake, end of argument"! The author informs us that there are "upwards of 20" enzymes in snake venom (there are in fact 26 that have been identified), but neglects to add that 12 of these are common to all snake venoms. I found the "fact" that a King Cobra has been known to kill an elephant, interesting but irrelevant, and the author's statement that "each snake had man in mind as an enemy as it evolved a capacity for storing large exaggerated amounts of venom", incredible!

An "advertisement" for the Poole Serpentarium is included, although he later condemns similar exhibits as "sensational pulls for the tourist"; whether anyone will want to go there again after reading Table 5, which purports to represent lethal doses for man from data taken from the Poole Serpentarium, remains to be seen. Regrettably there is no mention of the size of the snakes from which the venom yield data were obtained, neither does the author differentiate between subcutaneous and intra-venous venom injection when considering lethal dosages. There is advice given on the choice of the most venom-productive snakes for those of you going into the venom supply business and some pretty horrific pictures of the symptoms and gangrenous results of snakebite.

The closing paragraphs are a record of Mr Phelps' prowess at snake catching, although he freely admits that the fifteen venomous bites he has received were the result of his own carelessness. It is curious that a few pages later under his next chapter heading, Snakes and Man, he castigates snake-handlers who boast about the number of times they have been bitten and recognizes this as a poor recommendation of their skills. Other apparent inconsistencies appear in this chapter; the author considers that the recent, much publicized "sit-ins" with highly venomous species "the height of stupidity", but goes on to applaud George "Snaky" Williams (a personal friend of Mr Phelps) as one of herpetology's most colourful characters, for "kissing" a King Cobra, a picture of which is included. This short chapter is concluded with yet more conservationist desk-thumping.

Chapter 9, entitled Poisonous Snakes in Captivity, is perhaps the best and most useful. It contains some very sound, if somewhat basic, practical information and advice on such topics as vivarium construction, management and a few "tricks-of-the-trade". There is an impressive list of 23 species bred in captivity at the Poole Serpentarium, for which Mr Phelps should be congratulated; I thought this section could have been expanded considerably. The section on ailments is, sadly, brief and contains no reference to the available literature which might be consulted in the event of a sick snake, particularly as the author apparently considers most veterinary surgeons incapable of dealing with poisonous snakes.

The final chapter deals with field study, and quite rightly highlights the need for continued and increasing efforts in ecological snake studies. It offers honest, practical advice on such things as study criteria, catching, equipment and safety. The second part of the chapter is devoted to the capture of particular species and proffers information on catching methods and temperament of species such as King Cobra, Black Mamba, Russells Viper and Western Diamondback Rattlesnake. The author might have quit there, whilst he was still marginally ahead but could not resist the platitude, "If common sense prevails then both snake and man will live to fight another day".

The "Selected Bibliography" is meagre, containing only 41 references from which some major works on poisonous snakes and their venoms are obvious omissions.

The book will no doubt find a place in the popular market, the title being appealing and emotive. There is, however, little to recommend it as a valuable addition to the library of the serious-minded amateur or professional herpetologist.

LIONEL G. KELLEWAY

AMPHIBIANS OF ARGENTINA. By J. M. Cei. **609** pp. Monitore Zoologico Italiano (Italian Journal of Zoology). NS Monografia 2.

This kind of monograph is automatically purchased by museum curators and librarians because it is always the latest comprehensive work on a particular fauna. Latest, of course, is always qualified by "possible", for research continues while compilation is in progress. This the author has attempted to rectify by inclusion of 12 appendices, detailing publications too late to be included in the main text. In this way work completed in 1978 is included in the book.

Not being a museum curator or having any particular professional involvement in the Argentinian fauna, I looked at this monograph to see if it had any other interest for the amphibian biologist or even general naturalist.

The first 56 pages are of general interest and use to classifiers of frogs; here is information on the different aspects of amphibian biology which have been used in taxonomy—morphology, voices, immunology, karyology. It is a useful summary of the multi-disciplinary approach that modern taxonomy requires. The rest of this section deals with physiology, sex cycles and zoogeography, and is generally interesting reading. Keys in English and Spanish follow.

The rest of the work is the systematic section, with detailed descriptions of all the species. The accompanying drawings are generally excellent and include the tadpoles in nearly every case. The photographs of live animals are also nearly always good but photos of preserved specimens convey little. Finally there are 23 plates of colour paintings, all of which look lifelike, though I have no means of judging the veracity of the colours. Earlier, there are 16 pages of black and white "habitat" photographs: I often wonder if these really convey much to the reader. After all, a temporary puddle in Argentina must look much like a temporary puddle anywhere else.

The bulk of the work is in English with the keys and summaries in Spanish as well. The English is studded with what I would call quaint phraseology and unusual adjectives, though this rarely made problems in comprehension. However, frog calls are notoriously difficult to describe in words comprehensible to those who haven't heard them. "Chickling voices" (of *Bufo variegatus*) did convey some sort of acoustic impression to me but I must admit to being puzzled by comparison (of *Hyla berthae*) with "the witty call of locusts".

On the whole, I think that this work is really of interest only to systematists and to those concerned with the South American fauna. The amount of non-taxonomic information is small and the price, though not stated must, for 600 pages, be high. On the other hand, having some knowledge of the frog fauna of other parts of Gondwana, I did find some interesting comparisons in the systematic section, and generally enjoyed browsing through it.

J. I. MENZIES

DISEASES OF THE REPTILIA, 2 volumes. Edited by J. E. Cooper and O. F. Jackson (1981). 584 pp. London, New York etc.: Academic Press, £47.80.

The aim of these two volumes, as stated in the Preface, is to provide "... an up-to-date guide to the diseases of reptiles with particular, but not exclusive, reference to those in captivity". Having read the 584 pages, I felt that this is perhaps a little misleading. Essentially the

*continued on p. 277*