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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 317–319 (1983)

THE HABITATS, DISTRIBUTION AND LIFE HISTORY OF *TRITURUS VITTATUS VITTATUS* (JENYNS) IN THE MOUNT MERON AREA (UPPER GALILEE, ISRAEL)

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(*Received* 22 *October* 1981)

SUMMARY

The habitats and life history of *Triturus v. vittatus* in the Mount Meron area have been studied. The newts in this area were found only in winter rain pools in late winter and spring; no newts were found in perennial streams or rock pools. The adult terrestrial newts reach the area of the pond as soon as it fills with water at the beginning of, or during winter. They enter the ponds and breed in late winter and spring. The males leave the ponds between the end of January and March. The females leave the water after oviposition, from the end of February to May. Oviposition time of captive females was found to extend over one or two months, and between 18 and 68 eggs were laid. The tadpoles hatch after 17 to 29 days, depending on water temperature. They were found from March to July. Tadpoles were found even later in ponds situated at higher elevations.

INTRODUCTION

Triturus vittatus vittatus is found in south eastern Turkey and in Israel, reaching the southern limit of its distribution there (Halliday, 1977). In Israel, *T. v. vittatus* populations are found in Mediterranean semi-arid habitats that have winter rains and a dry summer. The winter rains create pools, most of which dry up in the spring or at the beginning of summer. In the Mount Meron area many different kinds of water bodies are available, including winter rain pools, rock pools, springs and streams. In northern and central Israel the newts are found mostly around bodies of water. During the winter the adults are found in their aquatic phase in winter rain pools and streams, breeding and spawning on plants. They leave the water after breeding and begin the terrestrial phase.

No papers have been published on the distribution, habitats, life history or breeding of *T. v. vittatus* in its southern distribution in Israel. The information reported here was observed during research on *Salamandra salamandra* in Israel (Degani & Warburg, 1978; Degani & Mendelssohn, 1979).

MATERIALS AND METHODS

A survey on the distribution and life history was carried out in the Mediterranean oak-woodland of the Mount Meron area from autumn 1980 through to the summer of 1981. The common plant association is of *Quercus calliprinos* and *Pistacia palaestinae* (Degani & Warburg, 1978). All the main types of aquatic habitats in the Mount Meron area have been studied (Fig. 1). Every body of water marked in this Fig. was visited, generally four times during the winter, and three selected ponds were visited twice every month throughout the year. The adults were collected around or in the water, weighed and measured as described previously by Degani & Mendelssohn (1979), and released at the place of capture. Ten pairs were placed in separate aquaria in order to observe breeding and oviposition.

RESULTS AND DISCUSSION

Adult *T. v. vittatus* were found in the Mount Meron area only in winter and spring. In all the winter rain pools in which newts have been found, the water remained throughout spring; in some of them, until mid-summer (Fig. 1). Some ponds, however, retained their water throughout the year when the winter rains had been abundant. No newts were found in winter rain pools that had dried up before the spring.

Three ponds were visited twice each month throughout the year. Newts were found in only one of them (Sasa pond—see detailed description in Degani & Mendelssohn, 1979).

The fact that in this area newts do not breed in spring may be connected with two factors.

1. The temperature of these bodies of water is colder than the temperature necessary for the development of the newt tadpoles. In most cases it is below 16°C (Degani & Mendelssohn, 1979; Warburg, Degani & Warburg, 1979). These low temperatures are more suitable for *S. salamandra* tadpoles.
2. If the temperature is about 20°C, the *S. salamandra* tadpoles can develop together with *T. v. vittatus* tadpoles. The salamander tadpoles can eat newt tadpoles and they are better adapted for competition for food (Degani & Mendelssohn, 1979; Degani, Goldberg & Warburg, 1980).

In the Sasa pond both salamander and newt tadpoles were found to eat the same invertebrates. In winter, however, when the temperature was between 1° and 10°C (Warburg *et al.*, 1979) only salamander tadpoles were found, and in summer when the temperature was between 10° and 30°C, newt tadpoles were found in

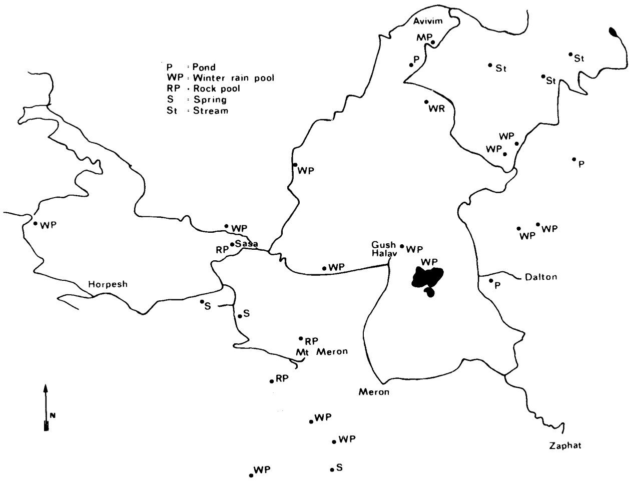

FIG. 1. The main types of aquatic habitats in the Mount Meron area.

this study. Newt tadpoles lived together with four species of anuran tadpoles (*Hyla arborea*, *Bufo viridis*, *Rana ridibunda*, *Pelobates syriacus*)—see Table I.

The adult newts reached the Sasa pond in December and January (Table III). At this pond they were found under stones around the pond when it was empty. As soon as the pond filled, the adult newts entered the water and changed to the aquatic phase. In December most of the newts were found around the pond, and in January, in it. The males left the water after breeding from late January to March, whereas the females sometimes remained in the water until May.

Males were on average larger than females (Table II) and the difference between body sizes was significant. At the aquatic phase, however, when the females were full of eggs, they were heavier than the males ($P < 0{\cdot}05$, Table II).

The females spawned from February to early May (Tables III, IV), depositing between 18 and 68 eggs each. Oviposition and development of the eggs and tadpoles depended on water temperature. Tadpoles in Sasa pond were extant during the four months from March to July. Tadpoles may be found at different times in other ponds. In the Beit Gan pond, for instance, which is the highest pond in the area (920 m) small newt tadpoles were found in May, whilst in the Nahalit pond (660 m) there were well-developed tadpoles at that time of year.

The newt tadpoles measured in Sasa pond (Table V) can be described by the following equations:

$$W = 0.21\, e^{0.02T} \qquad (r = 0.95, P < 0.01)$$
$$L = 0.04T + 2.51 \qquad (r = 0.99, P < 0.001)$$

where W = weight (g), L = length (cm), T = age in days. The newt tadpoles increased in weight slowly during the spring and more rapidly with advancing summer, as do *S. salamandra* tadpoles (Degani & Mendelssohn, 1979; Warburg *et al.*, 1979).

In Europe, tadpoles of *Triturus* species are found in summer. Those of *T. vulgaris* in Sweden are found in the ponds from June to September or October (Hagstrom, 1974). A similar time for spawning and tadpole growth was found by Bell & Lawton (1975).

TABLE I. Different types of aquatic systems where newts were found (1980–1981). (The dates concern newts and not other amphibian species)

Ponds	Dates (months)	Type	Nat. Grid Ref.	Altitude (m)	Other species
Sasa AT	Dec. Jul.	Winter pond	271187	800	S.s., B.v., P.c., H.a., R.r.
Iron T	Apr. Jun.	Winter pond	276193	680	B.v., R.r., P.c., H.a.
Dovav T	June	Winter pond	273189	720	S.s., B.v., H.a., R.r.
Matityahu T	April	Winter pond	274193	688	P.c., B.v., H.a., R.r.
Nahalit	April	Winter pond	276193	660	P.c., H.a., B.v., R.r.
Beit Gan T	June	Winter pond	263187	920	S.s., P.c., H.a., B.v.

T = tadpoles; A = adults; S.s. = *Salamandra salamandra*; P.c. = *Pelobates syriacus*; H.a. = *Hyla arborea*; B.v. = *Bufo viridis*; R.r. = *Rana ridibunda*.

TABLE II. Comparison between male and female sizes

Sex	No. of newts	Weight g ± SD	Significance of difference		Body size mm ± SD	Significance of difference		Body size with tail mm ± SD	Significance of difference	
			t	*P*		*t*	*P*		*t*	*P*
Terrestrial										
males	10	3.8 ± 0.4	2.2	<0.05	55 ± 3	8.6	<0.001	104 ± 8	4.9	<0.001
females	20	2.9 ± 0.7			47 ± 3			90 ± 7		
Aquatic										
males	5	3.5 ± 0.6	2.8	<0.05	57 ± 6	2.1	NS	106 ± 4	5.8	<0.001
females	6	4.5 ± 0.6			48 ± 8			92 ± 7		

TABLE III. Capture of adult newts during the year in the Sasa pond area

Date	Number of males	Number of females
Dec. 1980	7	15
Jan. 1981	6	7
Feb. 1981	—	3
May 1981	—	1
Dec. 1981	2	1

TABLE IV. Time of deposition, culture and hatching of newt eggs

Date of deposition	No. of eggs	Duration of deposition (days)	Time from deposition to hatching (days)	
			start	end
21.2.1981	32	13	23	29
23.2.1981	18	11	18	21
13.3.1981	54	12	17	25
14.3.1981	20	9	20	26
13.3.1981	67	10	20	28

TABLE V. Growth rate (weight and length) of tadpoles in Sasa pond

Date	Sample size	Mean weight (g ± SD)	Mean length (mm ± SD)
4.6.81	2	0.21 ± 0.1	46 + 4.2
18.6.81	11	1.0 ± 0.3	49 ± 10
3.7.81	20	2.6 ± 0.6	62 ± 8
16.7.81	20	3.7 ± 0.8	69 ± 8

There are no published works in the literature on experiments carried out in the laboratory on growth rates of newt tadpoles dependent on water temperature and food, as described in *S. salamandra* tadpoles (Degani *et al.*, 1980). The results of the Bell & Lawton study, however, together with the work reported here, may indicate that the growth rate of newt tadpoles depends to a large extent on both water temperature and food available. The growth period of *T. v. vittatus* tadpoles in the Mount Meron area is earlier and shorter than that of newts in Europe. In other parts of Israel where the winter is not as cold as in the Mount Meron area, the growth period is in winter, and newt tadpoles complete metamorphosis in spring before the winter rain pools and ponds dry up (unpublished data).

ACKNOWLEDGEMENTS

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HISTOLOGY OF A TRIPLE TAIL REGENERATE IN A GECKO, *HEMIDACTYLUS PERSICUS*

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Lizards from the wild with two, or more rarely with three, tails have been reported (*e.g.* Fraisse, 1885; Brindley, 1898; Gräper, 1909; Das, 1933). The condition may result from a regenerate growing from an original tail or from another regenerate and is of sufficient interest to merit histological examination. The present specimen (Fig. 1) was taken from an adult *Hemidactylus persicus* captured in Bahrain. There was

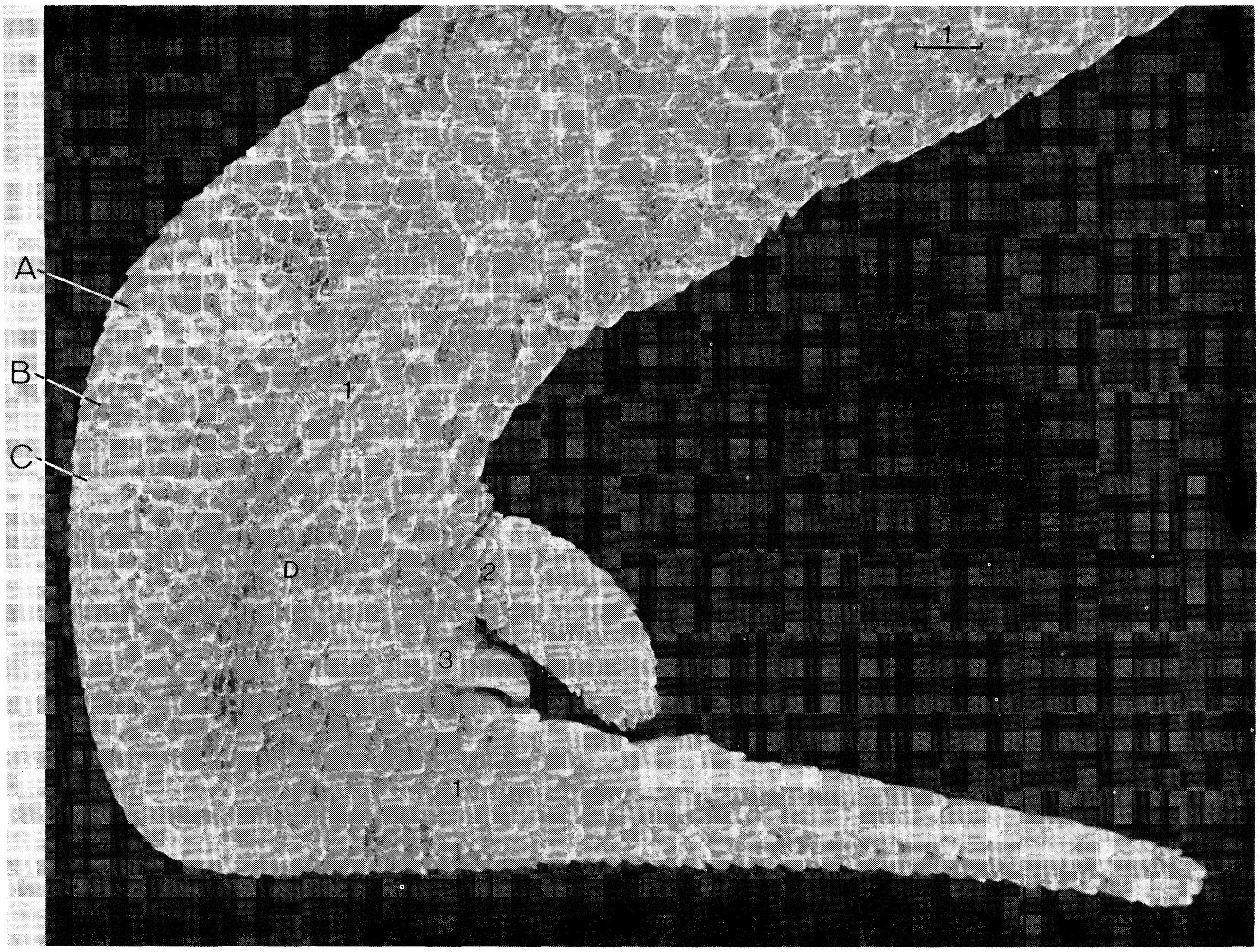

FIG. 1. Regenerated tail of *Hemidactylus persicus* with two accessory regenerates, seen from above. Approx. planes of section in Fig. 2, A, B, C shown on left. D, depression in main regenerate. 1, main regenerate. 2, 3, accessory regenerates. Scale = 1 mm.

a large main regenerate (1) which had apparently developed after autotomy near the tail base. Its distal portion was bent at a right angle and it measured about 50 mm in total length. The regenerate was flattened dorsoventrally, and its right lateral aspect, facing the angle, was set off from the rest by a depression. Two, much smaller, accessory regenerates projected within the angle, the larger (2; Fig. 1) being 4 mm, and the smaller (3) 1.5 mm long. The tail was cut off through the main regenerate and serially sectioned.

The main regenerate (Fig. 2A) has for the most part the typical structure of the regenerated saurian tail (see Shah & Chakko, 1968; Simpson, 1970; Bellairs & Bryant, in the press). The vertebrae are replaced by an unsegmented tube of cartilage (Fig. 2E) which contains the imperfectly regenerated spinal cord, consisting mainly of a tube derived from its ependymal lining and some descending nerve fibres. A new fat layer corresponding with the submuscular, perivertebral fat layer of the original tail is present and is traversed by nerves and blood vessels. Peripheral to this are muscles covered with connective tissue and scales, resembling (though not entirely similar to) those of the original tail. In geckos of many species the subcutaneous tissues of the tail, and to a lesser extent of the dermis, contain fat cells; these are also present in the regenerate. The layers of dense collagenous tissue in the deep dermis and perimuscular fascia are also regenerated.

The cartilage tube passes round the bend in the main regenerate and reaches nearly to its tip. However, at a level just proximal to the larger accessory regenerate it shows evidence of previous injury, probably amounting to fracture. The morphologically right side of the tube is partly separated from the rest and a layer of cartilage arising from it seems to have spread over its other side, suggesting a kind of callus formation (Fig. 2A). Further distally the two portions of the cartilage tube reunite and the integrity of the structure is restored. The ependymal tube also continues throughout the regenerate, but passes very close to the damaged cartilage, perhaps adhering to it.

The larger of the accessory regenerates (2) contains muscle, fat, connective and other tissues, but no branch of the cartilage tube from the main regenerate passes into it (Fig. 2B; D, left). The smaller accessory regenerate (3) is likewise devoid of cartilage (Fig. 2C; D, right); it contains the various layers of fat and connective tissue, but the muscles of the main regenerate do not extend into it. It is covered with large scales. Both accessory regenerates contain large bundles of

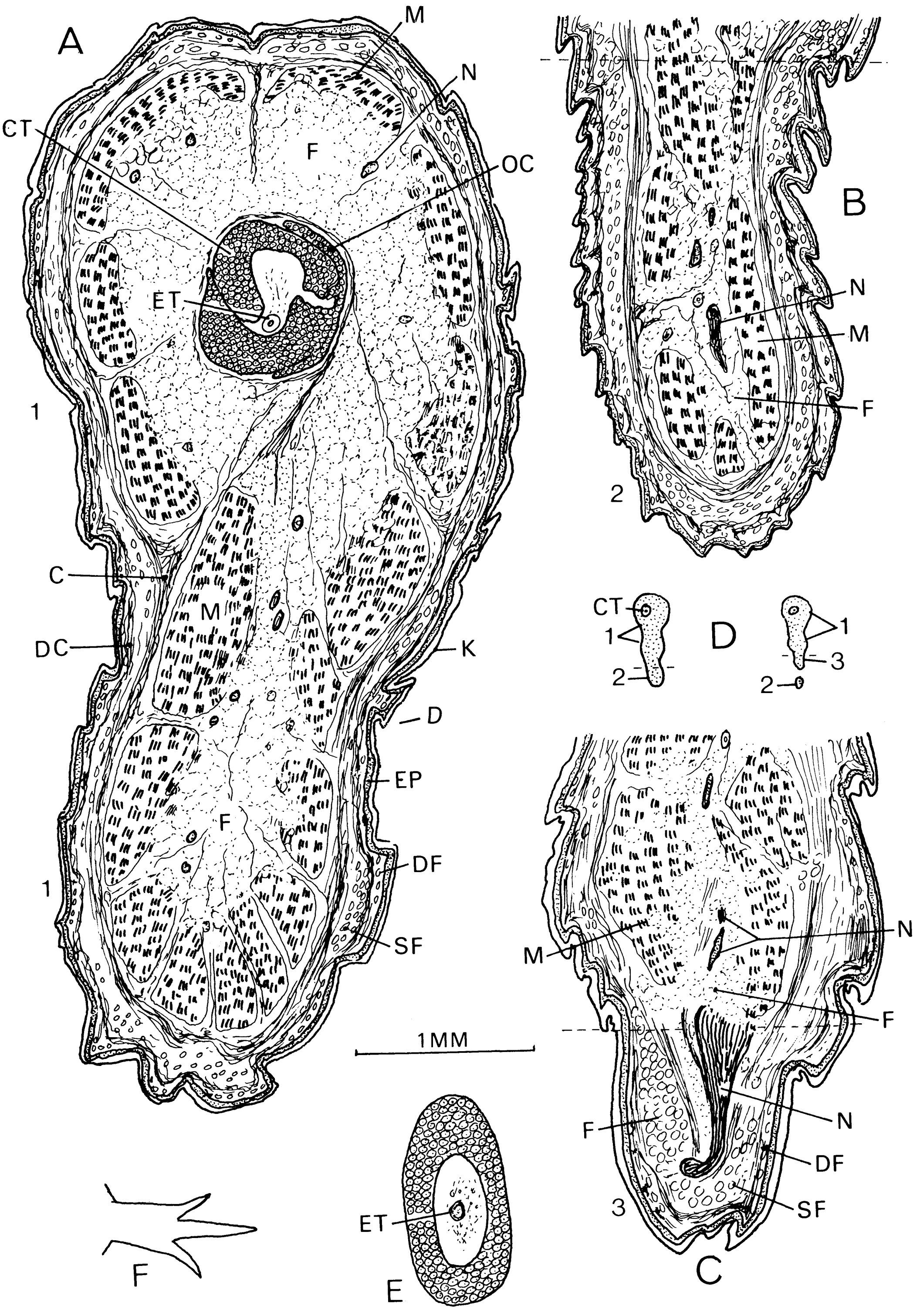

FIG. 2, A–E. *Hemidactylus persicus*. A, section through main regenerate. B, C, sections through accessory regenerates: planes of section shown in Fig. 1. D, much reduced outlines of sections of whole tail at level of B (left) and C (right). The areas of the accessory regenerates are beneath the broken lines in B, C and D. E, transverse section through cartilage tube of main regenerate at level proximal to sites of accessory regenerates in Fig. 1. In A–E the originally dorsal aspects of the regenerates are on the right. F, triple tail of *Hemidactylus flaviviridis*, after Das (1933); not to scale. C, dense subcutaneous tissue; CT cartilage tube; D, depression in main regenerate; DC, dense connective tissue of dermis; DF, dermal fat; EP, epidermis; ET, ependymal tube; F, deep fat layer (submuscular where muscles are present); K, keratin layer of epidermis, partly detached; M, regenerated muscle; N, nerves; OC, overgrowth of cartilage from damaged part of tube; SF, subcutaneous fat. 1, main regenerate; 2,3, accessory regenerates.

nerve fibres which arise from nerves in the main regenerate and which seem to terminate in the connective tissue and subcutaneous fat (Fig. 2C).

All three regenerates appear to be mature, lacking the growth blastema and apical cap of thickened epidermis which are characteristic of young regenerates; it seems unlikely that they would have grown any larger.

DISCUSSION

The specimen described here differs from the two examples of *Hemidactylus flaviviridis* studied by Das (1933) in that the accessory regenerates arise close together from the same side instead of from different sides of the main regenerate (Fig. 2F). It resembles them, however, in that the accessory regenerates lack the cartilage tubes and their contained tubes of ependyma which are characteristic of normal regenerates. Similar conditions were found by Woodland (1920) and also by Das in multiple regenerates which had been experimentally provoked by wounding the tail. The extra tails produced in the experiments by Tornier (1897) and found in a wild *Lacerta agilis* by Gräper (1909) were different. In these cases the vertebrae of the original tail had been damaged; both cartilage and ependymal tubes were seen in the regenerates and in some specimens individual regenerates contained more than one cartilage tube.

The injuries to the skeleton in these last specimens could well have been accompanied by damage to the spinal cord and its ependyma. It is well known that the presence of ependyma near the wound site is important in initiating tail regeneration, especially the regeneration of the cartilage tube (Simpson, 1970). The absence of cartilage from the accessory regenerates described here, like those observed by Woodland (1920) and Das (1933), may have been due to the lack of ependymal influence. It is uncertain whether the ependymal tube was injured in our specimen, or whether its influence could have spread beyond the broken cartilage; it is in any case separated from the site of the accessory regenerates by some 4–5 mm of differentiated tissue of the main regenerate. The growth of these two small regenerates may perhaps be attributed to the influence of nerve fibres, which are conspicuous within their substance, and which are also known to play an important part in many types of regeneration (see Simpson, 1970).

It is suggested that the sequence of events responsible for the conditions in the specimen described here was as follows. (1) The gecko underwent high autotomy and produced a mature regenerate (the main one): (2) the distal part of this regenerate was injured in turn, probably by a predator, and bent out of its normal shape so that the cartilage tube was partly broken: (3) the accompanying injury to the superficial tissues of the main regenerate was followed by the development of both accessory regenerates from adjacent regions of the wound surface; alternatively, the smaller accessory regenerate could have been elicited by a second injury to the main one.

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LAPAROSCOPY OF THE GREEN SEA TURTLE, *CHELONIA MYDAS*

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SUMMARY

Laparoscopy has proved to be a valuable aid in assessing the reproductive state of the green sea turtle. Diagnostic evaluation of abnormal conditions and a possible route for artificial insemination have also been investigated using laparoscopic techniques. The procedures have been performed safely and quickly with minimum stressing of the animal.

INTRODUCTION

Laparoscopy, examination of the peritoneal cavity via an endoscope, has been used with a variety of domestic and zoo animals (Harrison & Wildt, 1980). The technique has been primarily adapted as a diagnostic and research aid on animals ranging in size from laboratory mice to horses and cows. The adaptability of the technique and the availability of the suitable equipment prompted laparoscopic investigations of the green sea turtle *Chelonia mydas*.

Chelonia mydas, as well as the other six species of sea turtles, have been the subject of considerable recent research because of their endangered species status. As a green sea turtle may not develop secondary sexual characteristics until it is at least 8 years old (Wood & Wood, 1980), means of sexing the live turtle are needed. Blood testosterone levels have been used with reasonable success on 4 year old turtles (Owens, Hendrickson, Lance & Callard, 1978). Sexing by examination of chromosomal karotypes has not been successful as both sexes of the green sea turtle are karyotypically identical (Bickham, Bjorndal, Haiduk & Rainey, 1980).

Cayman Turtle Farm, Ltd, Cayman Islands, British West Indies, maintains a captive stock of the green sea turtle for commercial and research purposes. Techniques for sperm collection by electroejaculation have been developed (Wood, Platz, Critchley & Wood, 1982). Laparoscopic techniques used to sex the green sea turtle, to examine the reproductive state of the turtle during different periods of its reproductive cycle and to develop a possible route for artificial insemination are discussed below.

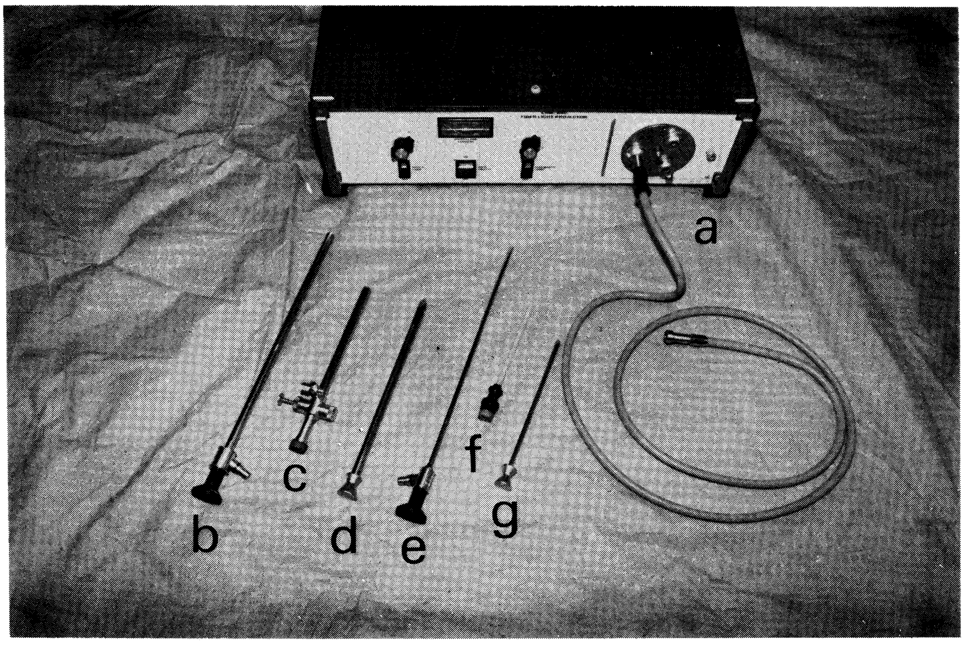

FIG. 1. Laparoscopic equipment routinely used consisting of a light source and cable (a); 10 mm telescope, trocar sleeve and trocar (b, c, d); and 5 mm telescope, trocar sleeve and trocar (e, f, g).

MATERIALS AND METHODS

Laparoscopic equipment was obtained from Richard Wolf Medical Instruments Corp. (Rosemont, Illinois, U.S.A.). Equipment routinely used consisted of a Model A5000.40 Cine Arc Fibre Light Projector, a 10 mm Lumina telescope 180° No. 8934.40 plus extra long trocar sleeve and trocar, and a 5 mm telescope 180° No. 8935.30 plus trocar sleeve and trocar (Fig. 1). Photography was done with a Canon AE-1 and 135 mm lens and adaptors using the 10 mm telescope.

All turtles examined were part of the stock maintained at Cayman Turtle Farm, Ltd. Examinations took place in air-conditioned laboratory facilities on the farm. Aseptic techniques were routinely employed. Equipment was sterilized by immersion in the germicidal solution Amerse (Vestal Laboratories, St Louis, Missouri) for 10 min prior to use. Animals were anaesthetized with ketamine hydrochloride (Ketaset, Veterinary Products, Syracuse, New York), sodium pentobarbital (Fort Dodge Laboratories, Fort Dodge, Iowa) or sodium thiopental (Pentothal, Abbott Laboratories, North Chicago, Illinois; Intraval, May & Baker Ltd, Dagenham, England). Details of anaesthesia have previously been published (Wood, Critchley & Wood, 1982). Animals were also electro-

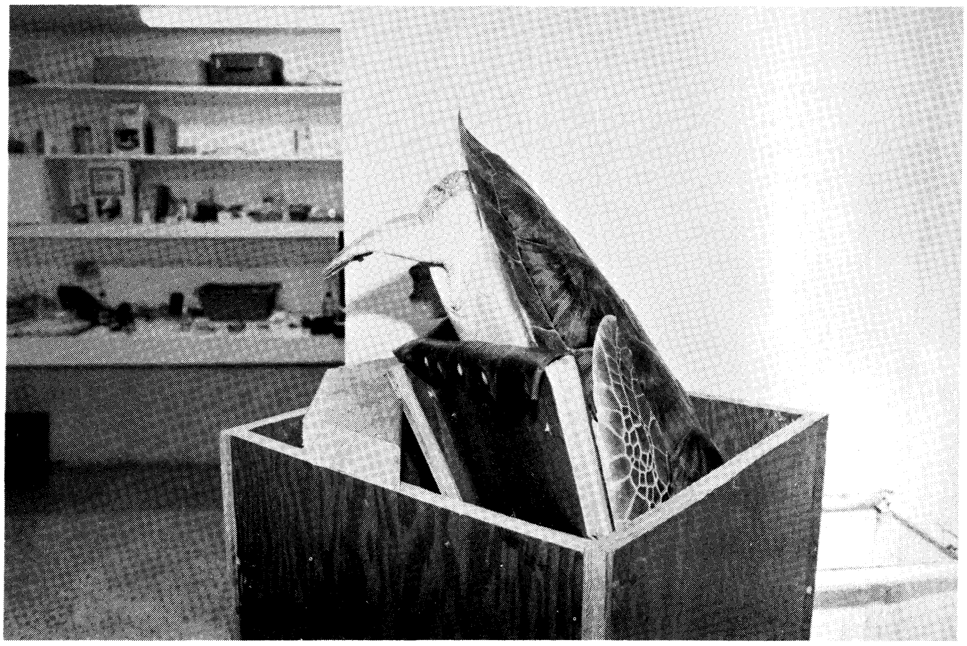

FIG. 2. A 20 kg turtle supported within a wooden box for laparoscopic examination.

FIG. 3. A 105 kg turtle supported in a rope sling for laparoscopic examination.

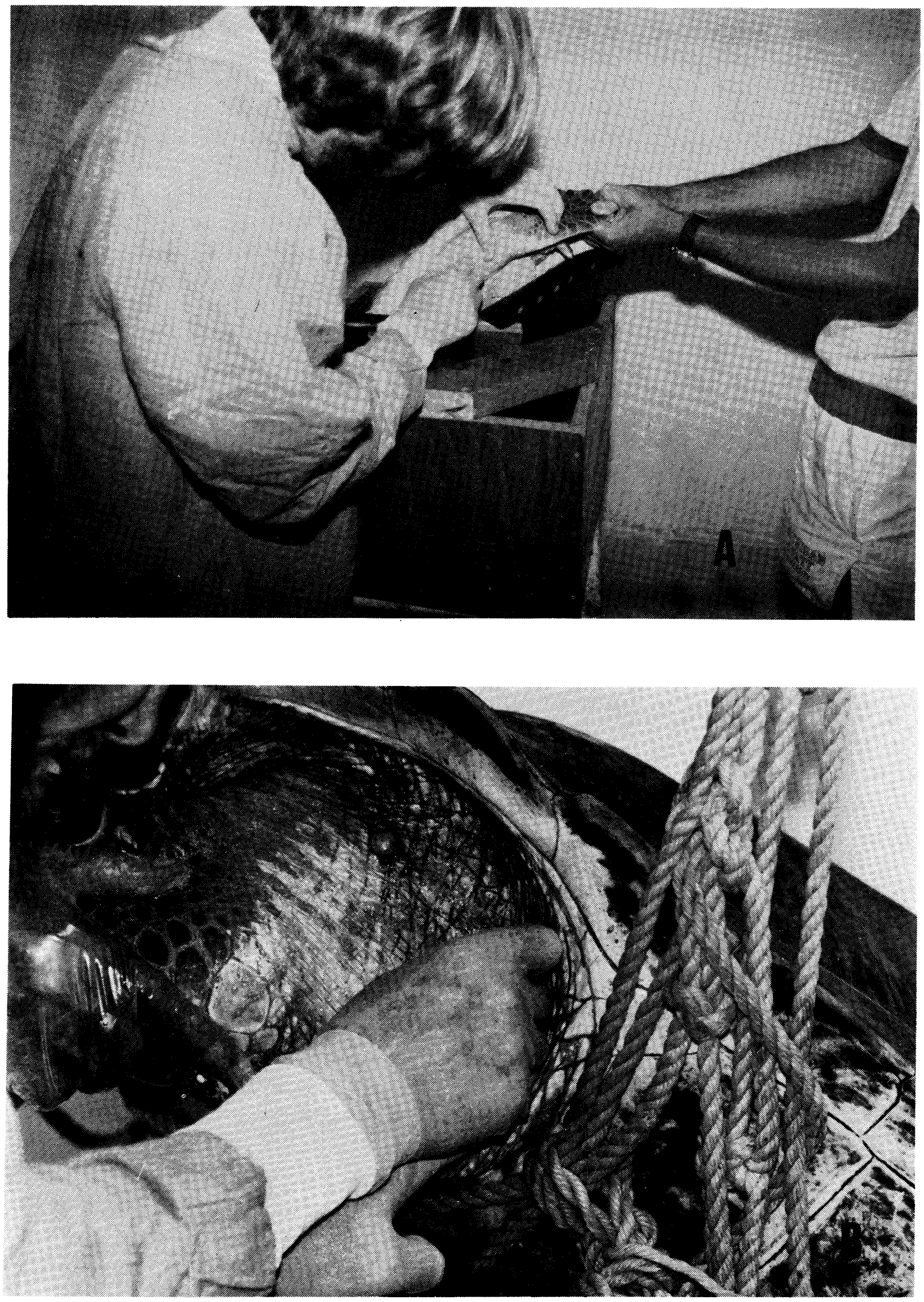

FIG. 4. Entry into the abdominal cavity through the skin laterally to the rear flipper A, for a 15 kg turtle, and B, for a 105 kg turtle.

anaesthetized using a Feenix Stockstill Mark I electro-anaesthesia unit (Feenix International Pty. Ltd, Tarlee, South Australia). Electro-leads were inserted under the skin in the shoulder and rear flipper, opposite the side of examination. A current of .25 ma was sufficient to maintain surgical anaesthesia. The entry area was cleansed by scrubbing with an ethanol-iodine surgical solution (I0 Surgical Solution, Hart Delta Inc., Baton Rouge, LA).

For the examination, the turtle was positioned in one of two restraining devices. For a turtle less than 20–30 kg, the turtle was placed on its ventral surface, head down, in a plywood box (46 × 46 × 30 cm) with slanting boards constructed so that the turtle rested at an approximate 60° angle (Fig. 2). Internal blocks enabled the turtle to be lowered or raised, depending on size, and supported the turtle on its shoulders so that the head rested easily in the base. For turtles up to 200 kg (the largest examined) the turtle was placed in a rope sling which was attached to four pulleys enabling the turtle to be raised and positioned at the appropriate angle (Fig. 3). Positioning of the turtle was important, preventing the need for insufflation to create an intra-abdominal air space to lessen the possibility of puncturing any organs. The turtle rested so that the intestines fell away from the kidneys, gonads, lungs and liver, enabling less obstructed viewing of the organs after entry. The turtle was also slanted so that the side on which entry was made was slightly above the other side. Entry was made laterally to the rear flipper as it was held back to expose the skin. Correct entry position, as seen in Fig. 4, prevented severing the femoral vein which in one instance was cut when entry was made too anteriorly to the rear flipper and the turtle was not positioned at the correct angle. Figure 5 illustrates the approximate position of the endoscope to view the gonads. In most instances, particularly with the younger turtles, the gonads were located by first finding the lung and moving the endoscope posteriorly over the kidney and attached gonad.

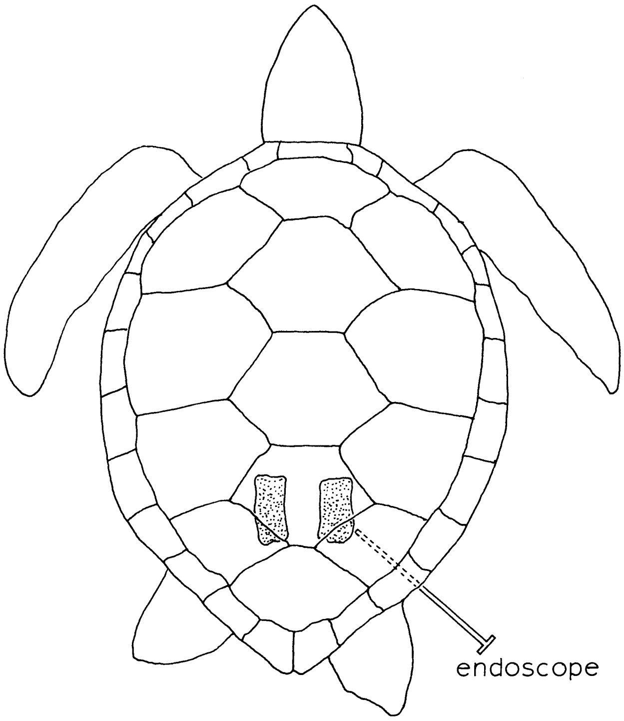

FIG. 5. Proper positioning of the laparoscope, in relation to the scutes, for viewing the gonads.

Actual entry into the peritoneal cavity was made by first making a 1–2 cm cut in the skin with a scalpel blade to allow easy manipulation for the size of trocar-cannula used. An additional cut for insertion of an accessory trocar-cannula can be made within a few cm of the initial cut. The trocar-cannula was cautiously pushed into the turtle with slight rotation. Once passage into the abdominal cavity was made, the trocar was partially withdrawn into the cannula to prevent puncture of the intestines and the cannula pushed in slightly more. Proper entry to the body cavity was verified with the endoscope and the trocar again inserted, if needed. In the larger, mature females, it was occasionally necessary to fully insert the extra long trocar (length = 23 cm) and cannula cautiously to penetrate the membrane supporting the oviduct, allowing direct view of the ovary. After examination the endoscope and cannula were removed and the skin incision(s) closed with 2–3 stitches (Dexon "S" absorbable surgical suture, Davis & Geck, Manati, Puerto Rico). Procedural details and instrumentation use are elaborated upon for various conditions in Harrison & Wildt, 1980.

RESULTS AND DISCUSSION

Over 50 turtles ranging in size from 5–200 kg have been examined by laparoscopy. The majority of these were examined to assess the sex. In sexing a turtle, entry, examination and closure of the entry site were completed within five minutes following anaesthesia of the turtle. The use of ketamine hydrochloride as the

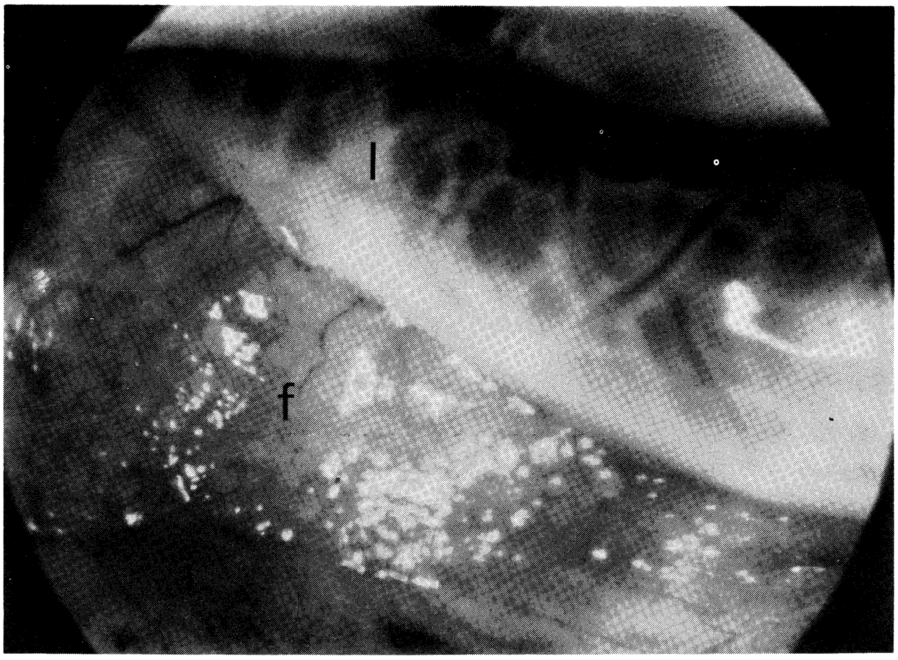

FIG. 6. Endoscopic view of developing follicles (f), lungs (l), and intestines (i) of a 39 month old green sea turtle.

FIG. 7. Endoscopic view of testes (t), lung (l), and intestines (i) of a 48 month old green sea turtle.

anaesthetic allowed for rapid induction of anaesthesia and rapid recovery for this procedure (Wood *et al.*, 1982). None of the turtles examined was adversely affected by the laparoscopic procedure. Laparoscopy is a positive, quick and efficient way of sexing immature turtles and offers the advantage over blood testosterone level determinations in that no laboratory analysis is required. Figures 6 and 7 show the developing follicles of a 39 month old female and the testes of a 48 month old male, respectively. Positive sex identification would be feasible with the appropriate size endoscope for turtles as young as 4–6 weeks old, at which time the green sea turtle can be positively sexed by the gross appearance of the gonads.

Evaluation of the gonadal development of the green sea turtle as well as investigations into artificial insemination are possible by laparoscopy. Both are important to the program of captive propagation of the green sea turtle at Cayman Turtle Farm, Ltd. Artificial insemination was attempted by introducing freshly collected sperm (Wood *et al.*, 1982) over the developing follicles of the female through an operating endoscope or a separate cannula inserted in a secondary incision made 2 cm from the original incision. Although initial attempts were unsuccessful in producing fertilized eggs, this route for artificial insemination is one presently being investigated at the farm.

Although used with only two turtles, laparoscopy may be valuable in evaluating an abnormal condition in the turtle. The two turtles examined, one weighing 5 kg and the other 114 kg, were found to have blocked intestines. The stress associated with anaesthetizing the turtle restricts the applicability of the technique, but as corrective surgical procedures become feasible for the sea turtle, diagnostic laparoscopy may become a more valuable tool.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 329–333 (1983)

MALE COMBAT AND REPRODUCTIVE BEHAVIOUR IN CAPTIVE *BITIS CAUDALIS* (A. SMITH)

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SUMMARY

Although male combat has been recorded in a number of species of Viperidae, it appears that it has not so far been observed in *Bitis caudalis*. A report of male combat in this species, together with observations of breeding behaviour, is presented. Possible reasons for male combat in this and other species of adders are examined.

INTRODUCTION

Male combat behaviour in African Viperidae has been reported in *Causus resimus* (Curry-Lindahl, 1956), *Bitis gabonica* (Akester, 1979), *Causus defilippii* (D. G. Broadley, pers. comm.), *Causus rhombeatus* and *Bitis arietans* (W. R. Branch, pers. comm.). An account of mating activity in *Bitis arietans* (Harvey, 1964) would appear to be a misinterpretation of male combat. A list of all snake species, worldwide, in which male combat has been recorded, is given by Shine (1978).

It would appear that male combat has not so far been recorded in the Horned Adder, *Bitis caudalis* (A. Smith). This paper describes a series of observations of male combat in this species, together with an account of reproductive behaviour.

The nature of male combat in snakes poses many questions, the answers for which are not easily provided. Patterns of behaviour differ from one species to another, so that theories suggested by observations made of one species do not necessarily hold good for others. However, there appear to be some areas of common ground, from which possible reasons for this behaviour may be put forward.

METHODS

Five adult *B. caudalis* (two females and three males) were obtained from the Beitbridge area of Zimbabwe. These individuals were released into an outside enclosure 8 m^2 in area, with sides of clear plastic sheeting and a substrate of coarse sand. A number of rocks together with raised, flat, stones were provided as refuges. The whole enclosure was protected by a wire-netting cover, providing a support for palm fronds which were arranged on top so that some part of the enclosure was shaded at all times of the day. A pool of water was provided, but no snake was ever seen to drink from it: from time to time the enclosure was watered with a fine spray and it was only then that the animals were observed to drink from water running off the rocks as well as from their own bodies. During the summer months the snakes were left in the enclosure at all times, but at the onset of the colder weather (May–September) they were removed to a heated cage. On warmer days they were returned to the outside enclosure, but were always housed in the heated cage at night until it became warm enough to leave them outside continuously.

OBSERVATIONS

The larger of the two females, C1, was released into the enclosure in September 1981, followed in November 1981 by the two males, C3 and C4, but the three apparently completely disregarded each other. In March 1982 a further male, C5 and a female, C2, were added to the community. No interaction was apparent between the occupants of the enclosure until 16 April 1982, when copulation between C4 and C1 was observed—lasting for approximately ten minutes.

29 May 1982:	Combat between all males. Copulation between C4 and C1.
30 May 1982:	Combat between all males. No mating activity.
5 June 1982:	Copulation between C4 and C1. No combat activity.
12 June 1982:	Copulation between C4 and C1. No combat activity. Copulation between C3 and C2.
3 July 1982:	Combat between all males. Copulation between C4 and C1. After the animals were returned to the cage, apparent homosexual activity occurred between C3 and C4 (see Discussion).
8 July 1982:	Apparent homosexual activity in the cage between C4 and C5.
10 July 1982:	Combat between all males.
11 July 1982:	No combat. Unsuccessful mating attempt between C4 and C1.
18 July 1982:	No combat. Mating activity between C4 and C1. C1 was apparently very reluctant, but copulation did occur at 1200 h.

No further combat or mating activity was observed after 18 July 1982.

Courtship in this species is initiated by the male approaching the female with a jerky action. On making contact with her, the male moves up over her body with this same characteristic jerky movement, while at the same time rubbing his chin along her back. This movement is associated with rapid tongue flicking and as he reaches the anterior part of her body, he tries to pass his tail underneath her and, if after reaching her head he has not succeeded in eliciting any response from her, he reverses direction and moves down towards her tail. This procedure is repeated until the female becomes responsive, signified by the raising of her tail and its movement from side to side in exactly the same manner that is employed by the species for the caudal luring of prey. As contact is made between tails male and female mutually intertwine them—the female taking just as active a role as the male. Usually copulation was observed to take place around noon, and lasted for approximately ten minutes.

Six matings were observed between C4 and C1, one between C5 and C1 and one between C3 and C2. C1 became progressively less responsive to C4's attentions and after 18 July 1982 mating activity ceased completely. C2 gave the appearance of being most reluctant to take part in mating activity at any time. Although the history of C2 in captivity is not completely known, it is believed that she was old and had been in captivity for some considerable time. It was originally thought that she might be too old for breeding purposes.

19 November 1982: C1 gave birth to 16 live young (9 females, 7 males).
18 December 1982: C2 gave birth to 6 live young (3 females, 3 males).

No infertile eggs were voided by either of the females.

Although the three males were well matched in both length and mass, C4 was by far the most aggressive, exercising complete dominance over the other two males and being at all times the initiator of combat. He was alert and active and any movement from either of the other males would bring an immediate response from him. Raising the anterior third of his body above the ground, he would move rapidly across the enclosure, using the same jerky movement that was so characteristic of mating activity. Upon reaching the other male, he would commence to move up over its body (Fig. 1), more often than not causing the other male to take immediate flight, only to be pursued at speed around the enclosure until it made good its escape. However, if the other male stood his ground, C4 would try to

FIG. 1. C4 having moved up over the body of C3, attempts to press the head of C3 downwards.

force its head down, at the same time attempting to twist his body in a "corkscrew" around the other male (Fig. 2). This would usually result in the male taking flight, but should he be challenged, C4 would become very violent—striking at his opponent with closed mouth and lashing his body from side to side. Often the consequence would be that both males were flung apart (Fig. 3), on some occasions landing in an inverted position. During one period of combat C4, on being challenged by C3, struck with open mouth—driving one fang into its head. All these combats inevitably resulted in the flight of C3 and C5. If, during the pursuit of one male, the other male was disturbed and made some movement, C4 would immediately attack this second male, and it was not unusual for him to transfer his attentions from one male to the other. There were occasions when C4 gave chase to both C3 and C5 at the same time.

It was interesting to note that movement from either of the females would be ignored by C4, but should he be paying court to a female, any movement from another male would cause him to leave her immediately to go off in pursuit. However, should copulation have started, C4 would pay no attention to either of the other two males. Combat usually lasted for approximately one hour, after which time C4 would settle down quietly or commence courtship with C1.

Occasionally combat of lesser intensity took place after the snakes had been transferred back to the cage, but this was usually of short duration. Two instances of homosexuality were also noted in the cage when a male happened to be resting on top of the female C1. This homosexual behaviour was interesting for both males intertwined their tails without any sign of either combat or flight taking place.

All three males sloughed immediately prior to the onset of male combat, while the two females sloughed shortly after combat and mating activity had ceased.

Photography of combat activity proved to be very difficult due to its short duration, and the speed at which C4 pursued the other males around the enclosure.

DISCUSSION

When considering male combat in *B. gabonica*, it seemed probable that territorial defence, competition for food, sexual domination and homosexuality did not play a part, and that the ritual had its roots in sexual

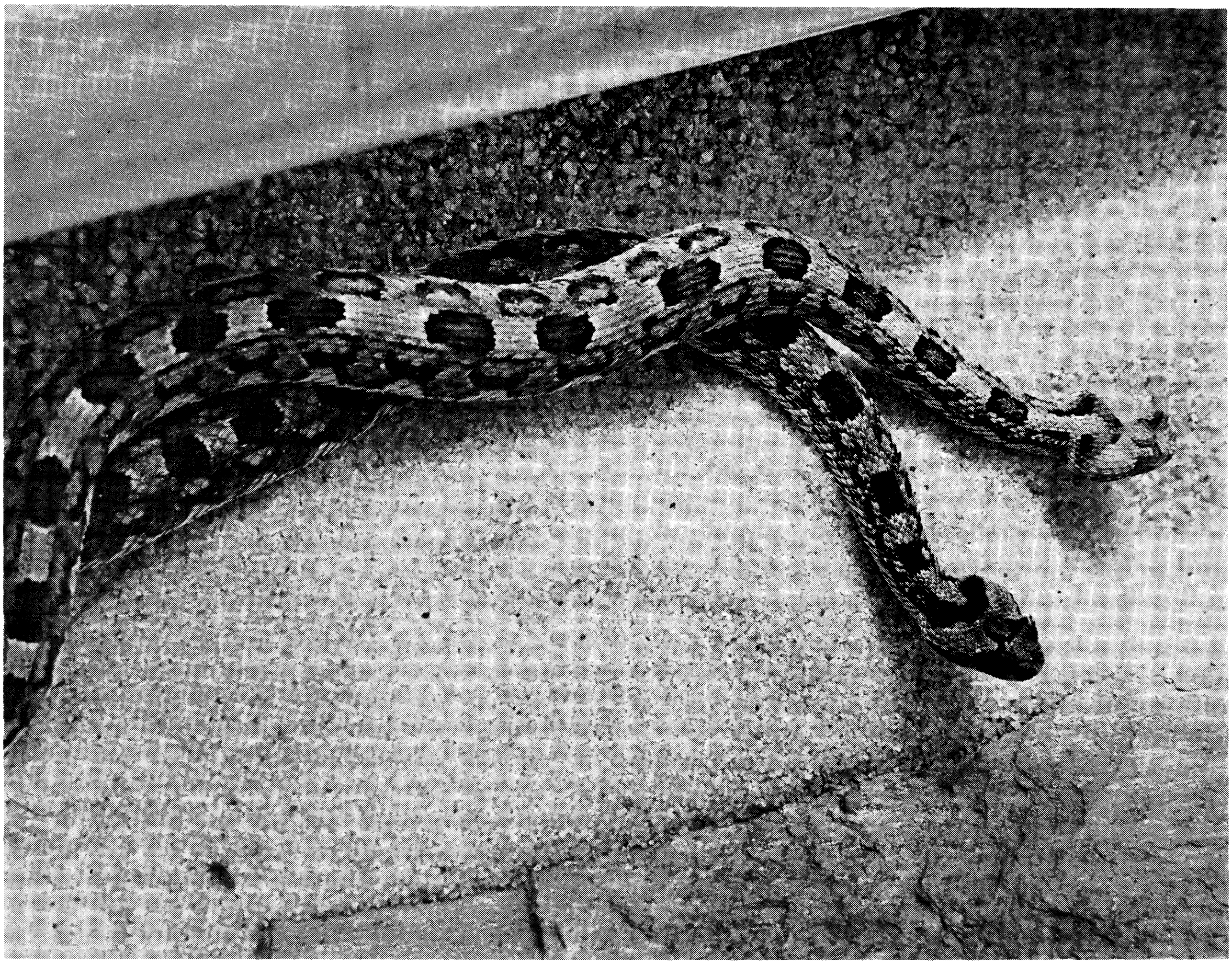

FIG. 2. C4 attempting to twist his body around C3, but being prevented from doing so by the non co-operation of C3.

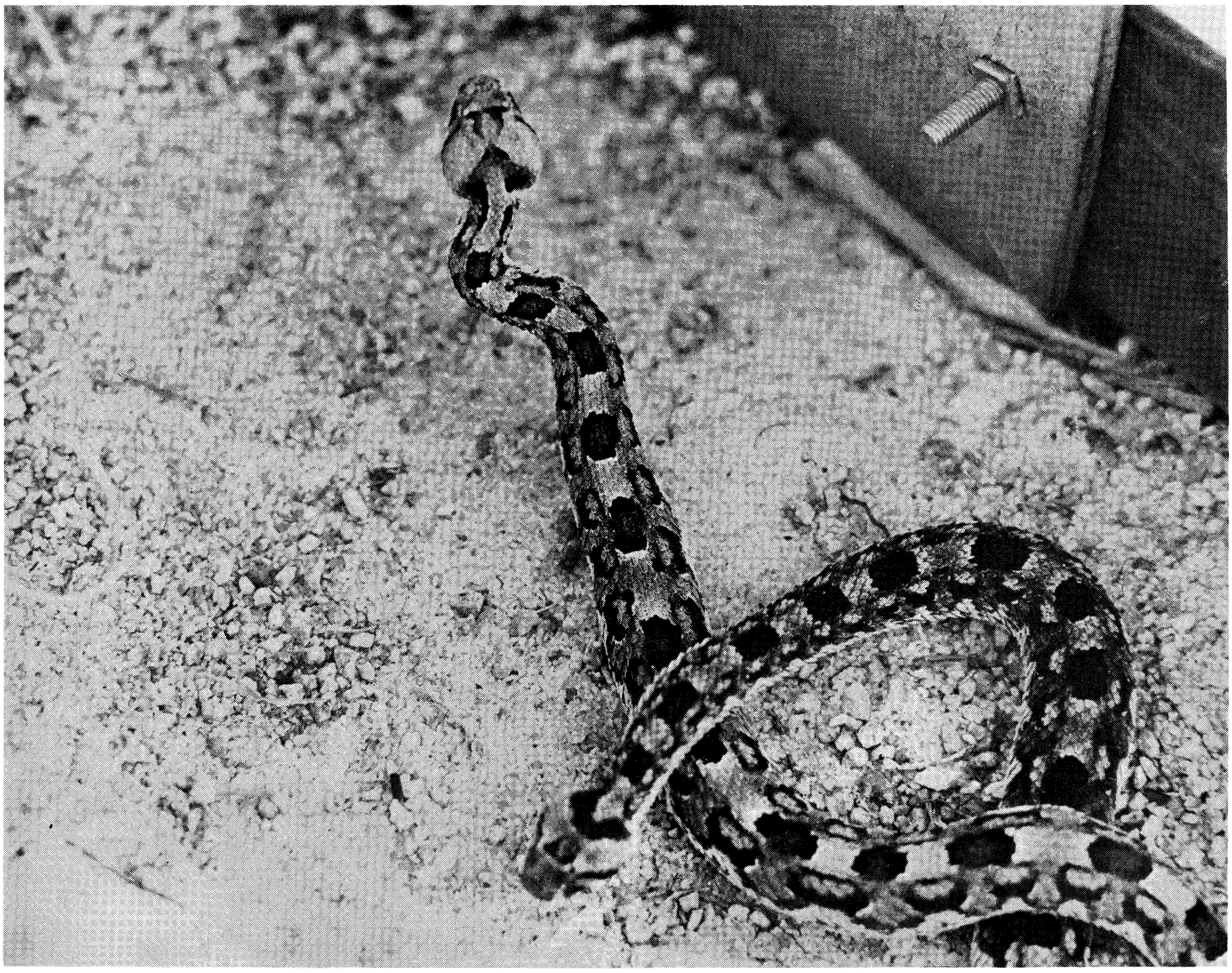

FIG. 3. C4 and C3 being flung apart as C4 reacts violently to the challenge of C3.

rivalry at a time when mature, aggressive males made contact with each other (Akester, 1979). However, the combat observed between male *B. caudalis* seems to run contra to the majority of these assumptions.

Although the dominant male did not have a particular territory to guard, he seemed to consider that the area immediately around himself constituted a zone where no other male was allowed to trespass. Any movement by another male within approximately 1 m of his position would elicit an immediate response from him. If he happened to be with the female, he did not return directly to her immediately after chasing the other male, but would wander restlessly about the enclosure until he eventually found her again. Once copulation had started, C4 paid no further attention to other males and would tolerate movement by them even in close proximity to the copulating pair. A female moving within the 1 m zone would be completely ignored by C4, and it is interesting to speculate how he differentiated between male and female at this distance.

When the snakes were dispersed over the limited area of the enclosure contact between them appeared to be predominantly visual, due no doubt to the close proximity of the individuals to each other, together with the lack of significant cover. However, once bodily contact had been made, it became apparent from the increased tongue flicking that chemical communication was then involved.

Andrén (1982) in discussing male combat in *Vipera berus* suggests that the release of a volatile substance, important in communication between males, seems to increase dramatically at sloughing, and it is interesting to note that all three male *B. caudalis* sloughed immediately prior to the period of male combat behaviour. Unfortunately, in these observations, the absence of a non-sloughed male for comparison purposes makes it impossible to assess the significance of sloughing on male combat behaviour in *B. caudalis*. However, from personal observations, it appears tht sloughing has no part to play in the male combat activity of *B. gabonica* as shedding in this species usually occurs once annually (October/November) some five to six months before male combat takes place.

Sutherland (1958) reported combat occurring between two male Timber Rattlesnakes which were aroused by the presence of food, and Kelleway (1982) describes predatory combat in *V. berus*. Combat in male *B. caudalis* takes place at a time when all feeding activity has ceased for the duration of the cold season, and at no time has there been any evidence that combat takes place between males after feeding has restarted.

It is quite clear that dominance by one male over another does take place in *B. caudalis* as evidenced by the complete domination of C4 over the other males—this despite the fact that there was almost no difference in length between the individuals and only a very slight weight advantage in C4's favour over each of the other males. The males, C3 and C5 gave little sign of any attempt at positive retaliation to the attacks of C4. Copulation occurred between C4 and C1 in all instances excepting one isolated occasion when C5 and C1 mated in the cage. However, this was out of their usual environment and it was probably an exceptional occurrence.

Male combat as a defence against homosexuality can be considered a possibility in this species, as evidenced by the two incidents observed to take place in the cage. In each example of homosexuality one of the males was resting on top of the female C1, when approached by another male. As the approaching male tried to pass his tail underneath, the second male actually assisted in the intertwining of tails, and no attempt at flight or combat took place. If combat is a defence against homosexuality, then it is possible that in these two incidents the close proximity of the female caused a breakdown in the defence mechanism which in turn led both males to believe that they were, in fact, actually courting the female. The initial stages of mating and combat are very similar—the only difference being that of the reaction of the female on one hand and the passive male on the other. Once the active male has reached the anterior third of the other individual, should it be a female she will remain quiescent or even assist in effecting copulation, but a male will either immediately take flight or engage in combat. It is possible that combat is a warning sign which prevents homosexuality from taking place. This reaction could be compared to the "release" calls of certain anurans—for example, *Ptychadena taenioscelis* (Passmore, 1976). If combat is a defence against homosexuality, this could explain why, in some instances, combat can take place without the presence of a female.

In *B. caudalis* it would appear that there are no clear-cut parameters in male combat and there is considerable overlap in a number of areas of behaviour. Territorial defence, sexual domination and defence against homosexuality all seem to be possible factors, but competition for prey items would appear to be an unlikely explanation.

It is interesting to draw comparisons between male combat in this species with observations on *B. gabonica* (Akester, 1979) and, although on examination there seems to be a wide divergence in behaviour patterns, a number of these factors can be explained by the very different characteristics of the two species. Gaboon Vipers are heavy-bodied, lethargic animals, in contrast to Horned Adders which are slender, active and alert.

For the greater part of the year Gaboon Vipers remain inactive for most of the time, only becoming restless for the duration of the breeding season: certainly a heavy-bodied snake such as this could not indulge in the vigorous combat and pursuits undertaken by male *B. caudalis*.

Male Gaboon Vipers disregard movement from other males until actual contact is made between them, appearing not to arouse themselves until it is absolutely necessary for them to do so—this would seem to lessen the possibility that territorial defence is a reason for combat in this species. In combat between male Gaboon Vipers there is no evidence of a victor or vanquished in direct contrast to the absolute dominance of one male *B. caudalis* over his fellows. Again it would appear that Gaboon Vipers do not have the bodily characteristics necessary for long chases in pursuit of rival males.

Although defence against homosexuality was not thought to be a factor in the male combat of Gaboon Vipers, subsequent personal observations seem to suggest that it could very well play an important role. Indeed, on examining the evidence of homosexual behaviour in both Gaboon Vipers and Horned Adders it would seem that future observations may well demonstrate that this may be, after all, a most important factor to be considered when seeking explanations of male combat in these and other species.

ACKNOWLEDGEMENTS

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BODY TEMPERATURES OF A DESERT POPULATION OF THE STRIPE-NECKED TERRAPIN, *MAUREMYS CASPICA*

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SUMMARY

Measurements have been made on the body temperatures of a population of *Mauremys caspica leprosa* Schweigger, in a desert habitat in North Africa. The results indicate that *M. caspica* employs heliothermy to only a limited degree and generally operates at body temperatures which are lower than air and substrate temperatures and only slightly higher than water temperatures.

INTRODUCTION

Heliothermy in reptiles is a behavioural strategy principally evolved to enable the elevation of body temperatures above the temperatures of the environment. This thermoregulatory strategy is found amongst all the major reptilian groups but is most prevelant and perhaps developed to its highest degree in species from the temperate regions where daily environmental temperatures may be low. When the temperatures of the habitat are high, heliothermy may be employed to only a limited degree or even become a seasonal phenomenon. Such a situation has been found in desert reptiles (Gauthier, 1967; Cloudsley-Thompson, 1971) where very high summer temperatures may alternate with cool winters. This paper reports on the body temperatures and basking behaviour of the stripe-necked terrapin *Mauremys caspica*. This chelonian is semi-aquatic and during the summer months the populations inhabiting the pools and streams of North West Africa frequently encounter environmental temperatures above those that may be lethal for reptiles.

Thermoregulation and thermoregulatory behaviour in semi-aquatic chelonians have been mainly investigated in North American species (see Boyer, 1965; Cloudsley-Thompson, 1971; Avery, 1982 for reviews). In the Mediterranean region there are only two species of terrapin *Emys orbicularis* and *M. caspica*. Cherchi (1958) has studied thermoregulation in *E. orbicularis* in the laboratory but there have been no such studies on *M. caspica* other than general observations on basking (*e.g.* Stubbs, Hailey, Tyler & Pulford, 1981).

MATERIALS AND METHODS

Body (cloacal) temperatures were recorded from basking terrapins during a two day period in May 1980 and one day's field work in September 1981 at an irrigation channel running through a desert region in Southern Morocco. The irrigation channel was approximately 2 m wide and had a concrete perimeter with a base of fine sand. The water running through the channel was slow moving and clear. Measurements on the body temperatures of basking terrapins are perhaps more difficult to obtain than in other reptile groups. The method used in this study was by entering the water and approaching the animals from this direction. Nets with adjustable handle lengths (up to 3m) were then used to capture the animals when they dived. This method produced the best results, the initial method of approaching from the bank was largely unsuccessful. A total of 30 captures were made; 6 in May (carapace lengths from 44–88 mm) and 24 in September (carapace lengths from 39–168 mm).

Temperatures were recorded in May with a mercury bulb thermometer, in September with a Whitley digital thermometer. The Whitley thermometer was battery operated and had a range from −50°C to 150°C and an error of ±0.5°C. Substrate temperatures were measured by inserting the probes 8 mm into the soil, water temperatures to a depth of 15 cm and air temperatures 30 cm above the ground with the probe shaded. Environmental temperatures were recorded simultaneously with body temperatures or every 30 mins or so. Body temperatures were tested for correlation with associated air and water temperatures and with carapace lengths. When appropriate a *t*-test with *n*-2 degrees of freedom has been used to test the levels of significance of the *r* value when *n* is low (Bailey, 1959).

RESULTS

During the period that body temperatures were gathered, sand temperatures around the channel varied from 45–55°C in May and 55–60°C in September, water temperatures from 24–25.2°C in May and 25.9–31°C in September, air temperatures from 30–33°C in May and 33–39°C in September. Only relatively few *M. caspica* were observed basking at either time of year. Basking took the form of the terrapins hauling themselves onto the concrete perimeter of the channel, at most a few centimeters clear of the water line and occasionally with the rear of their shells submerged.

Table I summarizes the results recorded between

TABLE I. Summary of *Mauremys caspica* body temperatures (°C) at two periods in the year

Period	n	Range	Mean	1.96 SD
May	6	24–26.5	25.4	1.84
September	24	24.8–29.5	26.8	2.54
Pooled	30	24–29.5	26.4	2.63

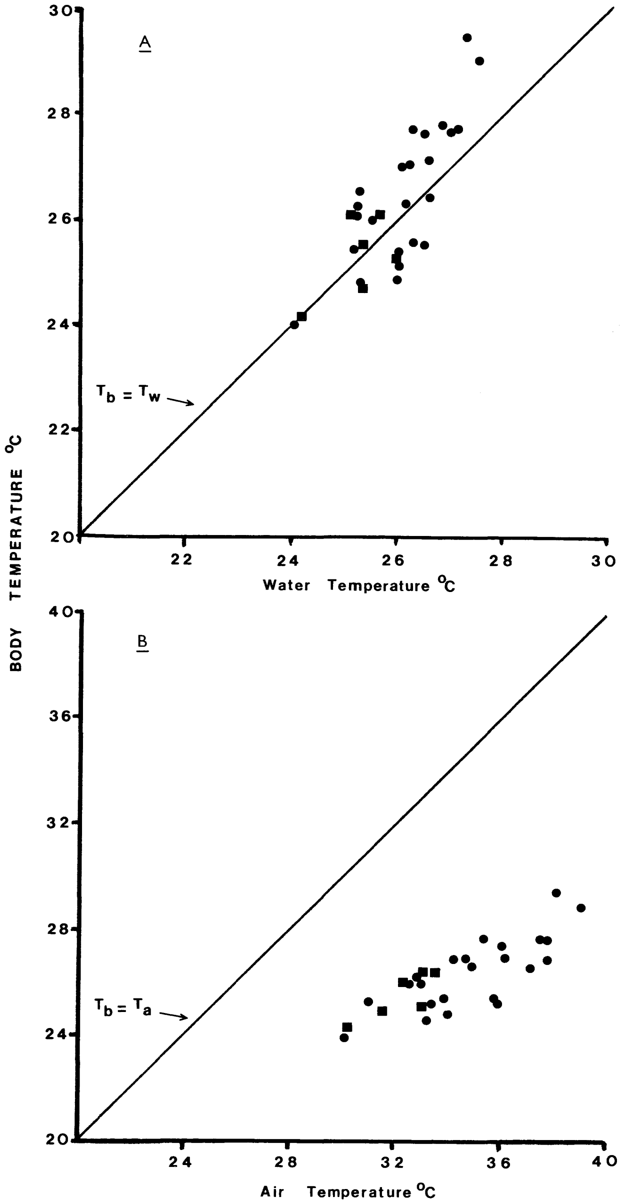

FIG. 1. Graphs showing *Mauremys caspica* body temperatures plotted against water temperature (A) and air temperature (B). Slanting lines indicate where body temperatures equal air or water temperature. September = ●, May = ■.

1200–1327 h in May and 1000–1800 h in September. In September, body temperatures were generally higher in mid-afternoon, the time when environmental temperatures were also highest. Figure 1 shows *M. caspica* body temperatures in relation to associated air and water temperatures. There was a significant correlation between air temperature and body temperature in September ($r = 0.70$, $P < 0.001$), but not in May ($r = 0.62$, 4 d.f., $P > 0.10$). Body temperatures were significantly lower than air temperatures (May: $t = -18.0$, 5 d.f., $P < 0.001$; September: $t = -27.1$, 29 d.f., $P < 0.001$). The majority of terrapins (70%) had body temperatures higher than or equal to water temperatures but there was no significant difference between mean body temperature and mean water temperature (May: $t = 1.53$, $P > 0.10$; September: $t = 1.58$, $P > 0.10$). Body temperatures were positively correlated with water temperature (May: $r = 0.76$, 4 d.f., $P < 0.10$; September: $r = 0.72$, 23 d.f., $P < 0.001$). Body temperatures were tested for correlation with carapace length. The results were not significant (May: $r = 0.53$ 4 d.f., $P > 0.10$; September: $r = 0.21$, 23 d.f., $P > 0.10$.

The mean body temperatures of males ($\bar{x} = 26.4$°C) and females ($\bar{x} = 26.8$°C) in September were not significantly different ($t = 0.74$, 15 d.f., $P > 0.10$) nor was the difference between the overall means of the May and September samples, $t = 1.02$, 28 d.f., $P > 0.10$ (See Table I).

DISCUSSION

In the desert areas of North Africa *Mauremys caspica* is regularly confronted with environmental temperatures that surpass the known critical maximum of chelonians (Hutchison, Vinegar & Kosh, 1966). However, by adopting a behavioural strategy of limited heliothermy and a large degree of thermoconformity with environmental temperatures *M. caspica* effectively maintains stable body temperatures to within a narrow range. Thermoconformity with water temperatures has been recorded in *Sternotherus oderatus*. Edgren and Edgren (1955) found that in this species body temperatures closely follow water temperatures when they are in the region of 28–30°C but that body temperatures are elevated above water temperature when these are low (17–19°C). They concluded that since this differential is not maintained in the laboratory it is presumably achieved by behavioural thermoregulation. The concrete basking areas used by *M. caspica* may also be influencing their thermoregulatory behaviour since Boyer (1965) noted that terrapins basking on concrete, which has high conductivity, did not remain emergent for long in contrast to those basking on logs, which spent long periods basking.

Thermoregulatory behaviour is believed to influence the presence of algal growth, flaking scutes and leeches on the shells of terrapins (Boyer, 1965). It has been suggested that basking and drying the body helps to keep the terrapins free of such animal and plant parasites and that non-basking terrapins in clear water would be the most subject to attack (Cagle, 1950; Neill & Allen, 1954). This hypothesis appears to be in good agreement with the limited basking of *M. caspica* since algal growth, flaking scutes and leeches have been found on the shells of over 20% of the terrapins examined at this study area (Meek, in preparation).

The maximum body temperature of 29.5°C attained by *M. caspica* is several degrees below the critical maximum body temperature of 41.5 °C found for emydids by Hutchison *et al.* (1966) and the 37.4°C at which the loss of righting response begins. It is of interest to note also that *M. caspica* does not appear to elevate body temperatures as high as those found for two species of amphibian at this study area (Meek, 1983) and are also lower than the maximum body temperatures found in North African *Testudo graeca* from a cooler coastal habitat (Meek & Jayes, 1982).

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INCUBATION AND HATCHING OF EGGS OF *GAVIALIS GANGETICUS* IN HATCHERIES

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SUMMARY

An account of captive hatching of the eggs of *Gavialis gangeticus*, their incubation temperature and hatching success, is given. Incubation at temperatures of about 32°C lasted for 57–76 days. Very high levels of incubation success (>80%) were obtained in two out of three years despite the fact that eggs were collected in remote areas and needed to be transported over distances of about 500 km to the hatchery.

INTRODUCTION

In view of the endangered status of all Indian crocodilians, a husbandry programme has taken shape over the years. The main plank of this programme is captive hatching of wild-laid eggs in hatcheries and restocking of juveniles in their natural habitat.

The conservation programme can be said to have commenced at Samut Prakan Crocodile Farm, Thailand (Yangparapakorn, Cromin & McNeeley,

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1971) where captive farming of *Crocodilus porosus* and *C. siamensis* was initiated in 1950, and is continuing with considerable success. Bustard (1969) recommended captive hatching of the eggs of *C. porosus* and *C. novaequineae*, natives of Papua and New Guinea, to build up their depleted populations in order to make the crocodilian skin industry a commercial proposition. Conservation in an exactly similar manner of *C. niloticus* in Africa (Pooley, 1971) and of *C. porosus* and *C. johnsoni* was taken up in Australia (Bustard, 1973) and is still continuing. In India also the conservation programme was initiated by Bustard (1974) when he proposed the "grow and release" technique to augment and conserve *G. gangeticus*, and also *C. porosus* and *C. palustris*. The present study is a logical extension of this programme.

MATERIALS AND METHODS

An account of the study area (130 km extent of the river Chambal), its physical features, individual sex identification of *Gavialis gangeticus* and their nest location in various river sections will be presented elsewhere (Chowdhury, Bustard & Tandan, in press).

Eggs were collected, usually 6–8 weeks after oviposition, in the second fortnight of May 1976, 1977 and 1978. The sandy plug of the nest was gently scooped out by hand and the top of each exposed egg marked with Indian ink. The eggs were carefully arranged in tiers, with their marked sides uppermost in 60 × 60 × 60 cm wooden crates, having a 10 cm thick layer of moist river sand at the bottom and, thereafter, covered with a 30 cm thick layer of moist sand. The sand was collected from the vicinity of the nests, and contained 5–7% water by weight. A separate carrier box was used for each clutch.

The wooden boxes were transported to the nearest negotiable ravine road either on boats or bullock carts. Therefrom they were transported on trucks to the Crocodile Rehabilitation and Research Centre at Kukrail, Lucknow, Uttar Pradesh, approximately 500 km away.

Two well-ventilated rooms measuring 3.65 × 3.05 × 3.04 m served as hatcheries, with each hatchery having 8–10 incubating chambers of brick and mortar, each chamber measuring 60 × 60 × 60 cm. The eggs were arranged in the incubating chambers, in their natural position, atop a 10 cm thick layer of moist sand and covered by a 30 cm layer of sand, with water content of the sand being maintained at 5–7% by adding a calculated amount of water. The temperature of the sand, at the level of the top-most egg, was recorded at 06:00 and 16:00 h and, as far as possible, maintained close to 32°C, the temperature that usually prevails in natural nests (Chowdhury *et al.*, in press). This was achieved by spraying the outer walls of the incubating chamber with water as and when necessary. The ambient temperature of the hatchery was also recorded for comparison.

Immediately before their hatching, a croaking sound emanated from the eggs; when the chorus became loud, the covering of sand was removed. In several eggs the snout was seen to have pierced through the shell.

RESULTS

Eggs from a total 30 nests were used for captive hatching (Table IV): 1976, 6 nests; 1977, 12 nests; 1978, 11 nests and one bottom nest. The mode of transportation of eggs to the hatchery, the distance over which they were transported and the manner of transport are given (Table I).

INCUBATION TEMPERATURE

From Table II, it will be seen that the temperature of the sand around the eggs, in the incubating chamber, ranged from 30.5° to 32.5°C, whilst ambient in the hatchery ranged from 24.0°–40.5°C.

NESTING SEASON AND INCUBATION PERIOD

Out of 30 nests, the date of oviposition of only 14 nests, 9 of 1977 and 5 of 1978, was known. Egg laying extended from the last week of March to mid-April. In the hatchery, the incubation period ranged from

TABLE I. Nest location and transportation of eggs for hatchery incubation during the 1977 breeding season

				Mode of transportation to hatchery			
Section of river Chambal	Nest no.	Nest location	Date of collection in 1977	By boat (km)	By bullock cart (km)	By truck (km)	Total distance (km)
(i) Barauli proper	1.1	River bank Barauli	20 April	—	6	520	526
(iii) Jhiri to Dholpur	3.1	Island at Bharra	17 May	6	5	493	504
	3.2	Island at Bharra	17 May	6	5	493	504
	3.3	Island at Bharra	17 May	6	5	493	504
	3.4	Island at Bharra	17 May	6	5	493	504
	3.5	River bank, Bharra	18 May	6	5	493	504
	3.6	River bank, Bharra	18 May	6	5	493	504
	3.7	River bank, Kalitir	15 May	—	5	493	498
(iv) Dholpur to Puraini	4.1	River bank, Puraini	24 May	7	—	533	540
	4.2	River bank, Puraini	24 May	7	—	533	540
	4.3	River bank, Puraini	25 May	7	—	533	540
	4.4	River bank, Puraini	25 May	7	—	533	540

TABLE II. Temperature of hatchery and incubating chamber during the 1977 breeding season

Date in 1977	Sand temperature in incubating chamber 06:00 h	16:00 h	Hatchery temperature 06:00 h	16:00 h
31 May	31.0	31.5	32.0	40.5
1 June	31.5	32.0	32.5	40.5
2 June	30.5	32.0	30.5	39.5
3 June	31.0	32.0	27.5	38.5
4 June	31.5	32.5	28.5	39.0
5 June	32.0	32.0	28.5	38.0
6 June	32.0	32.5	29.5	39.0
7 June	32.0	32.5	30.5	37.0
8 June	31.5	31.5	28.0	35.5
9 June	31.0	32.0	28.0	—
10 June	31.0	31.5	27.0	33.5
11 June	31.5	31.5	28.5	32.5
12 June	31.5	32.0	27.5	37.0
13 June	31.5	31.5	30.5	36.0
14 June	30.5	31.5	24.0	36.5
Range	30.5–32.0	31.5–32.5	24.0–32.5	32.5–40.5

57–76 days, in the 1977 nests from 61–76 days and the 1978 nests from 57–66 days (Table III).

The maximum number of nests harvested from any one section of the river was from section (iii)—seven in 1977: Table I. A comparison shows both the range and average of incubation periods of eggs collected from section (iii) (61–76 days, mean = 69) in 1977 to be slightly greater than that of eggs collected from section (iv) (57–66 days, mean = 62) in 1978.

HATCHING SUCCESS

According to the data of the 30 nests, hatching success ranged from 0 to 100% (Table IV). No hatching was recorded in two clutches, in one due to an extremely unfavourable substratum, in the other due to an accident. While the lowest hatching success of 21.87% was recorded for nest no. 3.5 (Table IV), this does not represent the normal figure because 23 eggs out of a clutch of 32 were predated leaving only 9 viable eggs. As 7 of these hatched, the hatching percentages calculated from 9 and 32 eggs are 77.8% respectively. The hatching success (62.5%) recorded for nest no. 3.4 (Table IV) likewise cannot be regarded as normal because 10 out of 32 eggs were predated. Of the 22 viable eggs, as 20 hatched, the hatching percentage calculated from 22 and 32 eggs come to 93.8% and 62.5% respectively.

The figure to be regarded as the lowest natural hatching success is 37.5%, recorded for nest no. 4.5, because this nest did not suffer any mishap. In view of the foregoing, the range of normal hatching success is 37.5–100%, the latter being for nest no. 4.2 (Table IV).

The hatching success based on the total number of eggs collected during each of the three breeding seasons is: 89.28% for 1976 seasons when 200 out of 224 eggs hatched, 86.48% for 1977 season when 448 out of 518 eggs hatched and 64.4% for 1978 season when 327 out of 500 eggs hatched (Table IV). Because one and three unsatisfactory clutches respectively of the 1976 and 1978 breeding seasons, have been included, as discussed above the percentages for these seasons are misleading.

Eggs which failed to hatch were either damaged during location of the nests, or were infertile or addled or underwent partial embryogenesis only. Hatchlings which died within 24 h of hatching have, for convenience, been included among unhatched eggs. Only 35 out of 518 (or 6.75%) eggs studied for captive hatching in 1977 were infertile.

TABLE III. Incubation periods of eggs collected during the 1977 and 1978 breeding seasons

Section of river Chambal	Nest no.	Date of: Laying	Collection	Hatching	Incubation (days): Period	In nature	In hatchery
1977							
(i) Barauli proper	1.1	1 April	20 May	31 May	61	50	11
(iii) Jhiri to Dholpur	3.1	28 March	17 May	28 May to 6 June	61–70	50	11–20
	3.2	28 March	17 May	2 June to 4 June	66–69	50	16–19
	3.3	2 April	17 May	6 June to 7 June	65–66	44	21–22
	3.4	1 April	17 May	6 June	66	45	21
	3.5	28 March	18 May	7 June to 10 June	71–74	51	20–23
	3.6	3 April	18 May	14 June	72	44	28
	3.7	4 April	15 May	14 June to 19 June	71–76	41	30–35
(iv) Dholpur to Puraini	4.1	—	24 May	6 June to 7 June	—	—	—
	4.2	—	24 May	8 June	—	—	—
	4.3	—	25 May	13 June	—	—	—
	4.4	8 April	25 May	8 June	61	47	14
					range		
					61–76	41–51	11–35
1978							
(iv) Dholpur to Puraini	4.1	8 April	30 May	13 June	66	52	14
	4.2	10 April	30 May	13 June	64	50	14
	4.3	10 April	30 May	12 June	63	50	13
	4.4	14 April	30 May	10 June to 12 June	57–59	46	11–13
	4.5	16 April	30 May	15 June to 16 June	60–61	44	16–17
					range		
					57–66	44–52	11–17

FATE OF EGGS OF DISTURBED NESTS

The hatching percentage of eggs that had been disturbed deserves consideration. Owing to its location, nest no. 3.4 (Table IV) of the 1977 breeding season was endangered by water logging; therefore 3 days after oviposition the eggs were transferred to an artificial nest, dug near by, but at a safer site, and arranged in it in their natural position. The hatching success of the clutch was 94.7%.

The bottom nest of the 1978 season was disturbed unwittingly, about one week after oviposition; the eggs were not rearranged with due care to their proper orientation, nor was the nest plugged with a sufficiently deep column of sand. Since no egg hatched even after the lapse of the normal incubation period, the eggs were examined. Fully formed active embryos were present inside, but the snouts of almost all were trapped in the network of umbilical blood vessels. On release of the snout from the network, the hatchlings were seen to be crooked or bent. All the 50 died within 48 h.

Nest nos. 3.2 and 3.3 of the 1977 season were collected respectively after undergoing 50 and 44 days of incubation in the natural environment, for transport to the hatchery. On the rough, pot-holed, narrow ravine road the bullock cart overturned and the two crates containing the eggs were thrown out. When they were immediately opened, the eggs were found tumbled and seriously disarranged, but as their tops were already marked, they could be re-arranged in their natural position. The hatching success of eggs from these nests was 91.66% and 95.31% respectively (Table IV).

DISCUSSION

In the experimental work of Bustard (1971) on the eggs of *C. novaeguinae*, incubated at 38°C, 3 young out of 10 eggs had to be helped out and they had a deformed tail; this deformity appears to indicate high temperature stress. In this light, the deformity in *G. gangeticus* young from the bottom of nests may well have been due to temperature stress resulting from an improper plug of sand.

McIlhenny (1934, 1935) recorded an incubation

TABLE IV. Hatching success of eggs collected for captive rearing 1976–1978

Section of river Chambal	Nest no.	Clutch size	Eggs hatched: Number	%	Eggs predated or disturbance	Unhatched eggs: Damage during location of nest	In-fertile	Addled	Partially developed	Hatchling died immediately after emergence
1976										
(i) Barauli proper	1.1	33	32	97	—	—	—	—	—	—
(iii) Jhiri to Dholpur	3.1	60	51	85	—	—	—	—	—	—
(iv) Dholpur to Puraini	4.1	53	50	94	—	—	—	—	—	—
	4.2	42	38	90	—	—	—	—	—	—
	4.3	31	29	94	—	—	—	—	—	—
	4.4	5	0	0	—	—	—	—	—	—
1977										
(i) Barauli proper	1.1	43	34	79	—	—	4	1	2	2
(iii) Jhiri to Dholpur	3.1	49	47	96	—	—	1	—	—	1
	3.2	48	44	92	—	—	4	—	—	—
	3.3	64	61	95	—	—	1	—	2	—
	3.4	38	36	95	—	—	—	—	2	—
	3.5	45	31	69	—	—	11	—	3	—
	3.6	35	24	69	—	—	7	4	0	0
	3.7	44	31	70	—	—	3	2	6	2
(iv) Dholpur to Puraini	4.1	14	6	43	—	—	2	6	—	—
	4.2	47	46	98	—	1	—	—	—	—
	4.3	50	49	98	—	1	—	—	—	—
	4.4	41	39	95	—	—	2	—	—	—
1978										
(iii) Jhiri to Dholpur	3.1	41	35	85	—	—	—	—	—	—
	3.2	41	36	88	—	—	—	—	—	—
	3.3	62	34	55	—	—	—	—	—	—
	3.4	32	20	63	10	—	—	—	—	—
	3.5	32	7	22	23	—	—	—	—	—
	3.6	46	41	89	—	—	—	—	—	—
(iv) Dolpur to Puraini	4.1	48	42	88	—	—	—	—	—	—
	4.2	44	44	100	—	—	—	—	—	—
	4.3	14	6	43	—	—	—	—	—	—
	4.4	50	47	94	—	—	—	—	—	—
	4.5	40	15	38	—	—	—	—	—	—
Outside study area (approx. 100 km below Puraini)	—	50	0	0	50	—	—	—	—	—

period of 62–64 days at 66–97°F (18.8°–36.1°C), for eggs in natural nests of *Alligator mississippiensis*. The incubation period of eggs of *C. niloticus* determined from observations on natural nests, has been reported to be from 77–91 days (Cott, 1961; Modha, 1967) and 77–98 days (Pooley, 1969). In eggs of *Alligator mississippiensis* incubated artificially at a temperature 80°–90°F (30°–32°C), an incubation period of 67 days was recorded (Chaffee, 1969). Recently, an incubation period of 70–84 days for eggs of *C. palustris*, incubated in a hatchery, has been reported (Whitaker, 1979). The corresponding figure for *G. gangeticus*, derived from artificial hatching of eggs at about 32°C, is 57–76 days. Any further comparison is precluded because previous workers have not always given the temperature of the nest.

The hatching success of crocodilian eggs under captive conditions is quite favourable. Joanen & McNease (1971) recorded 56% hatching of eggs of *A. mississippiensis*; Yangparapakorn *et al.* (1971) 40–50% of eggs of *C. palustris* and 50–60% of those of *C. siamensis* and Whitaker (1979) 23.8–100% of eggs of *C. palustris*. The hatching percentage, 37.50–100%, of eggs of *G. gangeticus* incubated in hatcheries, is on average rather better than these results.

The importance of maintaining reptilian eggs in their original position should be stressed. Bustard (1972) states that rotation of eggs may cause the yolk to lie on top of the embryo, resulting in death. A comparison of hatching figures for the two disturbed nests of *G. gangeticus* (Table IV) substantiates the importance of the original position of the eggs during their incubation.

Pooley (1971) opined that for their captive hatching, the eggs of *C. niloticus* should be collected soon after being laid, especially if the journey back to the hatchery involves a considerable distance over rough roads. In his reports on farming of all three Indian crocodilians, Bustard (1974, 1975) also made a similar recommendation, a practice adopted by him earlier (Bustard, 1972) in the course of conserving *Chelonia mydas*. While Pooley's view was based on the notion that transport of eggs in advanced states of incubation may rupture delicate vessels and cause premature hatching due to bumping or jolting, Bustard also stated that early collection saved the clutch from natural predation or loss due to unseasonal flooding.

As opposed to this, Blake (1974) and Blake & Loveridge (1975) hold the view that late collection of eggs of *C. niloticus* from natural nests brings high hatching success in hatcheries in comparison to early collection. This view was based on the notion that *C. niloticus* eggs are more susceptible to handling in early than in late state of incubation.

Late collection of *G. gangeticus* eggs, 6–8 weeks after oviposition, for captive hatching in the first year (1976) was an arbitrary decision. Since a hatching success of 85.0% or above resulted, the same practice was continued for captive hatching of eggs of the 1977 and 1978 seasons also. Since no gharial egg was collected soon after oviposition, it is not possible to comment on whether late or early collection is superior. Working on the eggs of the hawkbill turtle *Eretmochelys imbricata*, Raj (1976) concluded that provided care is exercised in maintaining the original orientation of the eggs and adequate precaution are taken to avoid mechanical shocks, turtles eggs may be moved at all stages of development over long distances and incubated with substantial greater success than in nature, allowing for natural losses due to predation or other hazards.

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AMPHIBIAN BREEDING SITES IN SUSSEX 1977–1983: POND LOSSES AND CHANGES IN SPECIES ABUNDANCE

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SUMMARY

The fates of breeding ponds and amphibian species using them in parts of Sussex have been investigated over a period of six years. Ponds continue to be lost, primarily as a result of neglect, both on the Downs and in lowland Weald areas. Common frogs *Rana temporaria* have nevertheless shown signs of increasing their range and abundance in recent years, but great crested newts *Triturus cristatus* show significant declines which may lead to widespread local extinctions within a few years if present trends continue.

INTRODUCTION

The changing fortunes of the various species of amphibians native to the British Isles have received considerable attention in recent years (*e.g.* Cooke, 1972; Cooke & Arnold, 1982; Beebee, 1973, 1975, 1976; Prestt, Cooke & Corbett, 1974). In most instances data on changes in abundance over long periods of time have been accrued by consulting historical records or by the polling of observers rather than by direct study of the animals themselves. In this paper I report on alterations of species distribution at a number of breeding pools in Sussex over a fairly short period of time (4–7 breeding seasons) but on the basis of direct observations rather than the use of indirect methods.

METHODS

The use of ponds by anurans was assessed by visiting the sites during and after peak breeding times to record the presence of adults or spawn. Newt populations were assessed by netting ponds during daytime and examining shallow areas at night, during early spring, with a powerful torch (Beebee, 1977, 1979). Wherever practicable both methods were applied to each pond, though in many instances (especially dewponds) the vegetation was too dense or the water too murky for night-torching to be effective. Ponds were selected initially using the 1:25 000 scale Ordnance Survey maps.

RESULTS

DEWPONDS

Dewponds on the South Downs are all of artificial origin, created at various times over the last few hundred years for the purpose of watering livestock. A depression in the porous chalk substratum was lined with clay or concrete and allowed to fill from rainfall and mist condensation. In the absence of maintenance such ponds inevitably have a finite lifespan, probably less than 100 years on average, since once the liner cracks or is pierced the water rapidly drains away. The sharp shift in farming practices on the Downs from sheep-rearing to arable, which began in the 1940s, has already resulted in the loss by neglect of more than 70% of previously-existing dewponds within less than 50 years (Beebee, 1977). Dewponds were good breeding sites for amphibians, especially newts, and where surrounding terrestrial habitat remained suitable (*i.e.* with rank grassland or scrub) sizeable populations of all three native species could be encountered though even in 1977 this favourable combination of circumstances was not common.

Twenty out of 31 dewponds still containing water when examined in 1977 were re-examined in 1983 (Table I). Of these, 3 had cracked and dried out completely (2 previously in the <0.5 m depth range and 1 in the 0.5–1.0 m range); a further 3 had partially cracked, with 2 entering the <0.5 m range from the 0.5–1.0 m range and 1 reducing from >1.0 m to 0.5–1.0 m depth. Conversely, 2 shallow ponds (<0.5 m) were restored over the same period to the 0.5–1.0

range and 1 new pond was created in this intermediate depth range. There was therefore a net loss of 2 (10%) of the dewponds over 6 years, with a likely loss of at least 3 more in the near future.

The dewponds chosen for re-examination in 1983 included all those found to contain breeding amphibians in 1977 together with four in which amphibians were not found but which were thought most likely on the basis of their condition and surrounding habitat to become used or to harbour animals previously undetected. An additional pond created in the intervening years was also investigated in 1983. Species located in 1977 and 1983 are shown in Table II. Many ponds yielded the same species in both years, but this was not always the case. Two smooth newt and 1 crested newt sites were lost through pond-cracking. Only a single string of toad spawn was deposited at site 4 in 1977 and none has been seen in subsequent years either there or in the adjacent site. 3. Smooth newts seem to have vacated the very shallow site 18 where only 2 individuals were found in 1977, but this pond has not changed visibly and it is possible that a very small newt population persisted undetected in 1983. The newly-constructed site 21, close to 18, had however, been colonized by smooth newts within 2 years of construction. The discoveries of crested newts in pond 13 and smooth and palmate newts in pond 20 in 1983 almost certainly reflect vagaries of the survey procedure rather than recent colonizations; pond 13 is situated in a vast tract of arable land with a small area of scrub immediately around the pool, and only 2 crested and 5 smooth newts were found there after intensive netting and torching in 1983. It is very likely that *Triturus cristatus* was present but missed in 1977, since dense reedbeds make this a particularly difficult

TABLE I. Fate of dewponds over 6 years

		Depth range (metres)		
Year	Dry	<0.5	0.5–1.0	>1.0
1977	0	6	9	5
1983	3	4	10	4

Figures are the numbers of ponds in each category.

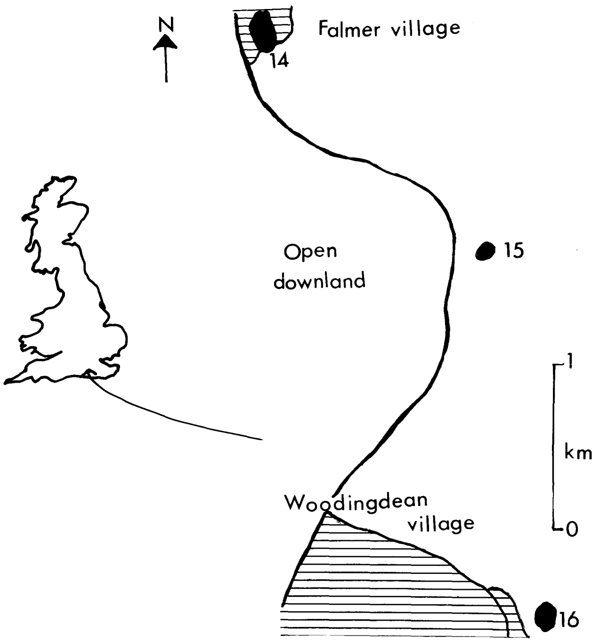

FIG. 1. Sketch map of the Falmer–Woodingdean area of Sussex, showing the road connecting these villages and the ponds 14–16 referred to in the text. Cross-hatch shows built-up areas; the remaining land is arable farmland.

TABLE II. Amphibians recorded in dewponds in 1977 and 1983

Site no.	Species found in 1977	Species found in 1983	Change in 1983 relative to 1977
1	TV TH TC	TV TH TC	0 (Pond restored)
2	TV TH	TV TH	0
3	TV TH TC	TV TH TC	0
4	TV BB	TV	–BB
5	TV TH TC	TV TH TC	0
6	TV	TV	0
7	TV RT	– (But pond in process of restoration)	
8	TV TH	TV TH	0
9	TV	–	–TV (Pond lost)
10	0	0	0
11	TV	–	–TV (Pond lost)
12	TC	–	–TC (Pond lost)
13	TV	TV TC	+TC
14	TC RT BB	RT BB ?TC	0
15	0	RT	+RT
16	TV	TV RT	+RT
17	0	0	0
18	TV	0	–TV
19	TV TC	TV TC	0
20	0	TV TH RT	+TV TH RT
21	0 (Newly created)	TV	+TV

TV = *Triturus vulgaris*; TH = *T. helveticus*; TC = *T. cristatus*; BB = *Bufo bufo*; RT = *Rana temporaria.*

pond to monitor. Pond 20 was virtually filled with rotting logs in 1977 and again difficulties in monitoring probably explain the failure to record the two newt species seen in the cleared-out (but cracked and almost empty) pond visited in 1983. Frog spawn would have been seen even in site 20 in 1977, however, and it is clear that frogs have extended their range in this part of Sussex in recent years. Pond 20 was first used by frogs in 1981, and ponds 15 and 16 for the first time in 1983. Dewponds more remote from human settlements still do not have frogs, and the 3 newly-used ones are those closest to built-up areas where frogs have recently proliferated in garden pond niches (Beebee, 1979). The positions of pools 14, 15 and 16 are shown in Fig. 1. in relation to nearby human settlements. Ponds 10 and 17 revealed no amphibians in 1977 or 1983.

LOWLAND PONDS

All 5 pools in the area of Weald immediately north of Brighton which contained crested newts when first investigated in 1980, together with 2 sites that did not have this species, were re-surveyed in 1983. Finally, the only other crested newt site known to me within the 300 km^2 I have studied, a large pond in a semi-urban area, was also included in the re-survey programme (site 8, Table III). Site 5 was discovered to be seriously damaged by cattle in 1983, with low water level and no aquatic vegetation or newts. Site 8 was in the process of destruction by a building development. Palmate newts could not be found in site 7 in 1983, but only 2 individuals were observed there in 1977. The appearance of this species in site 4 was a single individual. Neither of these pools or their environs had changed visibly, but both areas have been closely studied in recent years and these minor alterations in palmate newt distribution are thought to be real rather than artefacts of the surveying procedures. Frogs have also recently started to breed in sites 4 and 7.

OVERALL CHANGES IN COMMON FROG AND CRESTED NEWT STATUS

Common frogs and crested newts are of particular interest for different reasons. The former species seems to be expanding its range in the Brighton area after a nadir in the 1970s, whereas the latter seems to be declining continuously. Table IV summarizes data for these two species. Whereas there has been a net change of >100% increase in frog breeding sites within the sample of ponds studied in rural areas, there has been a coincident 20–25% loss of crested newt sites and another equal percentage is under imminent threat.

DISCUSSION

It is evident that amphibian breeding sites in rural areas of Sussex are still disappearing at a frightening rate. Conversely, terrestrial habitat changes which, at least in the case of arable farming, have probably had serious effects on amphibian populations in the recent past have virtually come to a halt in these study areas over the last few years. The future of dewpond habitats appears particularly bleak and on current trends all

TABLE III. Amphibians recorded in lowland ponds in 1980 and 1983

Site no.	Species found 1980	Species found 1983	Change in 1983 relative to 1980
1	TV TH TC	TV TH TC	0
2	TH	TH	0
3	TV TC	TV TC	0
4	TV TC	TV TH TC RT	+TH RT
5	TV TH TC	0	Pond damaged. –TV TH TC
6	TV TH TC	TV TH TC	0
7	TH	RT	–TH +RT
8	TH TC RT	0	Pond destroyed. –TV TC RT

Abbreviations are the same as in Table II.

TABLE IV. Overall changes in status of *Rana temporaria* and *Triturus cristatus*

Species	No. sites on first survey	Gains	Losses	Net change	No. sites on second survey
Rana temporaria	3	5	1	+4	7
Triturus cristatus:					
Small populations*	8	0	2	–2	6
Medium/large sites	5	0	1	–1	4
Total	13	0	3	–3	10†

Figures refer to numbers of ponds used as breeding sites.

* Those thought to contain very few newts, *i.e.* no more than 10's. Medium/large sites are thought to contain >50 newts.

† Of these, 1 medium/large and 2 small sites are either under imminent threat or the species could be already extinct there.

The assumption is made that site 13 (Table I) contained warty newts in 1977 though these were only detected in 1983 (see text).

other than the few receiving positive management (usually for amenity purposes) will have gone by the end of this century. As far as I am aware only 3 ponds within about 70 km^2 of downland are deliberately maintained at present, with the prospect of 1 more being built by the Nature Conservancy Council within a nature reserve in the near future. This would represent <4% of the ponds present on the Downs earlier this century. Some features of special interest are among those likely to be lost; site 19 (Table I) is well placed to act as a source of crested newt colonization for the proposed nature reserve pond, and the crested newts are notable for their small size (<100 mm); but this is one of the ponds which has recently cracked and is in danger of imminent loss. Lowland ponds have fared somewhat better, although one of the best of the small number studied is under threat of development, one has just been built over and another seriously damaged by cattle. The latter problem may of course by reversible but it is increasingly evident that many of the best surviving pools are in need of some form of management to maintain their status. Overgrowth with dense scrub and infilling with silt or fallen trees are particular problems in addition to cattle and very few pools are now actively maintained by farmers for livestock watering. Neglect is at least as much of a threat as positive development.

Considerations of changing amphibian species in the various ponds depend critically on the validity of the surveying procedures, a subject presently under scrutiny (Beebee, in preparation). The interpretations I have made are those I consider most likely to be true, but other explanations are obviously possible in some instances; it may be, for example, that *Triturus cristatus* has indeed recently colonized site 13 though circumstantial considerations render this unlikely. Anurans and their spawn are unlikely to be missed in the small pools of this study, but newts are generally more problematical. Of the 28 sites examined in at least two separate seasons, 23 showed no changes in newt species that could possibly be attributed to monitoring procedures and only in two instances is it thought likely that survey inaccuracy was responsible for the differences noted.

The apparent improvement in the status of *Rana temporaria* should be viewed in the light of the vagrant nature of this species. It was shown by Savage (1961) that within any particular area virtually no pond will always be used for spawning and there is a continual redistribution of sites from year to year. Large frog colonies may be more stable in this respect, but none of the ponds recorded here contained more than 10 spawn clumps. This opportunistic breeding pattern may explain the appearance of frogs in lowland pools 4 and 7 (Table III) but is unlikely to account for the dewpond observations. These seem to reflect a true expansion from urban areas of high frog population density; trivial explanations, such as human movement of spawn to these sites, can be ruled out on the basis of detailed observations. Whether the frogs traversed the large arable fields over kilometre distances or moved along apparently more suitable routes such as roadside verges to approach 15 (see Fig. 1) is not known, but either way the colonizing potential of *Rana temporaria* under these circumstances is impressive. Another important perspective however is the very low baseline level of rural frogponds in Sussex in the 1970s (Beebee, 1981) and any present tendency to expand is still small compared with the distribution that probably pertained in the recent past and likely to be strictly confined by the dwindling number of suitable ponds.

Toads remain rare in rural areas in this part of Sussex, though they are quite common in urban districts (Beebee, 1979). Smooth newt sites have shown a net decline of four, from 21 to 17, but there is little serious concern for this widespread species which also prospers in garden pools and palmate newts have lost (net) no more than one site out of 11. Crested newt declines give the greatest cause for concern and if present rates of site loss persist all but positively managed ones (only one at present) are likely to disappear within the next 10–20 years. A useful observation from this study is an idea of the minimal area of terrestrial habitat needed in the vicinity of a pond in order to support crested newts; at one site which has not changed significantly over 6 years it is possible to locate 1–2 adult crested newts by day-netting for 30 minutes or night-torching for 15 minutes, evidently a very small population in a pond of some 30 m diameter. This pool has no more than 600 m^2 of scrub and long grass in its immediate vicinity and is otherwise surrounded by arable fields for >1 km in every direction.

There must now be an urgent case for the establishment by the Nature Conservancy Council of a pond conservation programme aimed at maintaining a network of the better rural ponds in Britain; such a policy would of course not only enhance the prospects of our native amphibians but also of many other groups of fauna and flora which depend upon this much-neglected habitat type.

ACKNOWLEDGEMENTS

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A PRELIMINARY NOTE ON THE DISTRIBUTION OF *TRITURUS HELVETICUS* IN CATALONIA (SPAIN)

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SUMMARY

This note gives fifteen localities for *Triturus helveticus* in the Province of Catalonia, Spain, and extends the known distribution of the species in a southerly direction.

INTRODUCTION

The palmate newt, *Triturus helveticus* (Razoumowsky), has a distribution which extends from France, England and Scotland (where the species reaches its northern limit) eastwards to Belgium, the Netherlands, Switzerland and West Germany. In Spain, it has been recorded only from the northern part of the country (Salvador, 1974). There are few references to the presence of the species in Catalonia. Maluquer (1902) stated in relation to Sant Cugat de Vallès "... recullirem un *Triton*, segurament el *palmatus*, Schn., que hi abundava extraordinariament ...". In his comprehensive work on the Amphibians and Reptiles of N.E. Spain, Mertens (1925) does not mention this reference, nor include *T. helveticus* in the list of Catalonian herpetofauna. Alvarez-Lopez (1934) has recorded the species from Girona, Palaus (1974) from Hostalric (Girona Province) and Felix & Grabulosa (1980) from Lledo (also Girona Province). Salvador (1974) describes the species as being found through the greater part of the Catalonian Pyrenees, without giving specific localities.

RESULTS AND DISCUSSION

This note records eleven new localities for *T. helveticus* in Catalonia. Most of them are in the coastal zone at altitudes between 0–250 m, in areas with Mediterranean influence and temperate climates (Fig. 1). At Rupit (1) and Collsacabra (2), however, the species has been found at 950 m in a wet, oak-beech forest zone.

The remaining localities are in the lowland zone. At Lledó (3) the species was found in the improved land and bank forest habitats. An individual trampled on the road, was found at Sant Pere Pescador (4) in orchard land neighbouring a formerly extensive marsh. The specimens at Mont-ràs (5) were in vegetation on the bank of a canal running through improved land.

The site at Sadernes (6) is an artificial pond in a holm oak grove, at an altitude of 280 m. The Banyoles (8) and Girona (9) habitats are rather similar, as are Sant Esteve de Palautordera (9), Hostalric (10) and Tordera (11), although the newts were found on land in grassland associations (*Cypero-Caricetum otrubae*, *Irido-Polygonetum salicifolii* and *Acrocladio-Eleocharitetum palustris*), and also in the artificial canals which frequently flood the surrounding land.

The Sant Cugat de Vallès habitat (12) recorded in Maluquer (1902) has not been confirmed to date.

Locality (13) is in the delta of the Ebro. The final two localities are in the northern part of the Massís de Montsià, a calcareous ridge which runs parallel to the sea. Both populations are small; that at Font d'Amburga (Sant Carles de la Rapida) (14) was found at an altitude of 350 m in an artificial trough used for watering domestic animals, the population at Mas de Comú (Ulldecona) (15) at 540 m in a small (20 m^2) natural pond. *Rana ridibunda* and *Alytes obstetricans* are found with *T. helveticus* at both locations, which are in the zone of degraded "roure valencia" (*Violo-Quercetum valintinae*). Locality (15) is the most southerly recorded location for *T. helveticus*.

The small number of individuals which were col-

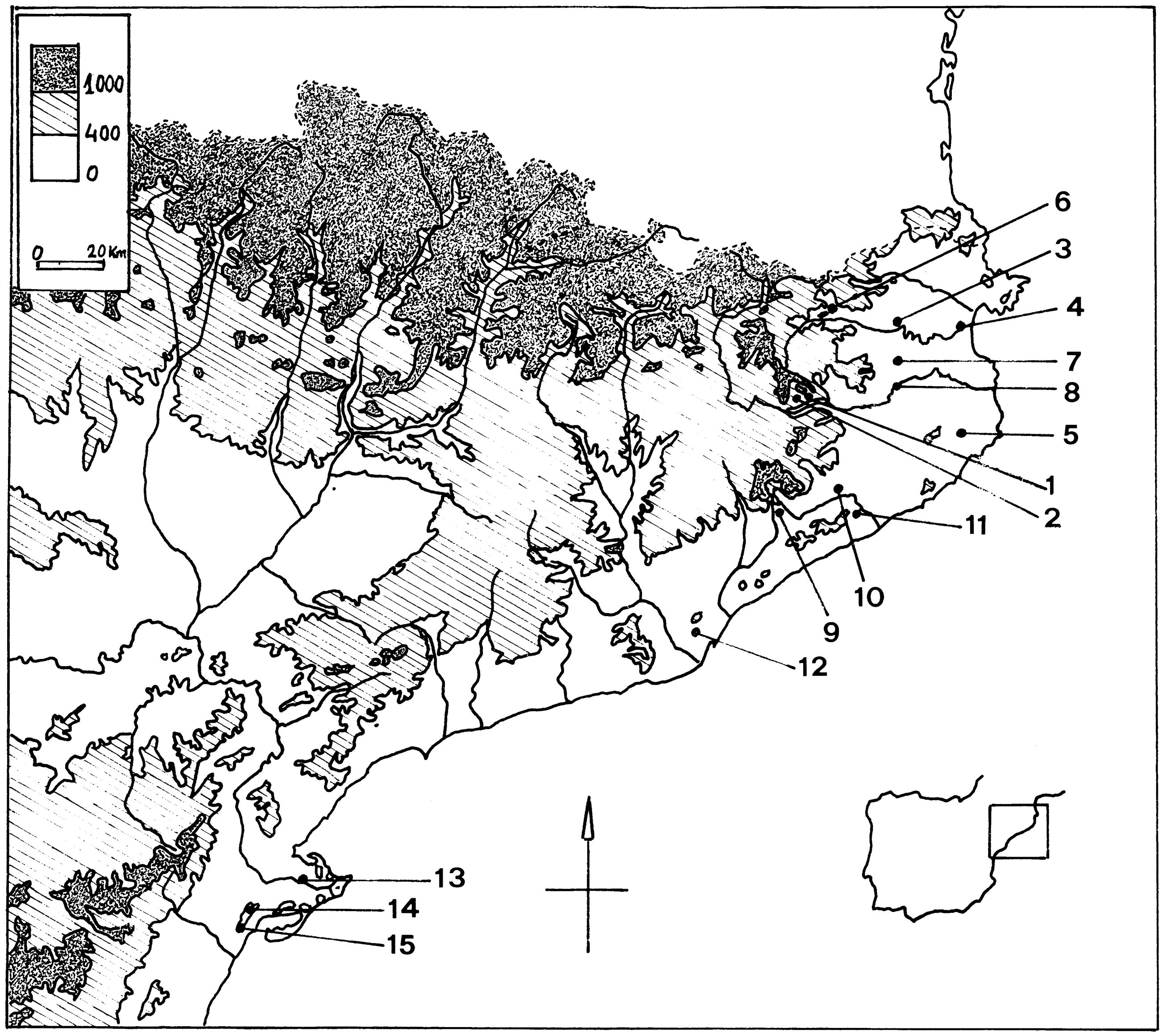

FIG. 1. Map of Catalonia showing places where *T. helveticus* has been found. Numbers on the map correspond to numbers referred to in the text.

lected from these populations all, irrespective of their origin, correspond both morphologically and biologically with the description of the subspecies *T. h. helveticus*.

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A NORTHERNMOST LOCALITY FOR *TESTUDO MARGINATA* SCHOEPFF 1792 IN GREECE (SHORT NOTE)

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(*Received* 19 *March* 1982)

Localities for *Testudo marginata* Schoepff in Greece are given by Werner (1938) and Wettstein (1953). According to Mertens & Wermuth (1960), the species occurs as far north in mainland Greece as Mount Olympus. The range of distribution of *Testudo marginata* in Greece has been outlined by Arnold, Burton & Ovenden (1978).

During field work on the Macedonian herpetofauna in the Summer of 1981, three specimens of *Testudo marginata* were found at different points at 400–500 m on the eastern slopes of Mount Vermion near Veroia (Fig. I.) in central Macedonia. These sightings are about 100 km further north than the previously stated northernmost limit of the species range in Greece.

The eastern slopes of Mount Vermion are covered by dense scrub vegetation. *Testudo marginata* was not recorded in the area at a lower altitude on the open plains, a habitat where Arnold *et al.* (1978) and we have recorded it in central and southern Greece.

The largest animal (a male in area 2) was collected and returned to the laboratory alive and has a carapace length of 33 cm. Clark (1970) reports an animal with a carapace length of 30 cm (Paros, Cyclades) and our specimen may be the largest recorded in the wild.

The Macedonian herpetofauna has been little explored and the three *Testudo marginata* were found in areas difficult for human access. The tortoises are unlikely to represent the translocation of the species by man, as in Sardinia (Mertens & Wermuth 1960), for none was found near human habitation in different habitats, unless, of course, they were unable to survive where placed by man initially. It is probable that *Testudo marginata* will be recorded elsewhere in Macedonia. It is, moreover, possible that the species

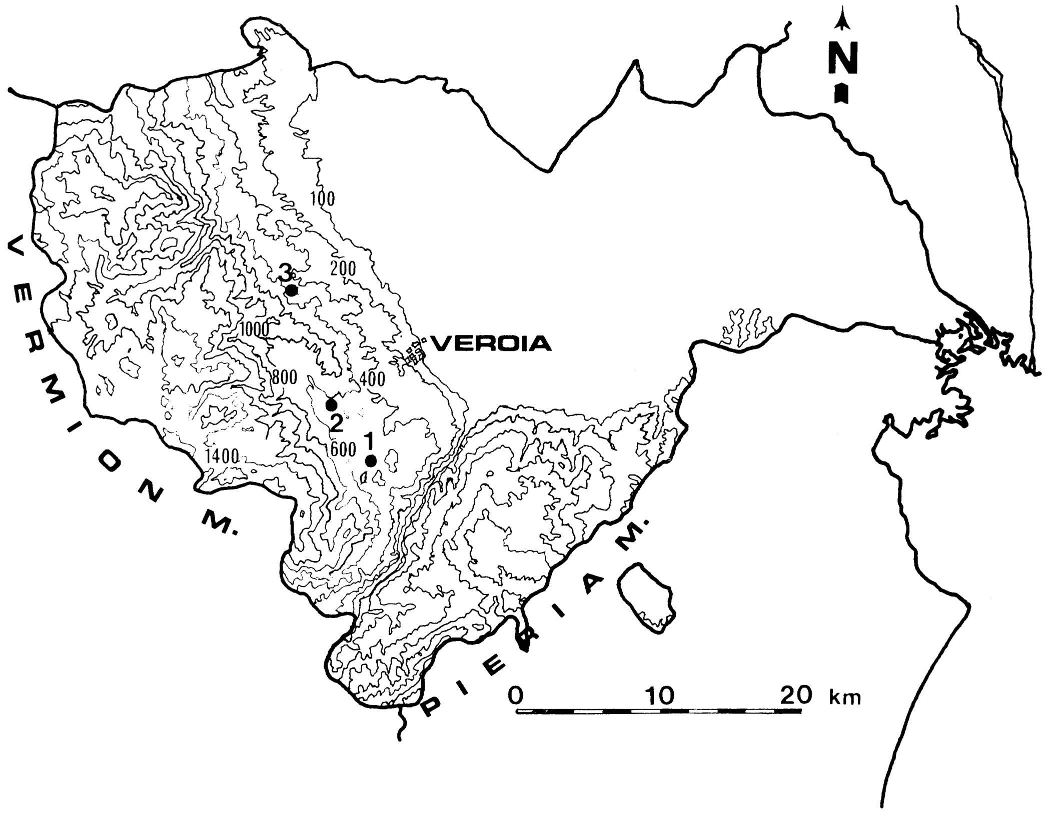

FIG. 1 The three locations in northern Greece where *Testudo marginata* was found.

extends further north in Macedonia, over into Yugoslavia, if the report of a Swiss importer of 25 *Testudo marginata*, stated to be collected around Bitola (Monastir), is true (Lambert, in litt.).

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BOOK REVIEWS

REPTILES AND AMPHIBIANS IN BRITAIN. By Deryk Frazer (1983). 256 pp. London: Collins. £11.00.

The appearance of *The British Amphibians and Reptiles* by Malcolm Smith in 1951 was a major event in European herpetology. The book was extremely well-received and very influential; one measure of its success was the requirement for four further editions, appearing at approximately six year intervals. The book bore the stamp of Smith's interests and personality in many ways. Descriptive aspects of herpetology were dealt with in detail—anatomy, taxonomy, geographical distribution. The sections on natural history tended to be descriptive too, but they were thorough and authoritative, being based on many years of painstaking observation in the field.

Herpetology has changed dramatically since Smith first wrote his classic. There are more herpetologists, and many of them are professionals—not necessarily full time herpetologists, but trained biologists who are imbued with the attitudes engendered by modern advances in genetics, evolutionary theory, biochemistry... They tend to see the facts which are the raw materials of herpetology not just as intrinsically interesting, but as adding to our understanding of how the natural world operates; as illustrating concepts and ideas. The complex courtship behaviour of the British newts, for example, is fascinating and beautiful at a descriptive level. It becomes even more meaningful when viewed from the standpoint of ideas relating to sexual selection, intra-sexual competition, species isolating mechanisms, the integrative rôle of *sequences* of "innate releasing mechanisms", and so on. In short, the questions "what?" and "how?" have become replaced by the questions "why?" and "what for?".

The volume under review is the eagerly awaited update of Smith's work. It has been given a new title, presumably to emphasize that it's a completely new book and not just a revised edition. How successful is it in incorporating the advances of the past thirty years?

Deryk Frazer, Past-President and Honorary Member of the BHS, has in many ways been faced with a more difficult task than Malcolm Smith, who simply needed to organize his descriptive material so that it was presented in a coherent and readable way. Frazer has additionally had to interpret the material in the light of modern conceptual advances, and find the right balance between a volume which will satisfy and inspire the huge readership of non-specialists for whom the "New Naturalist" series is primarily intended, and one which is sufficiently detailed that specialists will feel that justice has been done to their subject. I think he has succeeded in this. Others might have done it differently: I myself would probably have included rather more of work from the continent of Europe on species which are also found in Britain, for example the recent work on adders by G. Nilsen and C. Andren in Sweden, H. Saint-Girons and G. Naulleau in France. These, however, are details. There is nothing of major importance which has been omitted. The sections on reptiles emphasize the rôle of thermoregulation in their lives (this concept was just emerging when Smith wrote—it had not at that time gained general currency), and show how their social behaviour can be quite complicated. Those on amphibia show how it is the timing of the breeding migration and the organization of courtship activities which are amongst the key factors which help one to understand the biology of these animals.

I end with a complaint. The book is not as well finished as its predecessor. The paper feels coarser; the half tones are not as well printed, nor in many cases are they the best of their kind which are available. There are doubts about the accuracy of some of the captions (*e.g.* Plates 3, 10). I know only too well, as the person who is responsible for the production of this journal, that it's probably economic constraints which are to blame: but it seems a pity.

R. A. AVERY

BIOLOGY OF THE REPTILIA, Volume 13. *Physiology D, Physiological Ecology.* Edited by Carl Gans and F. Harvey Pough (1982). xiii + 345 pp. London etc: Academic Press. £40.00.

So many complimentary things have been written about the volumes of *Biology of the Reptilia* over the past few years that it would seem merely repetitious to add to them. Volume 13 contains six chapters. Four of them will be essential works of reference, not only for herpetologists, but others too, because they deal with topics of considerable importance for the expanding field of physiological ecology. These are "Reptilian hibernation" by P. T. Gregory, "The energetics of reptilian activity" by A. F. Bennett, "Environmental control of reptilian reproductive cycles" by D. Duvall, L. J. Guillette Jr. & R. E. Jones, and "Patterns of growth in reptiles" by R. M. Andrews. This is not in any way to belittle the contributions made by the remaining two, "Physiological adaptations to aquatic life" by R. S. Seymour and "Energy budgets and life histories of reptiles" by J. D. Congdon, A. E. Dunham & D. W. Tinkle; they are simply rather more specialized.

No-one who is interested in reptile physiology can afford to be without this book: it is worth every penny of the substantial price.

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