Volume 6, Number 10

June 1984
ISSN 0007-1056

BRITISH JOURNAL OF
HERPETOLOGY

Published by
The British Herpetological Society

BRITISH JOURNAL OF HERPETOLOGY

Volume 6, Number 10 June 1984

CONTENTS

Published by the British Herpetological Society
Computer typeset by SB Datagraphics, printed and bound by
Spottiswoode Ballantyne, Colchester and London

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 351–358 (1984)

FEEDING, GUT DYNAMICS. DIGESTION AND OXYGEN CONSUMPTION IN HATCHLING GREEN TURTLES (*CHELONIA MYDAS* L.)

JOHN DAVENPORT AND PETER J. OXFORD

NERC Unit of Marine Invertebrate Biology, Marine Science Laboratories, Menai Bridge, Gwynedd, U.K.

(*Received* 25 *May* 1983)

SUMMARY

Hatchling green turtles (*Chelonia mydas* L.) were found to be opportunistic, omnivorous feeders which would readily consume algae, sponges, invertebrates and fish. They appear to have a cellulose degrading gut microflora. Food transport along the gut is very slow with the mean total gut clearance time (TCT) being 394 h. Starvation totally inhibits faecal production and it is clear that continuous feeding is required to push material along the gut. However, residence times of food in stomach, small intestine and rectum appear to be relatively short; the material spends most of the TCT in the large intestine where some to and fro mixing of gut contents appears to take place. Oxygen uptake values were about 100 $\mu l\ O_2\ g^{-1}\ h^{-1}$, which is a similar rate to that of yearlings and adult turtles.

INTRODUCTION

In the past few years there have been several studies devoted to the nutrition and energetics of the marine green turtle *Chelonia mydas* L. (*e.g.* Bjorndal, 1979, 1980; Wood & Wood, 1981; Davenport, Ingle & Hughes, 1982; Hadjichristophorou & Grove, 1983). In the main these have been concerned with adult or yearling turtles weighing at least 500 g.

Adult green turtles, unlike all other extant marine species, are usually assumed to be exclusively herbivorous with a definite preference for seagrass (*Thalassia* spp.) and eelgrass (*Zostera* spp.), although there is some evidence to suggest that they are on occasion more catholic in their tastes; Kooyman (1972) reported observing an adult turtle feeding upon shrimps at a depth of 290 m. Adult animals certainly possess a cellulose-degrading gut flora (Bjorndal, 1979). Hatchling *C. mydas*, like the young of other marine turtle species, are generally believed to be carnivorous although direct field evidence to support this supposition is extremely scarce since few green turtle hatchlings have ever been seen after leaving the beach of their birth until they appear on seagrass beds as so called "yearlings". This gap in our knowledge of turtle biology has commonly been referred to as the "lost year question" (*e.g.* Carr, 1967) though, since it would appear that natural growth rates do not match those attained in the laboratory or upon turtle "farms" (Medonca, 1979), the period of uncertainty may possibly be longer than 12 months. Carr suggested that Caribbean turtle hatchlings spent much of their "lost year" living in association with sargassum rafts; this suggestion has since been confirmed by direct observation (Caldwell, 1968; Smith, 1968; Frick, 1976; Witham, 1980). Many of these observations apply to hatchlings of the loggerhead turtle *Caretta caretta* which is carnivorous as an adult. However, Carr & Meylan (1980) reported that sargassum floats and leaves made up most of the stomach contents of loggerhead hatchlings washed ashore by a hurricane in 1979; they also recorded observations of groups of hatchling green turtles upon sargassum mats 40 km off the Panamanian coast (though they were unable to catch the animals concerned). It is therefore possible that green turtle hatchlings also consume quantities of plant material.

The aims of the investigation reported upon here were to assess the range of acceptable food organisms in hatchling green turtles, to compare their nutrition with that of the yearlings studied by Hadjichristophorou & Grove (1983), to look for evidence of the ability to digest cellulose, and to monitor oxygen uptake for comparison with the data collected for older animals by Davenport *et al.* (1982).

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Six green turtle hatchlings were transported by air from the Department of Fisheries, Cyprus (where a conservation programme is in operation) to London, and thence by road to Menai Bridge. At the beginning of the study they weighed between 38.4 and 54.6 g. However, they grew very rapidly and were consequently reweighed before each experimental procedure. They were held in recirculating sea water of 33–34‰ at a temperature of 25 ± 1°C under constant illumination. A slow flow of sea water from the laboratory supply system gradually replenished the system. The turtles were routinely fed upon an artificial pelleted diet (Omega Trout food: floating—see Hadjichristophorou & Grove, 1983 for composition) at a rate of about 1.5% body weight per day unless otherwise indicated. As supplied, the pellets were too large for the hatchlings to eat. They were, therefore, ground to a paste with a little water and extruded through a syringe, dried and cut up into smaller pellets.

VARIETY OF ACCEPTABLE FOOD

At the start of the investigation, with the hatchlings as young and small as possible, the following marine organisms were offered to them as possible food: the sea lettuce *Ulva lactuca*, the purse sponge *Grantia compressa*, the sea anemone *Sagartia elegans*, the shrimp *Crangon vulgaris* and the small teleost *Gobiusculus flavescens*. They were also offered specimens of the earthworm *Lumbricus terrestris*. With all species offered, the reactions of the turtles were observed and recorded.

SATIATION AMOUNT AND GUT CLEARANCE TIME

Routine fed turtles were each fed a satiation meal of trout food labelled with the inert green marker chromic oxide (2.44% by weight—see Hadjichristophorou & Grove, 1983) 24 hr after their previous meal. Four grammes of pellets were prepared for each turtle, though one of the animals refused to feed and was subsequently excluded from feeding trials. The procedure employed during feeding of satiation meals was as follows. Pellets were offered to each turtle, in turn, until the turtle had refused 5 pellets within 10 min. The weight of pellets not offered to the turtle was measured; uneaten pellets left in the water were dried and weighed. Weights of unoffered and uneaten pellets were deducted from the original 4 g to determine the satiation amount.

Following feeding, the turtles were each confined in a floating polypropylene container two-thirds full of sea water. Every day the water in the containers was changed and any faeces produced were removed and inspected for chromic oxide. During this period the animals were starved ("starved clearance").

After 16 days of starvation, faecal production had ceased in all 5 turtles, yet no green faeces had been observed. Normal routine feeding was therefore resumed until green faeces had been eliminated and followed by normal faeces.

The above experiment was repeated, but on this occasion the satiation meal was followed by normal routine meals; faeces production was monitored until all green marker had been eliminated ("routine fed clearance").

BARIUM MEALS

To obtain further information about the progress of food along the gut of hatchling *C. mydas*, a barium meal was administered to one of the turtles. Barium sulphate pellets were prepared by mixing food pellets with barium sulphate (in the ratio 5 : 1 by weight). The mixture was ground into a smooth paste with water, ejected through a syringe, dried and cut up into small pellets.

The turtle was X-rayed before feeding and was fed a 1% body weight meal. It was X-rayed 30 min after feeding and subsequently at intervals as food progressed along the alimentary tract. During the experiment the animal continued to be routine fed; the appearance of white faeces (loaded with barium sulphate) gave another measure of routine fed gut clearance time.

To identify sections of the hatchling gut it would have been desirable to feed routine barium meals until the entire gut was filled with radio-opaque material. However, it was feared that this procedure might be harmful at such an early stage in development and it was consequently delayed until the animals were much stronger and larger. When one of the turtles had grown to about 750 g it was fed routine barium meals until white faeces had been observed for 2 days. It was then X-rayed. It should be noted that an alimentary tract full of barium sulphate labelled food created noticeable buoyancy problems for the turtle (the atomic weight of barium is 137.4) which spent far more time than usual resting at the bottom of its tank and clearly needed more effort than normal to take breaths at the water surface.

CELLULASE ACTIVITY

Ruminant cellulose breakdown is primarily accomplished by the action of anaerobic bacteria (Hungate, 1947). Therefore, to be absolutely certain that the gut of hatchling *C. mydas* contained a microflora capable of digesting cellulose, it would be necessary to remove material from the gut directly and investigate its properties in anaerobic culture, or perform the sort of biochemical analysis carried out by Bjorndal (1979) on gut contents taken from dead turtles. Such an invasive procedure was impermissible in the present study (the turtles were to be returned in good health to Cyprus), so experiments were carried out upon freshly voided faeces tested under aerobic conditions for cellulose activity. Two different culture media containing cellulose were employed (Kellerman & Macbeth, 1912; Dubois, 1928) and were inoculated with material taken from turtles held in tanks of filtered sea water which was changed daily. Faecal material was streaked onto culture plates with a sterile wire as was water from around the turtles. Control plates were also prepared, first with newly filtered sea water and secondly with food pellets.

After streaking, the plates were incubated at 25°C. When bacteria became apparent they were subsampled onto further sterile plates to ensure that the bacteria were only utilizing cellulose as a carbon source and were not relying upon carbon derived from faeces or food pellets. They were incubated for a further 4 or 5 days. Samples of bacteria were then stained with Grams stain and inspected with a light microscope.

OXYGEN UPTAKE

Oxygen consumption was monitored at 25°C in a respirometer of the type used by Davenport *et al.* (1982) to study yearling turtles, although a smaller chamber (532 ml) had to be used because of the hatchlings smaller size. Oxygen uptake was monitored over 24 hr periods in turtles which had been routine fed previously. The hatchlings remained still during their sojurn in the respirometer and showed no sign of distress, so that data collected should approximate to basal metabolic levels. It had been hoped to make estimates of specific dynamic action (SDA) after meals (as had been done for yearlings), but the potentially detrimental consequences of starvation revealed by the gut clearance studies made the necessary pre-meal food deprivation unacceptable.

RESULTS

ACCEPTABLE FOOD

Hatchlings *C. mydas* ate all of the food offered in a voracious manner, whether it was of plant or animal origin. Gobies and shrimp were readily chased, speared with the beak and swallowed whole. Sea lettuce, pieces of sea anemone and small sponges were all eaten with no hesitation or sign of distaste. Earthworms were consumed quickly, any broken off portions being caught before they fell to the bottom of the tank. It should be appreciated that these were the reactions of well fed animals which had not been in captivity for a long period; they consequently indicate an omnivorous, opportunistic feeding habit.

SATIATION AMOUNT AND GUT CLEARANCE TIME

The satiation amounts for the 5 turtles which accepted a meal are presented in Table I. The mean satiation meal of 2.63% body weight is rather higher than the 1.95 to 1.99% recorded by Hadjichristophorou & Grove (1983) for animals in the 509–887 g weight range. However, their results were obtained after 108 hr starvation rather than the 24 hr deprivation period used here; their results imply a satiation amount of about 1.4% body weight after 24 hr food deprivation, so it would appear that hatchling turtles have nearly double the relative food intake of yearlings.

TABLE I. Size of satiation meals in green turtle hatchlings

Turtle No.	Weight of turtle (g)	Size of satiation meal (% body weight)
1	54.3	2.28
2	55.0	2.77
3	75.9	2.66
4	55.3	2.42
5	61.5	3.02
	mean 60.4	2.63

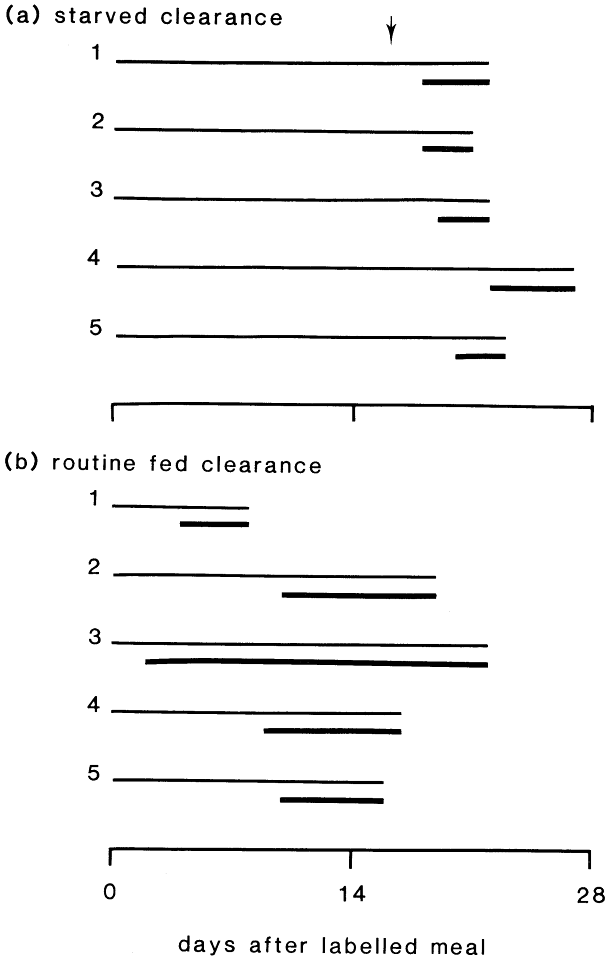


FIG. 1. Gut clearance times in hatchling green turtles. (a) "Starved clearance". (b) "routine fed clearance". Thin horizontal lines represent total gut clearance times, thick bars represent appearance of chromium dioxide labelled faeces after a labelled meal consumed at time 0. Arrow indicates resumption of feeding in starved animals.

The "starved" and "routine fed" gut clearance times at 25°C are illustrated in Fig. 1. First it was clear that prolonged starvation caused a profound reduction in faecal output; after 16 days of food deprivation it has ceased entirely, yet no green faeces had been observed. Three to seven days after feeding was resumed green faeces started to appear and all animals had completed gut clearance by the 27th day. If the total gut clearance time (TCT) is taken to be that interval between feeding and the elimination of the last green faeces, then the mean TCT of the starved hatchlings was 552 ± 56 hr. It is often assumed that the gastric emptying time (GET) is equivalent to the time elapsed between the appearance of the first and last faeces (see Hadjichristophorou & Grove, 1983), although this assumption relies upon a steady and unidirectional movement of food from one end of the gut to the other (a point which will be considered further later). On this basis the "starved clearance" animals had a mean GET of 81.6 hr.

The corresponding "routine fed" values were as follows: TCT = 394 ± 125 hr; GET = 230 ± 168 hr. It must therefore be concluded that starvation greatly increases TCT but shortens GET. The "routine fed" values are much longer than the corresponding values for food deprived yearling turtles (TCT = 176 hr; GET = 110 hr—Hadjichristophorou & Grove, 1983), so it would seem that food transport along the gut is much slower in hatchlings than in older turtles.

CELLULASE ACTIVITY

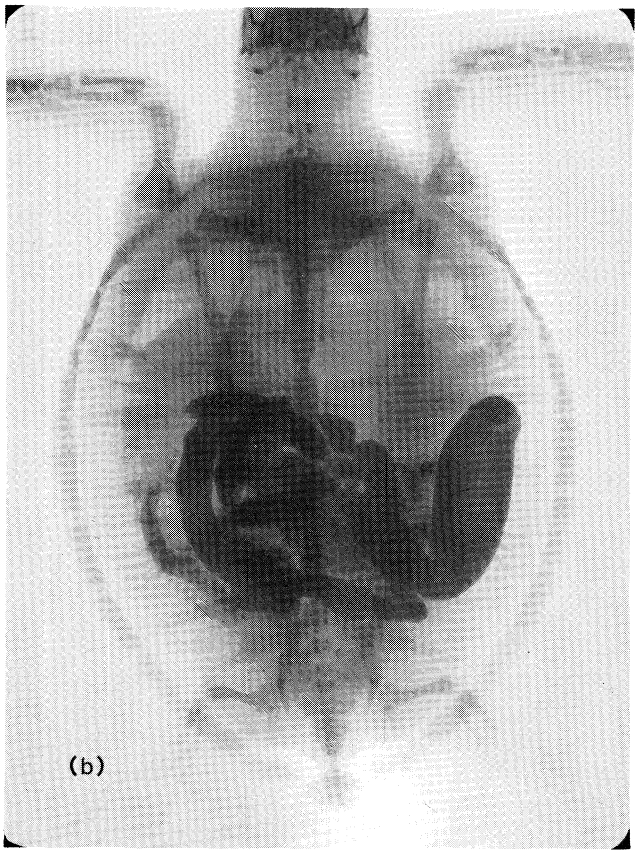
The results of the cellulase activity study were rather equivocal. Bacteria capable of digesting cellulose were present both on control plates (filtered sea water; food pellets) and on plates inoculated with material derived from the turtle (faeces, surrounding sea water).

However, the rich cultures derived from faeces and surrounding sea water consisted of short gram negative rods, whereas the bacteria on control plates were coccobacilli. It is conceivable that the rods were derived from the outer surface of the turtle and infected both sea water and faeces, but it seems more likely that they were of faecal origin and therefore characteristic of the gut microflora.

BARIUM MEALS

Figure 2 illustrates the whole digestive tract of a 750 g turtle. In Fig. 2a the large stomach can be seen as a rather diffuse shadow (despite a recent barium meal). The loops of duodenum and small intestine are impossible to identify positively from this photograph, partly because the coils of the gut seem to be quite mobile (cf. Fig. 2b photographed 24 hr later). However, the wide loops of the large intestine are more visible, and they, together with the stomach and rectum, are identified in the drawing displayed in Fig. 2c. Material appears to have a short residence time in both stomach and rectum judging by the differences shown between Figs 2a and 2b.

Figure 3 shows the sequence of X radiographs taken from a hatchling held at 25°C after a single barium meal (followed by normal daily meals). Thirty minutes after the meal the stomach is clearly outlined, but after 24 hr little barium remains in the stomach and most is concentrated in a loop which is probably part of the small intestine. From 48 hr after the meal to the last radiograph taken (after 220 hr) the barium appeared to be near stationary in loops of the large intestine.



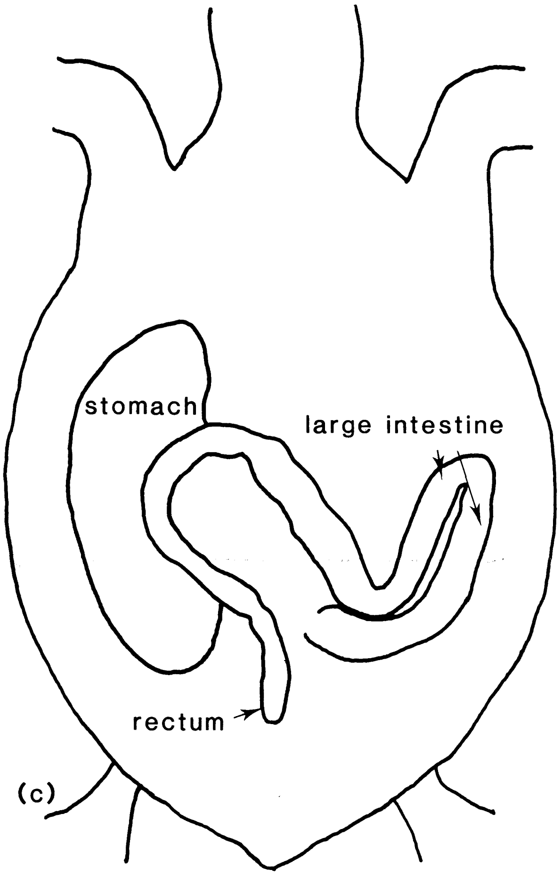
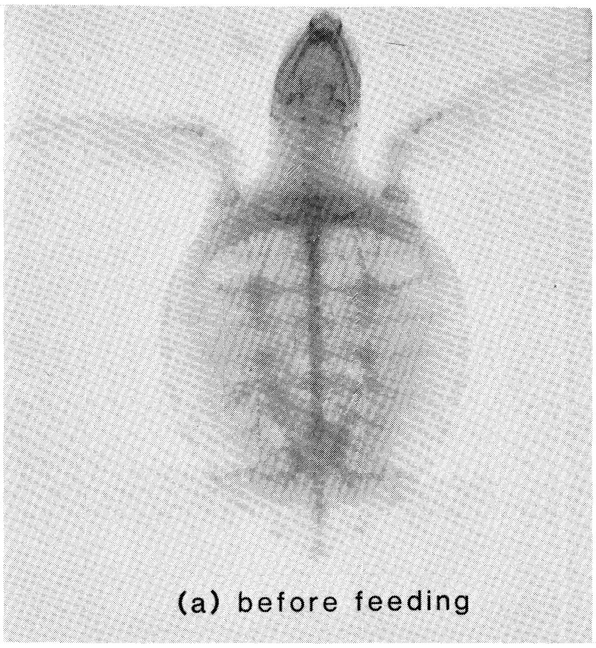
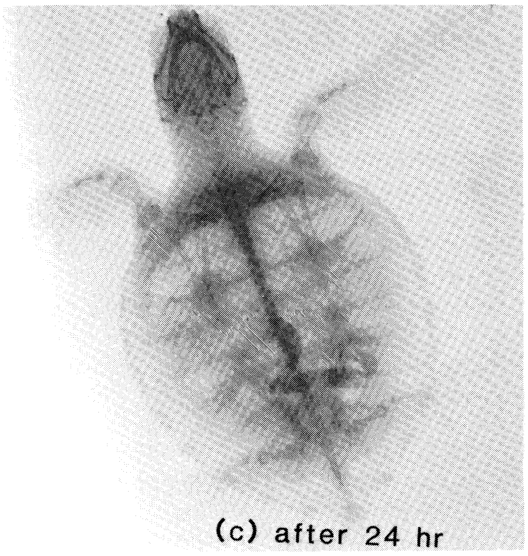
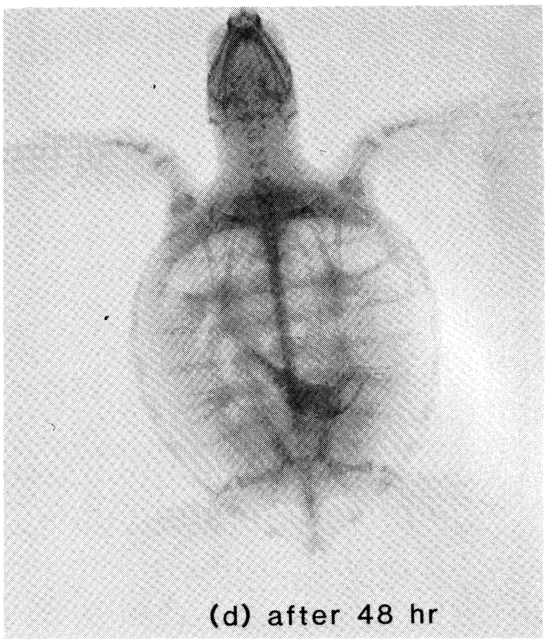


FIG. 2. Gut of 750 g yearling turtle visualized by barium sulphate. (a) Gut full of barium label from stomach to rectum. (b) After 24 hr of routine feeding; little barium in stomach, none in rectum. (c) Identifiable portions of the gut.

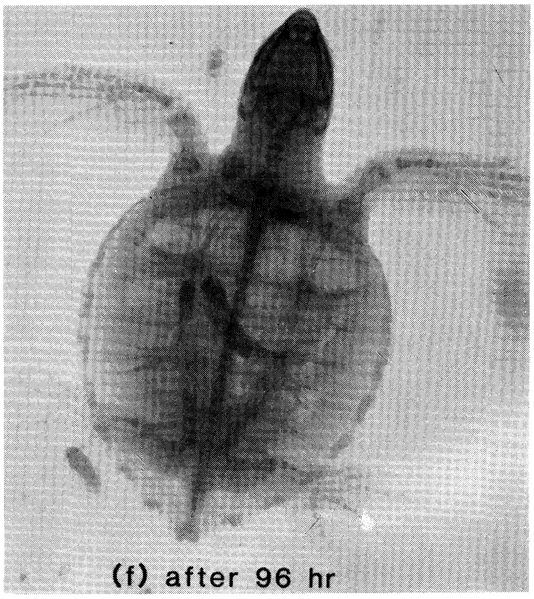

(a) before feeding

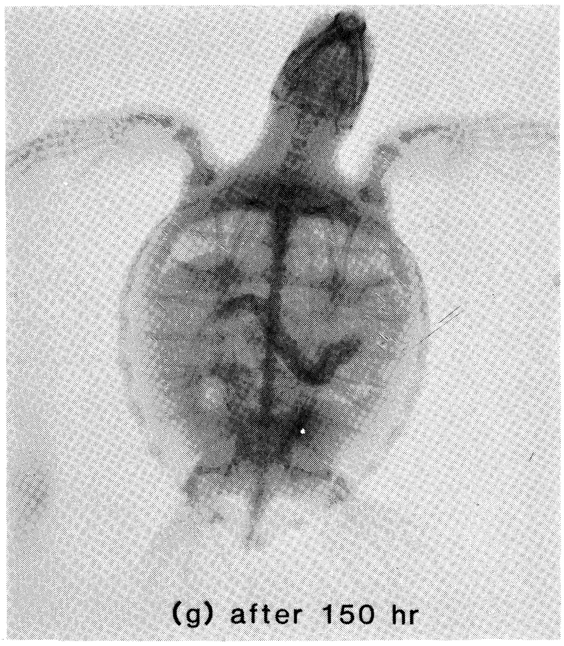

(b) 30 min after barium meal


(c) after 24 hr


(d) after 48 hr


(e) after 72 hr


(f) after 96 hr



(g) after 150 hr

(h) after 220 hr

FIG. 3. Passage of a barium labelled meal through the gut of a hatchling green turtle. See text for commentary.

Analysis is difficult because of the changing configuration of the loops, but there appear to be signs that between 48 and 150 hr after the meal there is some diffusion of radio-opaque label in both directions, suggesting to and fro movement of gut contents. No data beyond 220 hr is presented; in this and other turtles studied, the barium shadow in the large intestine simply gets fainter and fainter (the turtle photographed in Fig. 2a was the only one seen with radio-opaque material in the rectum) until it is impossible to decide whether any label is still present.

Although most attention was paid to the barium shadows, other anatomical features of the turtles may be seen. The majority of these are outside the scope of the present investigation, but it is noteworthy that the stomach and large intestine often contained gas. In the case of the former this could presumably be swallowed air, but in the latter must be a product of digestion.

OXYGEN UPTAKE

Basal oxygen uptake values are presented for all 6 turtles in Table II. Uptake values ranged between 96.6 and 137 $\mu l\ O_2\ g^{-1}\ h^{-1}$. This agrees well with the results of Prange & Ackerman (1974) who recorded 99 $\mu l\ O_2\ g^{-1}\ h^{-1}$ in newly hatched green turtles, and is also within the range of 96–142 $\mu l\ O_2\ g^{-1}\ h^{-1}$ recorded by Davenport *et al.* (1982) for yearling turtles weighing between 835 and 2185 g.

TABLE II. Oxygen consumption in green turtle hatchlings

Turtle No.	Weight of turtle (g)	Mean oxygen uptake ($\mu l\ O_2\ g^{-1}\ h^{-1}$)	±SD
1	41.7	113.8	4.9
2	38.5	112.1	8.1
3	58.3	106.9	7.0
4	56.8	137.2	20.3
5	44.2	128.8	19.1
6	40.6	96.6	10.7
	mean 46.7	115.9	

DISCUSSION

The results of the present study strongly suggest that hatchling green turtles are adapted to deal with a wider range of food organisms than previously realised. Although hatchlings probably prefer to eat fish and invertebrates if they can get them, and can even survive on a diet of jellyfish (Witham, 1980), they will certainly take plant material readily. In this they resemble some freshwater chelonians such as the yellow bellied turtle *Chrysemys scripta scripta* which prefers and grows best on a "high quality" animal diet available in some parts of its range, yet will subsist adequately (albeit with poorer growth) on a diet consisting mainly of vegetation (see Parmenter, 1980). Because sargassum rafts are a feature of the Caribbean turtle breeding areas and not of European waters we were not able to test the acceptability of sargassum floats and leaves. However, it seems most unlikely that *C. mydas* hatchlings would not eat sargassum, particularly in the light of the finding of Carr & Meylan (1980) that loggerhead hatchlings (also previously regarded as carnivores) consume considerable quantities of plant material. Certainly the long periods taken for food to pass along the gut, together with the evidence of a cellulose-degrading gut flora, are indicative of an animal well adapted to deal with a plant diet. Acceptance of the idea that green turtle hatchlings will take plant material on occasion, together with the observation that adult *C. mydas* sometimes consume animals (Kooyman, 1972), avoids the necessity for postulating a sudden change in feeding habit and physiology at some stage in the animal's life history. It seems likely that a high protein "animal" diet is necessary early in development to ensure the rapid growth rates which eventually reduce vulnerability to predation. As maturity approaches, the green turtle, which does not possess the massive jaws which allow the loggerhead *Caretta caretta* to exploit slow moving benthic prey (*e.g.* crabs, molluscs), presumably encounters suitable densities of animal material which it can cope with (prawns, small and slow fish) relatively rarely and so switches to a plant dominated diet.

In one respect the green turtle, whether hatchling or adult, is not a typical herbivore; the gut is only moderately convoluted and does not possess a pronounced caecum (see Fig. 2). In addition there is a conflict between the gastic emptying time calculated from observations upon chromium dioxide labelled faeces (GET = 230 hr at 25°C) and the rapidity with which barium meals appear to leave the stomach (24–48 hr; see Figs 2 and 3). Admittedly Grove & Crawford (1980) reported that X-radiography was not sensitive enough to record the passage of the last fragments of a barium meal, and will thus tend to underestimate GET, but the discrepancy in duration reported here appears to be too large for this simple reason alone to suffice. From the observations made here, it would seem that food spends little time in the stomach, small intestine or rectum, but is held for most of its transit time in the large intestine. There is some indication that it also moves to and fro in that part of the gut, which will not only prolong gut clearance time (and thus give a longer period for cellulose-degrading bacteria to act), but will also tend to mix material from "old" meals with more recent food intake and thus (in our experiments) spread green chromium dioxide label to material (and hence "meal times") it was not originally associated with. In support of this hypothesis, it should be noted that the "GET" values recorded were much shorter in the "starved" clearance experiment when later meals were not available to mix with the labelled material.

Although the residence time of food in the stomach appears to be relatively short, the organ itself is very large. Partly this is probably to allow the uptake of sizeable meals, but it does seem to be rather bigger than necessary for 2–3% body weight meals. However, from the diffuse nature of the barium shadows seen immediately after a meal, it would seem that there is a very copious gastric fluid, or that sea water is swallowed in some quantity along with food. Some X-rays taken from hatchlings show the stomach to contain a great deal of gas. Probably this is air rather than gaseous product of digestion and it is possible that such gas may be involved in the buoyancy mechanism of the species.

The oxygen consumption rates recorded from hatchling *C. mydas* are unremarkable except in that they provide further support for the suggestion that size has relatively little impact upon weight specific oxygen uptake in the species (Davenport *et al.*, 1982). Mrosovsky & Pritchard (1971) reported an uptake rate of about 70 μl O_2 g^{-1} h^{-1} from adult green turtles, while our results and those of Prange & Ackerman (1974) agree on about 100 μl O_2 g^{-1} h^{-1} for hatchlings. Thus a thousand-fold increase in body weight appears to be accompanied by a mere 30% reduction in weight specific oxygen uptake. Such a small effect of size is relatively unusual in the animal kingdom, but has been reported for other chelonians in the past (Baldwin, 1926; Benedict, 1932; Hutton *et al.*, 1960).

ACKNOWLEDGEMENTS

The authors wish to thank Mr A. Demetropoulos, Director of Fisheries, Cyprus for the loan of the turtles. Thanks are also due to Mr L. Roberts for technical assistance, Mr W. Rowntree for photographic help and Miss Sheila Davies for contributing to the care of the turtles. We are also grateful for the assistance rendered by Mrs J. Egan who gave microbiological advice.

We wish to thank Dr D. J. Grove for his encouragement and advice, and for his good offices in initiating cooperation between Menai Bridge and Cyprus.

REFERENCES

Baldwin, F. M. (1926). Notes on oxygen consumption in turtles, *Chrysemys marginata belli* and *Chelydra serpentina. Proceedings of the Iowa Academy of Science* **33,** 315–323.

Benedict, F. G. (1932). The physiology of large reptiles. *Publications, Carnegie Institution of Washington* No. 425, 1–539.

Bjorndal, K. A. (1979). Cellulose digestion and volatile fatty acid production in the green turtle *Chelonia mydas. Comparative Biochemistry and Physiology* **63A,** 127–133.

Bjorndal, K. A. (1980). Nutrition and grazing behaviour of the green turtle *Chelonia mydas. Marine Biology* **56,** 147–154.

Caldwell, D. K. (1962). Growth measurements of young captive Atlantic sea turtles in temperate waters. *Contributions in Marine Science* **50,** 1–8.

Carr, A. F. (1967). *So excellent a fishe.* New York: Natural History Press.

Carr, A. F. & Meylan, A. B. (1980). Evidence of passive migration of green turtles in sargassum. *Copeia* **1980,** 366–368.

Davenport, J., Ingle, G. & Hughes, A. K. (1982). Oxygen uptake and heart rate in young green turtles (*Chelonia mydas*). *Journal of Zoology, London* **198,** 399–412.

Dubois, R. J. (1928). The decomposition of cellulose by aerobic bacteria. *Journal of Bacteriology* **15,** 223–234.

Frick, J. (1976). Orientation and behaviour of hatchling green turtles in the sea. *Animal Behaviour* **24,** 849–857.

Grove, D. J. & Crawford, C. (1980). Correlation between digestion rate and feeding frequency in the stomachless teleost *Blennius pholis* L. *Journal of Fish Biology* **16,** 235–247.

Hadjichristophorou, M. & Grove, D. J. (1983). A study of appetite, digestion and growth in juvenile green turtle (*Chelonia mydas* L.) fed on artificial diets. *Aquaculture* **30,** 191–201.

Hungate, R. E. (1947). Studies on cellulose fermentation. III. The culture and isolation of cellulose decomposing bacteria from the rumen of cattle. *Journal of Bacteriology* **53,** 631–645.

Hutten, K. E., Boyer, D., Williams, J. C. & Campbell, P. M. (1960). Effects of temperature and body size upon heart rate and oxygen consumption in turtles. *Journal of cellular and comparative Physiology* **55,** 87–93.

Kellerman, K. F. & Macbeth, I. G. (1912). The fermentation of cellulose. *Centralblatt für Bakteriologie II* **34,** 485–494.

Kooyman, G. L. (1972). Deep diving behaviour and effects of pressure in reptiles, birds and mammals. *Symposium of the Society for Experimental Biology* **26,** 295–311.

Medonca, M. T. (1979). Growth rates of immature green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles in the wild. *American Zoologist* **19,** 953.

Mrosovsky, N. & Pritchard, P. C. H. (1971). Body temperature of *Dermochelys coriacea* and other sea turtles. *Copeia* **1971,** 624–631.

Parmenter, R. P. (1980). Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys s. scripta*). *Copeia* **1980,** 503–514.

Prange, H. D. & Ackerman, R. A. (1974). Oxygen consumption and mechanisms of gas exchange of the green turtle (*Chelonia mydas*). *Copeia* **1974,** 758–763.

Smith, W. G. (1968). A neonate Atlantic loggerhead turtle, *Caretta caretta caretta*, captured at sea. *Copeia* **1968,** 880–881.

Witham, R. (1980). The "lost year" question in young sea turtles. *American Zoologist* **20,** 525–530.

Wood, J. R. & Wood, F. E. (1981). Growth and digestibility for the green turtle (*Chelonia mydas*) fed diets containing varying protein levels. *Aquaculture* **25,** 269–274.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 359–367 (1984)

A REVIEW OF GEOGRAPHICAL VARIATION IN THE AFRICAN PYTHON, *PYTHON SEBAE* (GMELIN)

DONALD G. BROADLEY

National Museum, P.O. Box 240, Bulawayo, Zimbabwe

(*Received* 6 *July* 1983)

SUMMARY

A survey of the variation in Museum material and perusal of published illustrations of *Python sebae* suggests that *P. sebae natalensis* A. Smith should be revived as a southern subspecies and that the recently described taxon *P. saxuloides* Miller & Smith should be treated as a synonym of it.

INTRODUCTION

The African Python, *Python sebae* (Gmelin), has throughout this century been regarded as a monotypic species. However, in 1979 Miller & Smith erected a new species, *P. saxuloides*, on the basis of six live specimens in the United States which originated from the vicinity of Mwingi, Kenya. This new taxon was distinguished from *P. sebae* on twenty-three characters and it was suggested that these two pythons were widely sympatric in eastern Africa, but no material in museum collections was examined.

Miller & H. M. Smith (1979) listed *Python natalensis* A. Smith, 1840, as a synonym of *P. sebae*, without discussion. However, in his *Illustrations of the Zoology of South Africa*, Andrew Smith indicated differences between his new species and the Indian Python (*P. molurus*), although he states "The Indian species is doubtless an inhabitant of Africa, and there are several specimens of it, both from India and Western Africa in the museum at Fort Pitt, Chatham, which are precisely similar". He mentions the smaller scales and different disposition of the plates on the head and also differences in the pattern of markings. His sample of "the Indian Species" apparently included not only specimens of *P. molurus* and *P. s. sebae*, but also *P. regius*, as he refers to the presence of four or five labial pits in juveniles of "the Indian species". Nevertheless, all three species differ from *natalensis* and agree with one another in having large shields in the frontal-supraocular region and strongly contrasted dorsal markings.

Although in his 1840 publication A. Smith refers to a preliminary description of *P. natalensis* in the *South African Quarterly Journal*, new series, p. 64, October, 1833, there is no evidence that this ever appeared. The page cited has only the description of two Elephant Shrews (G. McLachlan, *in litt.*). Jan & Sordelli (1864) illustrated a typical *P. sebae* from Ghana and a topotypic "*P. sebae* var. *natalensis*". Peters (1882) and Bocage (1895) both regarded *natalensis* as a valid species, but Boulenger (1893) placed *natalensis* in the synonymy of *P. sebae* and this disposition has not subsequently been questioned.

In 1980 I examined the *Python sebae* material in the British Museum in an attempt to establish the status of *Python saxuloides*. Unfortunately, no specimens from Kenya were available, but the material examined strongly suggested that *P. sebae natalensis* A. Smith should be revived as a southern race (represented by two syntypes in London). These findings induced me to undertake a review of the geographical variation in *Python sebae*, because it has been proposed that all forms of *Python* should be placed on the schedule of endangered species (CITES and Red Data Book).

McDowell (1974) divided the genus *Python* into two groups, the *reticulatus* group, ranging from south-east Asia to Australia, and the *molurus* group, including the three African species and two Asiatic species (*molurus* and *curtus*). The *molurus* group differs from the *reticulatus* group in having the infralabial pits much more shallow than the supralabial pits and not set in a distinct longitudinal groove; the supralabial pits are square or triangular, not diagonal slits. The *molurus* group includes two large species (*molurus* and *sebae*) and three small ones (*curtus*, *regius* and *anchietae*). A few specimens of *P. molurus* were available for comparison with *P. sebae*, to which it appears to be closely related (Frazetta, 1966).

MATERIALS AND METHODS

Because of the large size attained by this species, most museum specimens are juveniles or consist of the skins or severed heads of adults. As some of the whole specimens are preserved in tight coils, it was not possible, in many cases, to obtain ventral counts. More or less complete scale counts were taken for approximately 14 specimens of *P. s. sebae* and 100 *P. s. natalensis*. Additional data for 4 specimens of *P. s. sebae* from Somalia (Hoevers & Johnson, 1982) were incorporated. No geographical variation (or sexual dimorphism) was observed in the counts for midbody scale rows, ventrals, subcaudals, supralabials, infralabials or number and position of labial pits. However, it was possible to differentiate two subspecies on the basis of the degree of fragmentation of the dorsal head shields and on the lateral head markings (Fig. 1).

Python sebae material was examined in the following collections (with acronyms in parentheses): A. J. Lambiris Collection, Harare, Zimbabwe (AJL); British Museum—Natural History (BM); National Museum of Kenya (NMK); National Museum of Zambia (NMZL); National Museum of Zimbabwe (NMZB) and the Transvaal Museum (TM). Specimens were borrowed from Peterhouse Museum, Zimbabwe (PM), the University of Dar-es-Salaam (UDS) and the J. P. Tello Collection, Zinave, Moçambique (JPT). In addition, I circulated a diagram, showing the characters that I had found diagnostic for the two subspecies, to all the European and American Museums with important African collections and asked the curators concerned to check their material of *P. sebae* against them. The relevant data were received from the following institutions: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Barry Hughes Collection, Legon, Ghana (BH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Institute Royal des Sciences Naturelles de Belgique. Brussels (IRScNB); Museum of Comparative Zoology. Harvard (MCZ); Museo Zoologico de "La Specola", Florence (MF); Museum d'Histoire naturelle, Geneve (MHNG); Museum National d'Histoire Naturelle, Paris (MHNP); Musée Royal de l'Afrique Centrale. Tervuren (MRAC); Naturhistorisches Museum. Vienna (NMW); Rijksmuseum van Naturlijke Historie. Leiden (RMNH); Staatliches Museum für Naturkunde, Stuttgart (SMNH); United States National Museum of Natural History, Washington (USNM); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK): Zoologisk Museum, Copenhagen (ZMUC) and Zoologisches Museum, Berlin, D.D.R. (ZMB). Data from these [illegible] covered an additional 306 specimens of *P. sebae* [illegible] and 72 specimens of *P. sebae natalensis*.

In the systematic section, the synonymies for the [illegible] subspecies are restricted to an allocation of the names applied to the species and a list of illustrations (plus a few descriptions) that can be positively identified to subspecies. In the lists of localities for each subspecies, to save space, individual catalogue numbers have not been listed, only acronyms for institutions holding material for each locality are given.

RESULTS

CHARACTER ANALYSIS

1. *Scale counts on body.* Table I shows the variation in number of midbody scale rows, ventrals and subcaudals for the two subspecies of *P. sebae* and the ranges for *P. molurus* (both subspecies; data from Smith, 1943, and 7 specimens examined). The races of *P. sebae* are indistinguishable on the basis of these scale counts, but have higher counts than *P. molurus* in all cases. Laurent (1956) suggested that there might be sexual dimorphism in ventral counts, males averaging higher, but no evidence of sexual dimorphism was observed in any of these counts.

2. *Counts of head shields.* Table II shows the variation in number of supralabials, infralabials, circumorbitals, minimum intrasupraoculars and supralabials in contact with circumorbitals for the two subspecies of *P. sebae*. They are indistinguishable on labial counts, but these are higher in *P. sebae* than in *P. molurus*, which has 11–13 supralabials and 16–20 infralabials.

Laurent (1956) noted that two females from Zaire

TABLE I

Character	Taxon	*N*	Range	Mean	SD
Midbody scale rows	*s. sebae*	17	76–98	86.88	4.86
	s. natalensis	115	78–99	86.64	3.67
	molurus		60–75		
Ventrals	*s. sebae*	12	265–283	276.17	4.59
	s. natalensis	87	260–291	276.63	4.87
	molurus		243–271		
Subcaudals	*s. sebae*	16	62–76	68.44	3.33
	s. natalensis	100	63–84	75.20	3.80
	molurus		58–73		

TABLE II

Character	Taxon	*N*	Range	Mean	SD
Supralabials	*s. sebae*	31	13–16	14.45	0.81
	s. natalensis	121	10–16	14.00	0.82
Infralabials	*s. sebae*	28	19–25	21.84	1.16
	s. natalensis	110	17–24	19.90	1.00
Circumorbitals	*s. sebae*	31	6–10	8.87	0.85
	s. natalensis	116	8–13	10.94	0.96
Minimum intrasupraoculars	*s. sebae*	30	2(3)	2.03	0.18
	s. natalensis	108	2–7	3.64	1.25
Supraoculars contacting circumorbitals	*s. sebae*	29	1–3	2.31	0.54
	s. natalensis	108	1–4	3.07	0.52

had pits in infralabials 2–4, whereas two males from Rwanda and Zaire had pits only in the second and third infralabials. I have noted no sexual dimorphism in this character: only the pits in infralabials 2 and 3 are distinct, ill-defined shallow pits may be detected in infralabials 4, 5 and 6. The posterior group of 3 or 4 pits covers infralabials 12–15 up to 15–18, depending on the total number of infralabials.

The more fragmented dorsal head shields of *P. s. natalensis* (Fig. 1) are reflected by the next two counts. The southern race has, on average, two more circumorbitals than the typical form (coefficient of difference = 1.14) and the minimum intrasupraoculars average 3.64 in *natalensis* whereas typical *sebae* almost invariably has only two and these may be partially fused (C.D. = 1.25). The number of supralabials contacting the circumorbitals averages higher in the southern race, but the difference is not significant.

Python molurus agrees with *P. s. sebae* in having a pair of large frontal shields (which may be fused) and the parietal region covered with moderately fragmented shields.

3. *Head markings*. The markings of *P. s. sebae* are much more contrasted and better defined than those of *P. s. natalensis*. These differences are most pronounced in the case of the lateral head markings (Fig. 1). The typical form has a subnasal pale stripe which runs diagonally back to the second supralabial. This is followed by an extensive preocular dark patch, a subocular dark triangle and a postocular dark stripe which is broader than the diameter of the eye. The subocular dark triangle is occasionally confluent with the preocular dark patch and/or the postocular dark stripe, but these areas are normally separated by pale streaks. There are usually solid dark markings on the infralabials and large dark blotches on the throat, but the underside of the head is always immaculate white.

In *P. s. natalensis* the dark marking in front of the eye is usually reduced to a dark line extending from eye to nostril. The subocular dark triangle is usually reduced or broken up and represented by one or more spots and/or a diagonal streak extending posteriorly. The postocular dark stripe is subequal in width to the eye diameter and may be pale centred. The markings on the infralabials and blotches on the throat are reduced to scattered dark flecks and there are also usually some dark flecks on the underside of the head.

The lateral head markings of *P. molurus bivittatus* are similar to those of *P. s. sebae*, except that a subnasal pale stripe is absent and the preocular dark patch is poorly defined. *P. molurus molurus* is more like *P. s. natalensis*, with a dark preocular line, a narrow dark postocular stripe and the dark subocular triangle often reduced to a diagonal streak extending posteriorly.

4. *Body markings*. These are much more variable than the head markings (Schmidt, 1923). This author gives a comprehensive description of the markings in a series of 18 *P. s. sebae* from north-east Zaire. *P. s. natalensis* seems to be even more variable in its body markings, which are less clearly defined. Details of body markings will be discussed under the section

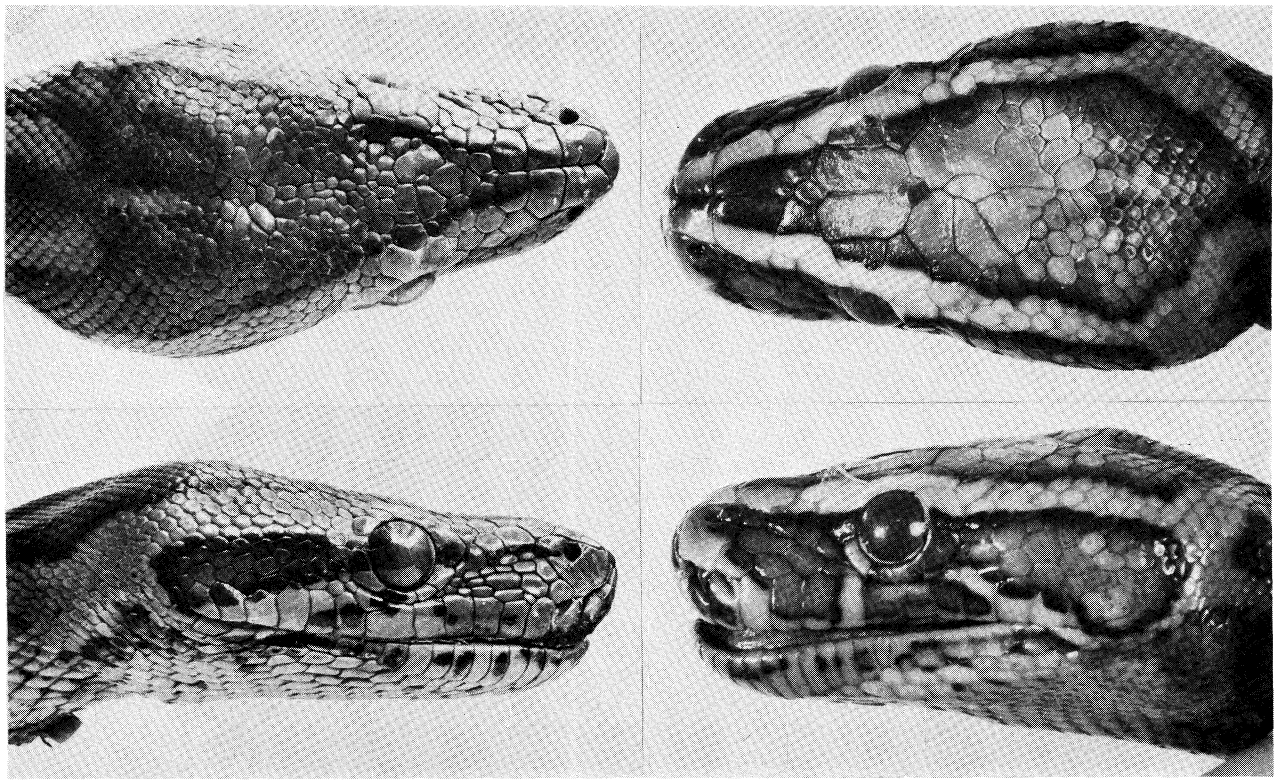


FIG. 1. Dorsal and lateral views of the head of (left) *Python sebae natalensis* (MHNP 364—Lake Ngami, Botswana) and (right) *Python sebae sebae* (MHNG 722.96B—Conakry, Guinea). Photographs by C. A. Domergue and G. Dajuz respectively.

dealing with the status of *P. saxuloides*. *Python molurus* has its light and dark body markings even more strongly contrasted than in *P. s. sebae*.

PYTHON SEBAE SEBAE (Gmelin) Northern African Python

Coluber Sebae Gmelin, 1789, *Syst. Nat.*, Ed. 13, **1**, Part 3, 1118 (based on Seba, *Thesaurus*, **2**, Pl. cxcix, Fig. 2). Type locality: "America" (error).

Coluber Speciosus Bonnaterre, 1789, *Encly. Méthod. Regnes Nat., Ophiol.*, 17. Type locality: "Brazil" (error).

Boa Hieroglyphica Schneider, 1801. *Hist. Amphib.*, **2**, 266. Type locality: "Cairo, Egypt" (by inference, as taken from Seba.

Python Houttuyni Daudin, 1803, *Hist. Nat. Rept.*, **5**, 254. No locality.

Heleionomus variegatus Gray, 1842, *Zool. Misc.*, 43, No locality.

Python Liberiensis Hallowell, 1845, *Proc. Acad. nat. Sci. Philadelphia*, 249. Type locality: Liberia (ANSP 6705).

Python sebae Jan & Sordelli, 1864, Pl. iii (Côte d'Or); Schmidt, 1923, Pl. i, Fig. 2 (NE Zaire); Pitman, 1938/1974, Col. Pl. A & Pl. iii, Fig. 1 (Uganda); Laurent, 1956, 85 (part); Pope, 1956, Pl. 68; Villiers, 1962, Fig. 99 and 1975, Fig. 117; Witte, 1962, Pl. ii (Kinshasa); Doucet, 1963, Pl. v. & Fig. 2 (Ivory Coast); Frazetta, 1966, Fig. 1; Roman, 1971, Fiche 19 (Houte-Volta); Skinner, 1973, Pl. 6 (Kenya); Miller & Smith, 1979, Fig. 1 (right), 3, 5, 7, 9 & 11; Hoevers & Johnson, 1982, 183.

Python molurus (not Linnaeus) Bellairs, 1969, Vol. 1, Pl. 30.

Habitat. Evergreen forest and moist savanna; in dry savanna restricted to riparian habitats. Found at 1350 m in Rwanda (Laurent, 1956), but reported to occur at altitudes up to 2250 m in Uganda (Pitman, 1938).

Distribution. Africa south of the Sahara, from Senegal east to Ethiopia and Somalia, extending southwards into northern Angola (as far south as Ambriz on the coast), the Shaba Province of Zaire, interdigitating and some areas intergrading with *P. s. natalensis* in Kenya and northern Tanzania (Fig. 2).

Recorded localities. SENEGAL: Bakel (BM), Boughari (BM), Dagana (ZMB), Darou (MHNP), Diattacounda (ZFMK), Fatick (FMNH), Rosombo (MHNG), Rufisque (RMNH). GUINEA BISSAU: Bijagós Archipelego (MHNP), Bissau (MHNP), Mansoa (NMW). MALI: Bamako (FMNH). GUINEA: Conakry (MHNG), Mont Nimba (MHNP). SIERRA LEONE: Bo (BM), Sandaru (BM). LIBERIA: Du River (MCZ), Harbel (FMNH), Monrovia (MCZ, MHNP, MRAC), Mount Coffee (USNM), Peáhtah (MCZ), Robertsport (RMNH), Suococo (AMNH). IVORY COAST: Adio Podoumé (MHNG, MHNP, MRAC), Bouna (USNM), Elima (MHNP), Flampleu (MRAC), Lamto (MHNG). UPPER VOLTA: Natiaboani (USNM), Ougarou (USNM). GHANA: Abonu (BH), Accra (BH, RMNH), Achimota (MCZ), Akosombo (BH), Amisano (BH), Asempanaye (BH), Bolgatanga (MCZ). Dabacrom (RMNH), Gbefi (RMNH), Kete Krakye (ZMB), Kpong (BH), Kumasi (BM), Legon (CAS), Mole National Park (BH), Secondi (RMNH), Suhum (BH), Tamale (FMNH), Volta River (NMW), Wa (BH). TOGO: Binaparba (MRAC), Nanergou (MRAC). BENIN: Zizonkame (USNM). NIGER: 11 km NW of Niamey (CAS). NIGERIA: Bamendo (ZMB), Lagos (SMNH), Mundame (ZMB), Samaru (BM). CAMEROUN: Bafout (ZFMK), Banjo Bamendo (ZMB), Bipindi (ZMB), Edea (ZMB), Koum (MRAC), Libamba-Makak (MHNG), Metet (AMNH), Mieri (MRAC), Nachtigal (MRAC), Tchollíré (ZFMK), Victoria (ZMB). EQUATORIAL GUINEA: Fernando Poo (ZMB), Rio Benito (MHNP). CHAD: Sar (NMW). GABON: Belinga (MHNP), Fernan Vas (USNM), Franceville (MHNP), Omboué (USNM), Talagouga (MHNG). CONGO: Nganchou (MHNP). ZAIRE: Bagbele (MRAC), Banana (MRAC), Biadimbi (MRAC), Bigba (MF), Boende (MRAC), Boma-Banana (MRAC), Bomili (MRAC), Bulape (MRAC, USNM), Busamba (IRScNB), Buta (MRAC), Butembo (MRAC), Chutes François-Joseph (MRAC), Djugu (MRAC), Eala (MRAC), Ekibondo (ANSP), Faradje (AMNH), Gamangui (AMNH), Ibembo (MRAC), Ibumba (IRScNB), Inkongo (MRAC), Ishango (MRAC), Itula (MRAC), Kalina (MRAC), Kalinga (MRAC), Kamina (MRAC), Kananga (MRAC), Kasaje (MRAC), Kasenye (IRScNB), Kawa Marsh (MRAC), Keseki (MRAC), Kiavitumbi (MRAC), Kiaviniongwe (IRScNB), Kifuku (MRAC), Kinshasa (MRAC), Kisangani (AMNH, MRAC), Kisantu (IRScNB, MRAC), Kunungu (MRAC), Kwamouth (MRAC), Lac Mayi Ndombe (MRAC), Lieke (IRScNB), Londo (MRAC), Luebo (MRAC), Makaw (MRAC), Mateba (MRAC), Mayumbe (IRScNB), Mbengi (MRAC), Molegbwe (MRAC), Mukandwe River (IRScNB), Mushie (MRAC), Mutsora (IRScNB), Panga (MRAC), Parc National Garamba (IRScNB), Paulis (MRAC), Penghe (MRAC), Poko (MRAC), Rutshuru (FMNH, IRScNB, MRAC), Semliki Delta (IRScNB), Temvo (MRAC), Tshela (MRAC), Ubangi (MRAC), Wilibadi River Source (MRAC), Tangambi (IRScNB, MRAC), Zobia (IRScNB), Zongo (MRAC). ANGOLA: Ambriz (NMW), Dundo (MRAC). RWANDA: Lac Ihema (MRAC), Ngarama (MRAC), Parc National Kagera (IRScNB). SUDAN: South of Khartoum (BM), Torit (FMNH), White Nile (BM, MHNP). ETHIOPIA: Amba Aradam (MF), Godare (BM), 30 km N of Kaalam (MHNP), Soddu and 70 km S (BM). SOMALIA: Alessandra Island (MF), Gelib (MF), Giohar (MF), Manamofa (USNM), Mareri (CAS, MF), Wabbi (ZMB). UGANDA: Sese Islands (BM). KENYA: Chemchem (NMZB), Lamu (ZMB), Lokuria (IRScNB), Malindi (NMK), Masabubu (AMNH), Mkonumbi (MCZ), Mombasa (ZMB), "near Nairobi" (ZFMK), Ngatana (MCZ), Nguni (NMK), Sabaki (NMK), Shimba Hills (BM), Songhor (CAS, NMZB), Tana River (ZMB). TANZANIA: Amani (BM), Dar-es-Salaam (ZMB), Kibaha (ZMUC), Kondoa-Irangui (MHNP), Mwanza (ZMB), Ukerewe Island (MCZ), Usambara Mts (NMW), Zanzibar (MCZ).

PYTHON SEBAE NATALENSIS A. Smith Southern African Python.

Python natalensis A. Smith, 1840, Pl. ix. Type locality: "Port Natal" = Durban. (syntypes: BM 1946.1.8.3

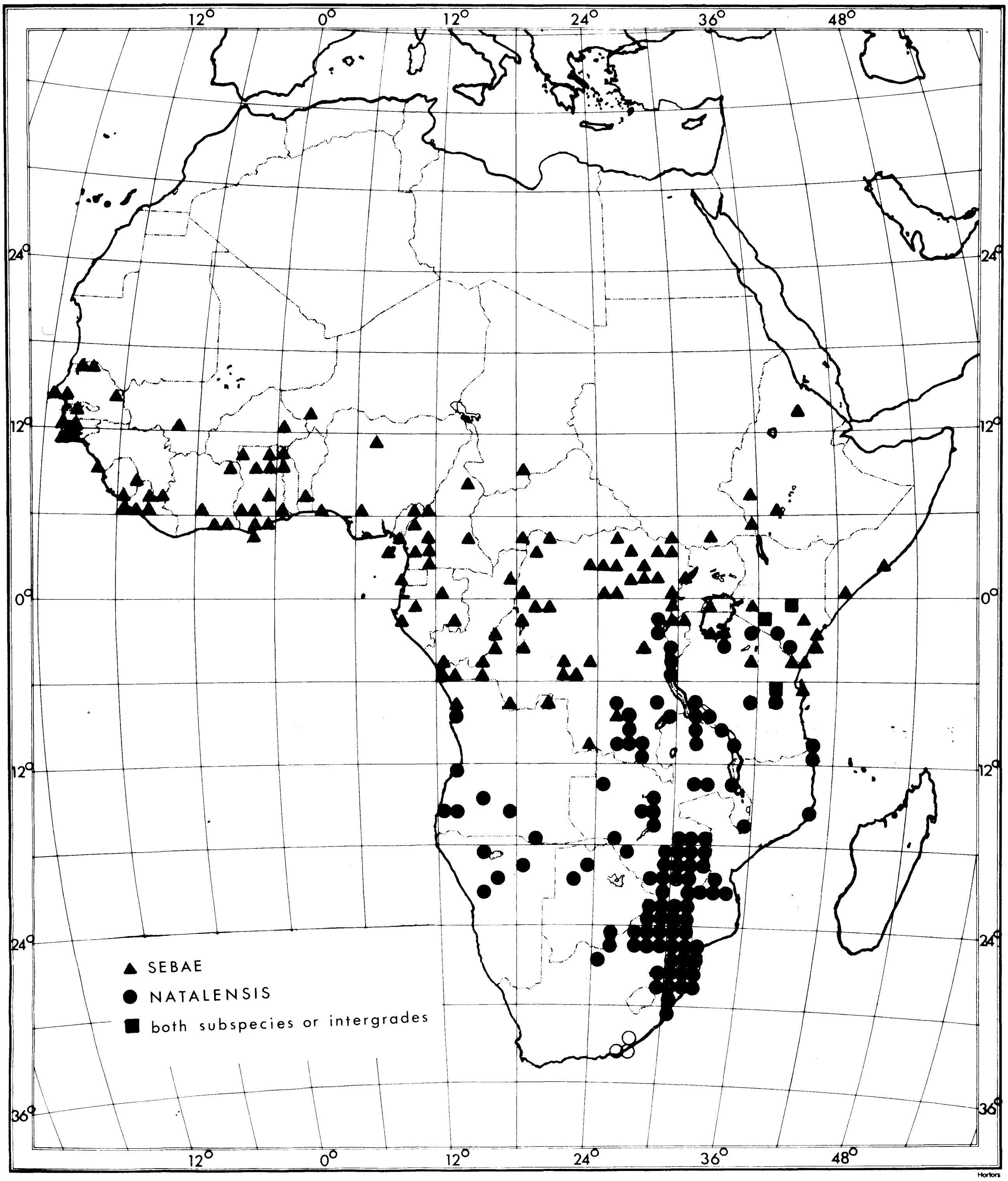


FIG. 2. Distribution of *Python sebae* by degree squares.

and 1946.3.27.2); Peters, 1882, 105; Bocage, 1895, 72.

Python sebae var. *natalensis* Jan, 1864, Pl. iv (Port Natal).

Python sebae (not Gmelin) FitzSimons, F. W., 1912, Figs. 26–29, 31, 1930, 20 illustrations and 1932, Pls. opp. pp. 80, 81 and 225; Rose, 1950, Fig. 157; Tasman, 1953, 2 photos (Harare, Zimbabwe); Isemonger, 1955, photos opp. pp. 4 & 5; Vogel (? 1955), Pl. 69; Laurent, 1956, p. 85 (part); Schmidt & Inger, 1957, Pl. 78; Vesey-FitzGerald, 1958, Pl. 6 (Mbala, Zambia); Sweeney, 1961, Pl. ii (Malawi); FitzSimons, V., 1962, Pl. 3; Pienaar, 1966, Pl. 59 (Kruger National Park); FitzSimons, V., 1970, Pl. 3, Fig. 1; Broadley, 1971, Pl. 7 (Mbala, Zambia); Visser, 1972, Pl. 1; Broadley & Cock, 1975, Pl. 62

(Mutare, Zimbabwe); Parker & Grandison, 1977, Pl. 3, bottom (Mutare, Zimbabwe); Pienaar, 1978, Pl. 54.

Python saxuloides Miller & Smith, 1979, Fig. 1 (left), 2, 4, 6, 8 & 10.

Syntypes. These consist of two adult specimens (BM 1940.3.27.1–2, re-registered BM 1946.1.8.3 and 1946.1.17.13 respectively) which were originally mounted, but now consist of flat skins rolled up and preserved in alcohol. The skins have darkened and markings are difficult to distinguish, but both have the fragmented dorsal head shields diagnostic for this subspecies.

Habitat. Savanna, most abundant in the vicinity of permanent rivers and lakes. Recorded at 1750 m on the Kundelungu Plateau in the Shaba Province of Zaire (Laurent, 1956), found at ca. 2000 m in the Inyanga District of Zimbabwe and probably reaching a similar altitude in Kenya and Tanzania.

Distribution. South-central Africa (*i.e.* southern Angola, south-eastern and eastern Zaire, Zambia, Burundi and southern Tanzania, south to northern Namibia, Botswana and the north-eastern parts of South Africa (Fig. 2). Formerly found in the eastern parts of the Cape Province, but now extinct (FitzSimons, 1962).

In central Africa, the range of *P. s. natalensis* extends northwards along the rift valley into the eastern Kivu Province of Zaire and western Burundi. From Lake Tanganyika it extends up the Rusizi River to Kamaniola, but the most northerly record from this area is a specimen from Hombo, Walikale District, which is just across the watershed on the edge of the Congo Basin. *P. s. natalensis* extends a little further north in central Kenya, being recorded from Ngomeni and Nguni, just south of the Equator.

Recorded localities. ANGOLA: Benguela (Bocage, 1895), Capelongo (AMNH), Chimporo (MHNG), Giraul, Luanda and Maconjo (Bocage, 1895). ZAIRE: Ganza (IRScNB), Hombo (MRAC), Kabwe (IRScNB), Kalemi (IRScNB, MRAC), Kamaniola (MRAC), Kanonga (IRScNB), Kaziba (IRScNB), Kiambi-Boudouinville (MRAC), Kikondja (MRAC), Kina (MRAC), Kundelungu (MRAC), Lubumbashi (IRScNB), Lukufu (MRAC), Mpala (IRScNB), Musosa (IRScNB), Mwera (MRAC), Nyonga (MCZ, MRAC), Panda (IRScNB), Uvira (MRAC). BURUNDI: Bujumbura (MRAC). KENYA: Kibwezi (NMW), Kyiro River (USNM), Mwingi (Miller & Smith, 1979), Nairobi (NMK), Ngomeni (NMK), Nguni (NMK), Sotik Lime Springs (USNM), Voi (IRScNB). TANZANIA: Engaruka Plains (SMNH), Iringa (MCZ, TM), Mikindani (MCZ), Momba River (IRScNB), Mwanyagi (UDS), Rukwa Valley (IRScNB), Shinyanga (USNM), Sopa (NMZB), Ujiji (MCZ), Zimba (IRScNB). ZAMBIA: Chipangali (NMZB), Chipata (NMZB), Chipopera (NMZB), Kabompo (NMZB), Kabwe (BM), Kafue River (USNM), Kaputa (IRScNB), Kasama (IRScNB), Kasauta (NMZL), Livingstone (NMZL), Lusaka West (NMZB), Mbala (IRScNB) and 41 km S (ZMUC). MALAWI: Chibotela (AMNH), Chipoka (MCZ), Kondowe to Karonga (BM), Lujeri Estate (NMZB), Misuku Hills (NMZB), Nyungwe (NMZB). MOÇAMBIQUE: Alves de Lima (JPT), Moçambique Island (Peters, 1882), Monzo (JPT), Namaacha (NMZB), Setache Po (JPT), Vamizi Island (BM), Zinave (JPT, NMZB). ZIMBABWE (all NMZB unless otherwise stated): Atlantica (AJL), Beatrice, Beitbridge, Bulawayo (MCZ, NMZB), Cashel, Chitora School, Esigodini, Goromonzi, Gwaranyemba, Harare, Haroni River, Headlands, Hwange Nat. Park, Imbezu Park, Inyanga, Kadoma, Kapami, Kariba, Khami Dam (AJL), Lake Kariba, Lake Kyle, Lilfordia, Mahenya, Mapembi, Maristvale, Marondera, Mazoe (NMZB, PM), Mutare, Odzi (BM, NMZB), Old Umtali, Penhalonga, Rusape (PM), Sabi-Lundi Confluence (TM), Selous, Triangle, Umfeseri, Whips Cross Farm. BOTSWANA: Kasane (NMZB), Khwai (FMNH), Lake Ngami (MHNP), Maun (FMNH, TM), Metsimaklaba (FMNH). NAMIBIA: Kaokoveld to Etosha Pan (FMNH), Rundu (TM). TRANSVAAL: Doornhoek (TM), Eureka (MCZ, TM), Karino (TM), Ohrigstad (TM), Pretoria (TM), Sterkwater (TM). SWAZILAND: Groenpan Farm (TM), Hlane (TM), Mliba (TM). NATAL: Durban (BM, TM), Lake Sibaya (TM), Mbazwane (TM), Mhlosinga (TM), Mkuzi (FMNH), Mtubatuba (TM), St Lucia Estuary (TM), Sodwana Bay (TM).

DISCUSSION

THE STATUS OF PYTHON SAXULOIDES

When *Python saxuloides* was described (Miller & Smith, 1979), the live holotype and two paratypes were compared with live specimens of *Python sebae sebae* and were considered to differ in 23 characters, which I will consider in turn.

1. Minimum scales between preoculars—2 in *sebae*: 3–6 in *saxuloides* (*natalensis* is similar).
2. Supraoculars and preoculars 4 to 5 times as large as other circumoculars in *sebae*: only 2 to 3 times as large in *saxuloides*. This is a somewhat subjective character, but *natalensis* generally agrees with *saxuloides*.
3. Two supralabials contacting circumorbitals in *sebae*: always 3 in *saxuloides*. This character actually shows considerable variation, as shown above, but *natalensis* averages 3.07.
4. Large subocular dark triangle in *sebae*: reduced to a small spot in *saxuloides* (*natalensis* may be similar or have several spots).
5. Postorbital dark mark broader then eye diameter in *sebae*: narrower in *saxuloides*. In *natalensis* the postocular dark stripe is subequal to eye diameter, but somewhat variable.
6. Supraocular-temporal light line not extending broadly onto lateral gular region, but narrowly continuous with light ventral colour between large dark blotches in *sebae*: widened in lateral gular area, not partially blocked by dark blotches in *saxuloides* (*natalensis* is similar).
7. Supraocular-rostral light line originating at tip of snout in *sebae*: in anterior prefrontal area in *saxuloides*. *P. s. natalensis* agrees with typical *P. sebae* in this character.
8. Loreal dark area separated from medium dark arrow on top of head by supraocular-rostral light line in

sebae: united in *saxuloides*. Again, *P. s. natalensis* agrees with the typical form in this respect.

9. A prominent diagonal subnasal light line in *sebae*: absent in *saxuloides* (with which *P. s. natalensis* agrees).

10. Loreal dark area confined at lip between second and anterior edge of fourth supralabial in *sebae*: extending from rostral to anterior edge of sixth supralabial in *saxuloides*. In fact the lower edge of the loreal dark area may be more extensive in *P. s. sebae* and in *P. s. natalensis* there is usually no clearly defined loreal dark area.

11. Rear edge of loreal dark area diagonally straight or concave in *sebae*: convex in *saxuloides*. There is no clearly defined loreal dark area in *P. s. natalensis*.

12. Throat and underside of head white, unmarked, except for large lineolate blotches on infralabial area, sharply distinct from profusely black-flecked ventral surfaces, posterior to throat in *sebae*: throat and underside of head black-flecked much like rest of ventral surface of body, but no blotchlike marks on infralabial area in *saxuloides* (*natalensis* is similar, but often there are only a few black flecks on underside of head).

13. A continuous dorsal caudal light stripe in *sebae*: discontinuous, absent except at base of tail in *saxuloides*. The supracaudal light stripe may be continuous in *P. s. natalensis* (ca. 25%), but is usually more or less broken up (50%) or absent (25%). In both subspecies the supracaudal light stripe may extend well forward onto the body as a continuous or broken vertebral light stripe; this is a characteristic of hatching *P. s. natalensis* that have been incubated at low temperatures (Branch & Patterson, 1975). There is no supracaudal light stripe in *Python molurus*.

14. Subcaudal surface irregularly mottled, no continuous light line in *sebae*: dark markings largely confined to sides, leaving a nearly straight continuous subcaudal light line in *saxuloides*. Many *P. s. natalensis* resemble *P. s. sebae* in lacking a medial subcaudal light stripe.

15. Light edging of dark marks on body in bold relief against dark ground colour as well as against dark marks in *sebae*: light edging poorly defined, ground colour but slightly darker in *saxuloides* (*P. s. natalensis* is similar).

16. Dorsolateral dark line or zone enclosing a very few, scattered light spots in *sebae*: enclosing numerous light spots, almost full length of body in *saxuloides*. *P. s. natalensis* agrees with *saxuloides*, but the light spots are often confluent to form elongate light blotches or stripes on the posterior half of the body.

17. Light spaces enclosed between dorsolateral dark lines or zones large, often continuous, commonly narrowed centrally and expanded anteroposteriorly in paravertebral area, much more extensive than dark areas between dorsolateral dark zones in *sebae*: small, highly irregular, but much less extensive than dark areas, not expanded in *saxuloides*. The dorsal pattern is in fact highly variable in both subspecies, but the light areas tend to be more extensive in the typical form. In *P. s. natalensis* the dorsal light markings usually form irregular broad crossbands anteriorly and often form broken longitudinal stripes posteriorly.

18. Iris brownish, pupil readily distinguishable in *sebae*: black, pupil scarcely distinguishable in *saxuloides*. This character can only be observed in live specimens. In Zimbabwe *P. s. natalensis* has a dark brown iris with the pupil not readily distinguishable.

19. Eyes obliquely positioned as seen in dorsal view, much exposed in *sebae*: nearly vertical, only apex exposed in *saxuloides*. I have not observed any difference between *P. s. sebae* and *P. s. natalensis*, but the eye seems to be more vertically positioned in juvenile and subadult snakes.

20. Intermidorbital distance narrow, about two-thirds distance from midorbit to snout, less than 40% distance from rictus oris to tip of snout in *sebae*: broader, about threequarters or more of distance from midorbit to tip of snout, more than 40% distance from rictus oris to tip of snout in *saxuloides*. In the small sample checked by me, the range for the first ratio was 65.0–81.6% and for the second 33.8–8–49.1%, with no difference between the two subspecies.

21. *P. sebae* is heavybodied; *P. saxuloides* slenderbodied. It is difficult to evaluate this subjective character. If it is valid, *P. s. sebae* would more closely resemble *Python molurus*.

22. Sexual maturity reached at about 300–350 cm, although maximum perhaps near 700 cm in *sebae*: comparable lengths for *saxuloides* are 250 and 450–500 cm. Female pythons grow larger than males, so presumably there would be sexual dimorphism in size at sexual maturity. Pope (1961) reported a specimen of *P. s. sebae* from Bingerville, Ivory Coast, which measured 9.81 m, whereas there seem to be no records of *P. s. natalensis* exceeding 6 m. Branch and Haacke (1980) give a maximum length of 5.8 m for pythons from southern Africa.

23. *P. sebae* invariably vicious, with rare exception of a few raised in captivity from hatchlings: only one out of six live specimens of *saxuloides* is vicious. This subjective character is difficult to evaluate. Temperament is certainly very variable in *P. s. natalensis*.

For the first 18 characters listed above, *P. sebae natalensis* agrees with *saxuloides* in 9 cases, *sebae* in 3, is intermediate in 3 and resembles neither in 3. It is not possible to evaluate characters 19 to 23, but *P. s. natalensis* apparently agrees with *saxuloides* in being a smaller snake than *P. s. sebae*.

When the localities for *P. s. sebae* and *P. s. natalensis* were plotted (Fig. 2), it became evident that the type locality for *P. saxuloides* falls in a region where the two subspecies are parapatric. The latter name is considered to be based on a somewhat aberrant peripheral population of *P. s. natalensis*. Unfortunately there are relatively few Kenyan pythons with precise locality data in museum collections. I examined a number of live pythons at the Nairobi Snake Park in December, 1981; these included both subspecies, with *natalensis* predominating.

PARAPATRY BETWEEN SUBSPECIES

The question of whether *natalensis* is a full species or merely a subspecies of *P. sebae* can only be settled by careful investigation of the areas where the two forms are parapatric, especially in Kenya and northern Tanzania.

I have examined a few specimens collected near Mwingi, type locality for *P. saxuloides*. From Nguni, 40 km to the north-east, there are single specimens of both *P. s. sebae* (NMK 2386/1) and *P. s. natalensis* (NMK 2386/2), with another specimen of *natalensis* (NMK 2389) collected at Ngomeni, 50 km NW of Mwingi. This area is indicated by the square immediately south of the Equator in central Kenya in Fig. 2. I have seen a *P. s. natalensis* from Nairobi (NMK 1620), but Dr Böhme has reported a *P. s. sebae* from "near Nairobi" (ZFMK 13868), which may well have come from a lower altitude. A large mounted specimen from Kenya (without precise locality), on public display in the Museum Alexander Koenig, has the head pattern of *P. s. sebae*, but the fragmented dorsal head shields of *P. s. natalensis* (Böhme, *in litt.*).

In Tanzania, there are no records of parapatry between typical *sebae* and *natalensis*, but I have examined one specimen from Morogoro (NMK 1575) that appears to be an intergrade and Mr J. L. Knight has reported that another from the same locality (MCZ 14948) has head markings and frontal shields like *P. s. sebae*, but the head shields anterior and posterior to the frontals are fragmented as in *natalensis*. A specimen from Ujiji (MCZ 48095) agrees with *P. s. natalensis* except for the presence of a dark postocular stripe broader than the eye.

There are no cases of parapatry between *P. s. sebae* and *P. s. natalensis* in Zaire or Angola. Two specimens identified as *natalensis* supposedly come from localities in Zaire far removed from the range of that subspecies (IRScNB 11035 Parc Nat. Garamba and MRAC 136 Mayumbe) and are either aberrant or have erroneous locality data.

ACKNOWLEDGEMENTS

I am grateful to the following colleagues for facilities granted whilst working on material in their collections: Ms A. G. C. Grandison (BM), Mr W. D. Haacke (TM), Mr A. Mackay (NMK), Mr A. Muyundu (NMZL) and Mr A. J. Lambiris. I am indebted to the following colleagues for providing data for material in their care: Mr M. Klemens (AMNH), Mr E. V. Malnate (ANSP), Dr B. Hughes (BH), Dr R. C. Drewes (CAS), Mr A. Resetar (FMNH), Monsieur J.-P. Gosse (IRScNB), Mr J. L. Knight (MCZ), Professor B. Lanza (MF), Dr J.-L. Perret (MHNG), Professor E. R. Brygoo and Monsieur Ch. A. Domergue (MHNP), Dr D. F. E. Thys van den Audenaerde (MRAC), Dr M. Häupl (NMW), Dr M. S. Hoogmoed (RMNH), Dr H. Wermuth (SMNH), Dr W. R. Heyer (USNM), Dr W. Böhme (ZFMK), Dr J. B. Rasmussen (ZMUC) and Professor Dr G. Peters (ZMB). I also thank Dr K. M. Howell (UDS) and Mr J. L. P. L. Tello for the loan of material.

REFERENCES

Bellairs, A. d'A. (1969). *The life of reptiles*. 2 vols. London: Weidenfeld & Nicolson.

Bocage, J. V. Barboza du (1895). *Herpétologie d'Angola et du Congo*. Lisbon: Imprimerie Nationale.

Boulenger, G. A. (1893). *Catalogue of the snakes in the British Museum (Natural History), Volume* **1.** London: British Museum (Natural History).

Branch, W. R. & Haacke, W. D. (1980). A fatal attack on a young boy by an African Rock Python *Python sebae. Journal of Herpetology* **14,** 305–307.

Branch, W. R. & Patterson, R. W. (1975). Notes on the development of embryos of the African Rock Python, *Python sebae* (Serpentes: Boidae). *Journal of Herpetology*, **9,** 243–248.

Broadley, D. G. (1971). The reptiles and amphibians of Zambia. *Puku* No. 6, 1–143.

Broadley, D. G. & Cock, E. V. (1975). *Snakes of Rhodesia*. Salisbury: Longman.

Doucet, J. (1963). Les Serpents de la République de Côte d'Ivoire. IIe partie. *Acta Tropica* **20,** 297–340.

FitzSimons, F. W. (1912). *The snakes of South Africa, their venom and the treatment of snakebite*. Cape Town: Maskew Miller.

FitzSimons, F. W. (1930). *Pythons and their ways*. London: Harrap.

FitzSimons, F. W. (1932). *Snakes*. London: Hutchinson.

FitzSimons, V. F. M. (1962). *Snakes of southern Africa*. Cape Town & Johannesburg: Purnell.

Frazetta, T. H. (1966). Studies on the morphology and function of the skull in the Boidae (Serpentes). Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus. Journal of Morphology* **118,** 217–296.

Hoevers, L. G. & Johnson, P. M. (1982). Notes on a collection of snakes from the middle Juba region, Somalia. *Monitore Zoologico Italiano*, N.S. Supplemento XVI, No. 8, 173–203.

Isemonger, R. M. (1955). *Snakes and snake catching in southern Africa*. Cape Town: Timmins.

Jan, G. & Sordelli, F. (1864). *Iconographie generale des Ophidiens*. Tome I, Livraison 8.

Laurent, R. F. (1956). Contribution à l'Herpetologie de la Region des Grands Lacs de l'Afrique Centrale. *Annales du Musée Royal du Congo Belge, Série in 8°, Sciences Zoologiques* **48,** 1–39, Pl. i–xxxi.

McDowell, S. B. (1975). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Anilioidea and Pythoninae. *Journal of Herpetology* **9:** 1–79.

Miller, T. & Smith, H. M. (1979). The Lesser African Rock Python. *Bulletin Maryland Herpetological Society* **15,** 70–84.

Parker, H. W. & Grandison, A. G. C. (1977). *Snakes—a natural history*. London & Ithaca: British Museum (Natural History) & Cornell University Press.

Peters, W. C. H. (1882). *Reise nach Mossambique … Zoologie III. Amphibien*. Berlin: G. Reimer.

Pienaar, U. de V. (1966). *The reptiles of the Kruger National Park*. Pretoria: National Parks Board of Trustees.

Pienaar, U. de V. (1978). *The reptile fauna of the Kruger National Park*. Pretoria: National Parks Board of South Africa.

Pitman, C. R. S. (1938). *A guide to the snakes of Uganda*. Kampala: Uganda Society.

Pitman, C. R. S. (1974). *A guide to the snakes of Uganda*. Revised Edition. Codicote: Wheldon & Wesley.

Pope, C. H. (1956). *The reptile world*. London: Routledge & Kegan Paul.

Pope, C. H. (1961). *The giant snakes*. New York: Knopf.

Roman, B. (1971). *Serpents de Houte-Volta*. Ouagadougou: B. Roman.

Rose, W. (1950). *The reptiles and amphibians of southern Africa.* Cape Town: Maskew Miller.

Schmidt, K. P. (1923). Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part II—Snakes. *Bulletin of the American Museum of Natural History* **49,** 1–146, Pl. i–xxii.

Schmidt, K. P. & Inger, R. F. (1957). *Living reptiles of the world.* London: Hamish Hamilton.

Skinner, H. A. (1973). *Snakes and us.* Nairobi: East African Literature Bureau.

Smith, A. (1840). *Illustrations of the zoology of South Africa ... Reptilia.* London: Smith, Elder & Co.

Smith, M. A. (1943). *The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. 3: Serpents.* London: Taylor & Francis.

Sweeney, R. C. H. (1961). *Snakes of Nyasaland.* Zomba: Nyasaland Society & Nyasaland Government.

Tasman, K. (1953). Every man's hand against him. *Rhodesian Graphic Annual* 1953, 17–37.

Vesey-FitzGerald, D. F. (1958). The snakes of Northern Rhodesia and the Tanganyika borderlands. *Proceedings and Transactions of the Rhodesia Scientific Association* **46,** 17–102.

Villiers, A. (1962). *Les serpents de l'ouest African.* 2e édition, and (1975) 3e édition. Dakar: IFAN.

Visser, J. (1972). *What snake is that?* Cape Town: Purnell.

Vogel, Z. (? 1955). *Reptile Life.* London: Spring Books.

Witte, G.-F. de (1962). Genera des serpents du Congo et du Ruanda-Urundi. *Annales Musee Royal de l'Afrique Centrale, Serie in 8°, Sciences Zoologiques,* No. 104: 1–203, Pl. i–xv.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, p. 368 (1984)

BOOK REVIEW

THE NATTERJACK TOAD. By T. J. C. Beebee (1983). 159 pp., 16 photos, 11 text figures. Oxford: Oxford University Press. £9.95.

Monographic books on the biology of single amphibian species are very rare. Each new one, written by a really competent worker, will be a valuable contribution from the first. Trevor Beebee's comprehensive work on the natterjack toad (*Bufo calamita*) is a model of how a lot of information obtained in decades of herpetological research on various aspects of morphology, physiology, behaviour and ecology of a species can be presented in clearly built up chapters which are as valuable for scientific specialists as for amateurs. It might be asked how a little toad species in heaths and dunes could not only deserve a whole book, but how this book could find enough buyers to be economically interesting for the publishers. Reading Beebee's book on *Bufo calamita* gives the answer. It contains a broad range of general biological information. Although this centres around one species only, and it concentrates on the biology of this species in only one part of its distributional area, *i.e.* Britain, the fascinating view of this one species helps the reader to learn more about the close correlation between ecological specialization and evolution, which is valid for any organism. That Beebee really intended to achieve this general goal is clearly demonstrated by the final chapter of his book, where he tries to give good advice to amateurs on how to make their own contributions to the study of amphibian biology.

HELMUT HEMMER

EDITORIAL NOTES

The Editor is grateful to the following people who kindly reviewed manuscripts during 1983: D. Bauwens, T. J. C. Beebee, C. Bishop, H. R. Bustard, A. S. Cooke, J. E. Cooper, S. P. Gittins, A. Goldsmith, T. R. Halliday, M. R. K. Lambert, C. J. McCarthy, R. Meek, T. J. Nicholls, C. J. Rose, I. F. Spellerberg, I. R. Swingland, T. E. Thompson, D. W. Yalden.

British Journal of Herpetology is currently limited in size by financial constraints; we have to turn away manuscripts of good quality which the Editor would like to be able to publish. The only way to increase the size of the journal is to increase membership and subscriptions: please check that YOU are a paid up member of the British Herpetological Society, encourage your colleagues and friends to join if they have not already done so, and persuade the Librarian of your institution to take out an institutional subscription to the journal.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 369–373 (1984)

THE INCIDENCE OF SPINAL DEFORMITIES IN MARINE TURTLES, WITH NOTES ON THE PREVALENCE OF KYPHOSIS IN INDONESIAN *CHELONIA MYDAS*

Anders G. J. Rhodin[1], Peter C. H. Pritchard[2] and Russell A. Mittermeier[3]

[1]*Orthopaedic Associates, P.C., Nichols Rd., Fitchburg, Mass.,* 01420 *and Museum of Comparative Zoology, Harvard University, Cambridge, Mass.,* 02138, *U.S.;* [2]*Florida Audubon Society,* 1101 *Audubon Way, Maitland, Fla.,* 32751, *U.S.;* and [3]*World Wildlife Fund—U.S.,* 1601 *Connecticut Ave., NW, Washington, D. C.,* 20009 *and Department of Anatomical Sciences, HSC, State University of New York, Stony Brook, N.Y., 11794, U.S.*

(*Received* 26 *July* 1983)

SUMMARY

Previously over-looked literature on spinal deformities in marine turtles is reviewed and analysed for data on incidence of kyphosis, lordosis and scoliosis. Field observations on the incidence of spinal deformities in *Lepidochelys olivacea* and *Chelonia mydas* are presented. The overall incidence of spinal deformities in the 11 726 marine turtles examined or reviewed is 0.11%, representing 0.08% kyphosis and 0.03% lordosis and scoliosis. Indonesian *Chelonia mydas* appear to have an unusually high prevalence of kyphosis (1.0%). Hypotheses regarding the etiologies of the various spinal deformities are discussed.

INTRODUCTION

The occurrence of spinal deformities in turtles has received little attention in the literature, and most articles have only documented the occurrence of kyphosis in one or a few specimens of a given species. Though many authors have dealt with the incidence of scute abnormalities in turtle populations, none have investigated the incidence of kyphosis and other spinal deformities. In addition, many literature citations on spinal deformities are buried in longer papers on chelonian natural history and morphometric investigations, and are easily overlooked. For example, the two most recent major papers on the occurrence of kyphosis in turtles (Plymale, Jackson & Collier, 1978; Wilhoft, 1980) are notably deficient in their analysis of previous literature. Plymale *et al.* (1978) in their "survey of all published accounts of chelonian kyphosis" provide only one citation for the occurrence of spinal deformities in marine turtles. They cite Coker (1910) as allegedly describing the occurrence of kyphosis in the loggerhead turtle, *Caretta caretta*. Our reading of that paper indicates no such description. On the other hand, one specimen described by Coker has a definite scoliosis and as such, does represent a case of spinal deformity in a marine turtle.

In order to remedy these shortcomings in the literature, we have initiated an investigation of kyphosis and other spinal deformities in turtles.

The three types of spinal deformity most common among turtles are kyphosis, lordosis and scoliosis. Kyphosis is commonly known as "hump-back" and is defined as a dorsally convex deformity of the spine in the sagittal plane of the animal (whether a turtle or other vertebrate, such as man). Lordosis is also known as "sway-back" and is defined as a ventrally concave deformity of the spine in the sagittal plane. Scoliosis is a lateral curvature of the spine in either direction within the frontal plane of the animal. In turtles this is normally a single curve, in humans usually a double S-curve. In addition, features of two or more of these deformities can be present in a single animal. Kyphoscoliosis, for example, is a complex deformity including deviation into both the sagittal and frontal planes.

METHODS

We performed an extensive literature review to identify as many previously overlooked citations as possible concerning spinal deformities in marine turtles. We also reviewed articles where the authors clearly paid specific attention to the possibility of the presence of skeletal abnormalities in marine turtles, yet where no cases of spinal deformity were noted. In all these reviewed literature citations, we have attempted to calculate the incidence of spinal deformities and kyphosis based on the population data presented, or the maximal possible incidence in those populations where no deformed individuals were noted. In addition, we have made preliminary field observations on the occurrence and incidence of kyphosis and other spinal deformities in marine turtles. This paper and Table I summarize our findings. The incidence of deformities has not been calculated for populations of less than 100 animals: for populations of 100 to 1000 animals the results have been calculated to the nearest one tenth percent, for those above 1000 to the nearest one hundredth percent.

RESULTS

Six previous articles have documented the presence of spinal deformities in marine turtles.

TABLE I. Incidence of spinal deformities and kyphosis in marine turtle populations

			Spinal deformities		Kyphosis		
Genus and species	Locality	*N*	No.	%	No.	%	Source
Chelonia							
C. agassizi	Baja California	2600	0	<0.04	0	<0.04	Caldwell 1962
C. mydas	Australia	984	1	0.1	0	<0.1	Moorhouse 1933
C. mydas	Indonesia	409	5	1.2	4	1.0	Present Study
C. mydas	Sri Lanka	214	0	<0.5	0	<0.5	Deraniyagala 1939
	Worldwide totals	4207	6	0.14	4	0.10	Above 4 Refs.
Lepidochelys							
L. olivacea	Sri Lanka	378	1	0.3	0	<0.3	Deraniyagala 1939
L. olivacea	Mexico	300	1	0.3	1	0.3	Present Study
L. olivacea	Guyana	241	0	<0.4	0	<0.4	Pritchard 1969
	Worldwide totals	919	2	0.2	1	0.1	Above 3 Refs.
Caretta							
C. caretta	South Carolina	398	0	<0.3	0	<0.3	Baldwin and Lofton 1959
C. caretta	North Carolina	208	1	0.5	0	<0.5	Coker 1910
	Worldwide totals	689	1	0.2	0	<0.2	Above 2 Refs. and Moorhouse 1933
Dermochelys							
D. coriacea	Guyana	5878	4	0.07	4	0.07	Fretey 1978
	Worldwide totals	5911	4	0.07	4	0.07	Above Ref. and Present Study
	Overall totals	11726	13	0.11	9	0.08	

Coker (1910), as mentioned above, described a case of scoliosis in a hatchling loggerhead (*Caretta caretta*) from North Carolina. He examined 208 specimens, thereby giving an incidence of 0.5% spinal deformities in the population, and <0.5% kyphosis.

Moorhouse (1933) examined 984 specimens of hatchling green turtles (*Chelonia mydas*) from Heron Island, Queensland, Australia and found one specimen with a mild spinal deformity causing depigmentation and tail loss. This represents an incidence of 0.1% spinal deformities in the population, and <0.1% kyphosis.

Deraniyagala (1939) examined 378 specimens of olive ridleys (*Lepidochelys olivacea*) from Sri Lanka and found one hatchling with lordosis. This represents an incidence of 0.3% spinal deformities in the population, and <0.3% kyphosis.

Villiers (1958) illustrated a single adult green turtle (*Chelonia mydas*) from West Africa with pronounced kyphosis. He made no mention of the population sample examined, but stated that shell deformities are apparently relatively common among sea turtles.

Witham and Futch (1977) illustrated and described the development of lordosis in captive-raised *Chelonia mydas* from Hutchinson Island, Florida. They indicated that at least 10 animals out of about 2500 developed lordosis, for an incidence of at least 0.4% spinal deformities. Since no deformities were noted at hatching and the lordosis developed during growth in captivity, this deformity may have represented a nutritional osteodystrophy secondary to a dietary calcium/phosphorous imbalance or other disorder of calcium metabolism. Because this population is a captive-raised one, the figures on incidence of spinal deformities are not included in Table I or in the analysis of the data.

Fretey (1978) examined 5878 mature female leatherback turtles (*Dermochelys coriacea*) nesting in Guyana and found 4 with "kyphotic" shells. He does not elaborate on this description other than stating that one of the specimens had a foreshortened carapace as a result. Whether his specimens represent true kyphosis or kyphoscoliosis remains unclear. The 4 specimens

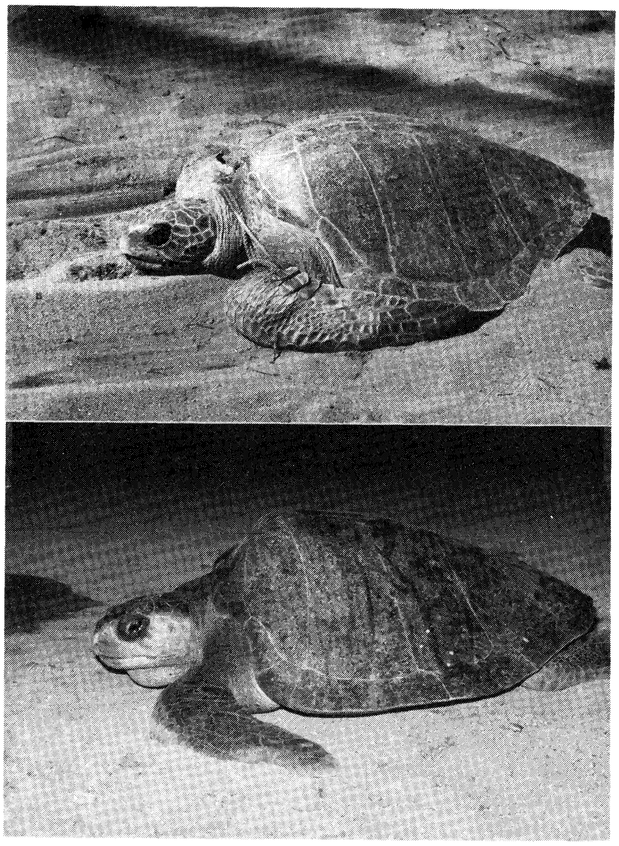


FIG. 1. *Top:* Normal female *Lepidochelys olivacea*, Guerrero, Mexico. *Bottom:* Kyphotic female *L. olivacea*, Oaxaca, Mexico.

represent an incidence of 0.07% spinal deformities in the population, and probably 0.07% kyphosis.

Five previous studies have addressed the question of occurrence of skeletal deformities in marine turtle populations without apparently discovering any cases of spinal deformity. Because a maximum possible incidence of spinal deformities in the population can be calculated from the number of animals studied, these citations are included for comparative purposes. Caldwell (1962) examined ca. 2600 *Chelonia agassizi* from the Gulf of California without noting any cases of spinal deformity, yielding an incidence of <0.04% spinal deformities. Deraniyagala (1939) found none among 214 *Chelonia mydas* from Sri Lanka for an incidence of <0.5%. Pritchard (1969) found none among 241 *Lepidochelys olivacea* from Guyana for an incidence of <0.4%. Baldwin & Lofton (1959) found none among 398 *Caretta caretta* from South Carolina for an incidence of <0.3%. Moorhouse (1933) found none among 83 *Caretta caretta* from Australia.

In addition to the above literature citations, we have made a few preliminary field observations on the occurrence and incidence of spinal deformities in marine turtles.

During a field survey of marine turtles in Oaxaca and Guerrero, Mexico in January, 1982, we (AGJR and PCHP) were able to examine ca. 300 olive ridleys (*Lepidochelys olivacea*) obtained from the slaughterhouse in Puerto Angel. We found one adult female with a kyphotic spinal deformity (Fig. 1), representing an incidence of 0.3% spinal deformities in the population, and 0.3% kyphosis. At the same time we examined 11 adult leatherbacks (*Dermochelys coriacea*), none with spinal deformities. In addition, AGJR has examined 15 adult *D. coriacea* from U.S. waters, and RAM 7 from Surinam, also all without spinal deformities. These 33 specimens have been added to Fretey's (1978) much larger sample for analysis of incidence of spinal deformities in *D. coriacea*.

During a visit to Bali, Indonesia in October, 1982, we (AGJR and RAM) surveyed the commercial sea turtle pens at Serangan and Benoa one day and examined 409 adult green turtles (*Chelonia mydas*). We found 5 animals with spinal deformities, of which 4 represented true kyphosis (Fig. 2) and one a case of lordosis (Fig. 3). This represents a total incidence of 1.2% spinal deformities in the sample, with 1.0% kyphosis and 0.2% lordosis. The turtle sample represented in these commercial pens probably does not constitute a single natural population, as the turtle fishery industry based on Bali encompasses a broad area within Indonesia, including Bali, Sumbawa, Flores, Timor, southern Sulawesi, and southeastern Kalimantan (Polunin & Sumertha Nuitja, 1982; Sumertha Nuitja & Akhmad, 1982). The turtles caught within this broad geographic region can well have originated from any one of several Indonesian green turtle nesting grounds. The most likely of these would be Ai-Ketapang on Sumbawa, Sukamade on Java, or Berau on East Kalimantan (see Polunin & Sumertha Nuitja, 1982).

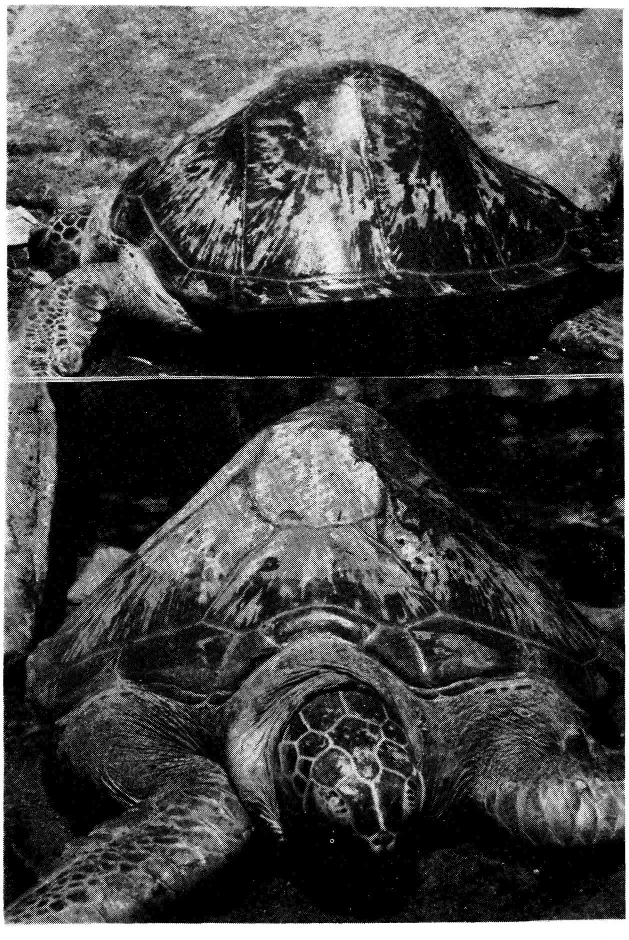


FIG. 2. Lateral and anterior views of kyphotic female *Chelonia mydas*, Bali, Indonesia.

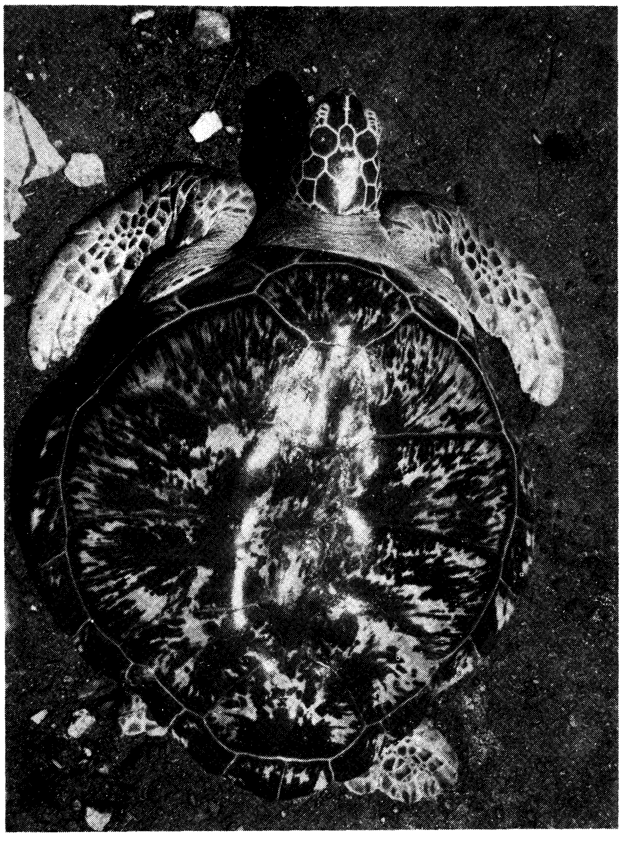


FIG. 3. Dorsal view of lordotic female *Chelonia mydas*, Bali, Indonesia.

DISCUSSION

The overall incidence of spinal deformities in the 11 726 marine turtles reviewed is 0.11%. Of this figure, 0.08% represents the incidence of kyphosis, 0.03% the incidence of other spinal deformities such as lordosis and scoliosis. There is little appreciable difference in the incidence of deformity between the three genera of the family Cheloniidae examined (*Chelonia*, *Lepidochelys*, and *Caretta*). The morphologically divergent *Dermochelys* of the family Dermochelyidae may have a lower incidence of spinal deformities than the hard-shelled Cheloniidae, but, despite hypotheses to the contrary (Nixon and Smith, 1949; Plymale *et al.*, 1978), does indeed develop kyphosis. The overall incidence of spinal deformities in the Cheloniidae is 0.15% based on 5815 specimens. The overall incidence in the Dermochelyidae is 0.07% based on 5911 specimens. For the incidence of kyphosis alone, the figures are nearly identical, with 0.09% in the Cheloniidae, 0.07% in the Dermochelyidae.

The prevalence of kyphosis (1.0%) among Indonesian *Chelonia mydas* is most unusual when comparing it to the data presented above on other marine turtle populations. However, the incidence of lordosis in the population (0.2%) falls within the general range for incidence of spinal deformities among other cheloniid marine turtles reviewed. As such, the incidence of total spinal deformities of 1.2% probably reflects primarily the comparatively high incidence of kyphosis alone.

At this stage, we can only hypothesize as to the cause of this unusual prevalence of kyphosis. Plymale *et al.* (1978) have listed the various theories already proposed in the literature for the development of kyphosis. Wilhoft (1980) also summarizes some of these. Neither of these authors, nor any previous workers, have differentiated between the various types of spinal deformity when discussing etiology. In fact, within the general field of chelonian teratology, the term "kyphosis" has unfortunately become more or less loosely synonymous with "spinal deformity". For example, Wilhoft (1980) described a purely lordotic snapping turtle (*Chelydra serpentina*) as "kyphotic", and MacCulloch (1981) described scoliotic painted turtles (*Chrysemys picta belli*) as "kyphotic". We believe that such laxity of definition can only lead to confusion and misdirected generalizations in any discussion of spinal deformity. We therefore urge a strict adherance to proper anatomic definitions.

In our opinion, the causes of spinal deformities are multiple. Initially, a distinction must be made between pre- and post-natally acquired deformities. Both kyphosis and lordosis can develop during growth as a result of nutritional osteodystrophy or other developmental factors. The lordotic green turtles discussed by Witham and Futch (1977) and the lordotic snapping turtle described by Wilhoft (1980) are representative of post-natal deformities. In addition, PCHP has observed one kyphotic green turtle (*Chelonia mydas*) raised at the Cayman Turtle Farm which might also fall into this post-natal category.

Pre-natally acquired deformities may be either congenital or secondary to alterations in the internal egg environment. For example, lordosis may well develop as a response to external pressure on the developing embryo, possibly as a result of excessive moisture loss and drying of the incubating egg (see Lynn & Ullrich, 1950, for experimental results on egg dessication). In turtle species with soft, pliable eggshells such as the marine turtles such deformation may occur as a result of collapse of the eggshell itself. In turtle species with hard, brittle eggshells such as the terrestrial tortoises of the family Testudinidae, such deformation can probably occur as the result of increasing size of the internal air bubble, also due to excessive moisture loss and drying of the incubating egg. Kyphosis, on the other hand, is more likely a congenital abnormality reflecting some internal defect. In humans, congenital kyphosis is due either to a partial failure of formation or failure of segmentation of the developing spinal vertebrae. Whether these mechanisms can account for chelonian kyphosis remains to be investigated. In addition, it would appear from preliminary observations on kyphosis in turtles in general, that there may be two different types of kyphosis, which may have different etiologies. Of these, one type is a smoothly high-domed deformity affecting the entire bony carapace which might well be related to post-natal developmental factors such as the yolk-retraction theory of Williams (1957). Kyphotic specimens of soft-shelled turtles (Trionychidae) appear to demonstrate this condition frequently (see Mertens, 1940; and Smith, 1947). The other type of kyphosis is the presence of an asymmetrical angular deformity in a smaller portion of the carapace which is more likely the result of a congenital defect. Most of the marine turtles reported on here, and most other hard-shelled turtles previously indicated in the literature represent this second type of kyphosis.

Further investigations will be required to delineate the causes of chelonian spinal deformities. Special attention should be focused on abnormal situations such as the high prevalence of kyphosis in the Indonesian population of *Chelonia mydas*. As Mitchell & Yntema (1973) have demonstrated, teratogens such as malathion and captan can cause an increased incidence of spinal abnormalities in turtles. Whether some unknown teratogenic effect is at work on the Indonesian green turtle population warrants further analysis.

A final note of caution must, however, be raised concerning any interpretation of the significance of the apparently high incidence of spinal deformities in Indonesian green turtles. These animals play an important role in social and religious contexts in Bali and it is not known whether these social factors influence the rate at which deformed specimens are sold in the market. It is possible that kyphotic or lordotic specimens accumulate in the commercial pens, either because they are highly valued by the seller, or because they are avoided by the buyer. If either case is true, then the actual incidence of these deformities in the natural Indonesian population would be much lower than that seen in the captive population in the commercial pens we examined. Further studies are clearly needed.

REFERENCES

Baldwin, W. P. & Lofton, J. P. (1959). The Atlantic loggerhead sea turtle, *Caretta caretta caretta* (L.) in America. III. The loggerhead turtles of Cape Romain, South California. *Bulletin of the Florida State Museum* **4,** 319–348.

Caldwell, D. K. (1962). Sea turtles in Baja Californian waters (with special reference to those of the Gulf of California), and the description of a new subspecies of northeastern Pacific green turtle. *Contributions to Science of the Los Angeles County Museum* **61,** 1–31.

Coker, R. E. (1910). Diversity in the scutes of Chelonia. *Journal of Morphology* **21,** 1–75.

Deraniyagala, P. E. P. (1939). *The tetrapod Reptiles of Ceylon. Volume* 1. *Testudinates and Crocodilians.* London.

Fretey, J. (1978). Mensurations du tortues luths femelles adultes, *Dermochelys coriacea* (Linne), en Guyane francaise. *Bullétin du Société Zoologique de France* **103,** 518–523.

Lynn, W. G. & Ullrich, M. C. (1950). Experimental production of shell abnormalities in turtles. *Copeia* **1950,** 253–262.

MacCulloch, R. D. (1981). Variation in the shell of *Chrysemys picta belli* from southern Saskatchewan. *Journal of Herpetology* **15,** 181–185.

Mertens, R. (1940). Der Knochenpanzer einer kyphotischen Weichschildkrote. *Senckenbergiana* **22,** 236–243.

Mitchell, J. T. & Yntema, C. L. (1973). Teratogenic effect of malathion and captan in the embryo of the common snapping turtle, *Chelydra serpentina. Anatomical Record* **175,** 390.

Moorhouse, F. W. (1933). Notes on the green turtle (*Chelonia mydas*). *Report of the Great Barrier Reef Committee, Brisbane* **4,** 1–22.

Nixon, C. W. & Smith, H. M. (1949). The occurrence of kyphosis in turtles. *Turtox News* **27,** 1–2.

Plymale, H. H., Jackson, C. G. & Collier, G. (1978). Kyphosis in *Chrysemys scripta yaquia* (Testudines: Emydidae) and other turtles. *Southwestern Naturalist* **23,** 457–462.

Polunin, N. V. C. and Sumertha Nuitja, N. (1982). Sea turtle populations of Indonesia and Thailand. In *Biology and conservation of sea turtles*, 353–362. K. Bjorndal (Ed.) Washington D.C.: Smithsonian Institution Press.

Pritchard, P. C. H. (1969). Sea turtles of the Guianas. *Bulletin of the Florida State Museum* **13,** 85–140.

Smith, H. M. (1947). Kyphosis and other variations in soft-shelled turtles. *University of Kansas Publications in Natural History* **1,** 117–124.

Sumertha Nuitja, I. N. & Akhmad, S. (1982). Management and conservation of marine turtles in Indonesia. *Manuscript submitted to Third World National Parks Congress, Bali.*

Villiers, A. (1958). Tortues et crocodiles de l'Afrique Noire Francaise. *Instut. Francaise de l' Afrique Noire* **15,** 1–354.

Wilhoft, D. C. (1980). Kyphosis in the snapping turtle *Chelydra serpentina. Bulletin of the New York Herpetological Society* **15,** 15–26

Williams, K. L. (1957). Yolk retraction as a possible cause of kyphosis in turtles. *Herpetologica* **13,** 236.

Witham, R. & Futch, C. R. (1977). Early growth and oceanic survival of pen-reared sea turtles. *Herpetologica* **33,** 404–409.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 375–378 (1984)

A COMPARATIVE STUDY OF PHOTOTAXIS AND THE RESPONSE TO SUBSTRATE MOISTURE IN NEWTS AND SALAMANDERS

R. A. Griffiths

Department of Zoology, Birkbeck College, University of London, Malet Street, London WC1E 7HX

(*Received* 14 *October* 1983)

SUMMARY

Phototaxis and the response to different conditions of substrate moisture were investigated in adult *Triturus vulgaris*, *T. cristatus* and *Salamandra salamandra* throughout the light and dark phases of a LD 12:12 cycle, using choice chamber apparatus. Under moist conditions, *T. vulgaris* was photopositive, and *T. cristatus* and *S. salmandra* were photonegative, during subjective daytime. Under the dim subjective night-time intensity, however, *T. vulgaris* and *T. cristatus* were both photopositive whereas *S. salamandra* showed no apparent preference. There was little variation in the response to light during each phase of the diel cycle. When offered a choice of moist or dry conditions, however, the phototactic response was overridden in all three species and moist areas were selected whatever the ambient light intensity or phase of the diel cycle.

INTRODUCTION

Substrate moisture levels are known to affect the horizontal and vertical distribution of terrestrial salamanders (*e.g.* Vernberg, 1953; Taub, 1961; Heatwole, 1962). In soil moisture gradients salamanders generally seek areas of optimal moisture, but the response may vary between species and according to the seasonal condition of individual animals (Vernberg, 1955; Anderson, 1972; Marangio & Anderson, 1977; Keen, 1982). Phototaxis may also be involved in microhabitat selection but there is a paucity of information relating to the effect of moisture levels on this and other behavioural responses.

In North American urodeles the effect of thigmotaxis on the light response has been documented for *Plethodon cinereus* and *Ambystoma macrodactylum* (Test, 1946; Anderson, 1972). In both normal and blinded *Necturus maculosus*, Cole (1922) found that the phototactic reaction time bears an inverse relationship to temperature. Pearse (1910) discovered that *Notophthalmus viridescens* gives a positive response to light, but Stier (1926) observed a negative reaction in starved individuals of the same species. Moisture preference in relation to water balance was studied in two species of *Plethodon* by Jaeger (1971), and in *A. opacum* by Marangio & Anderson (1977). In European salamanders, Degani & Warburg (1980) found that juvenile *Salamandra salamandra* respond significantly more to areas of high moisture than adults. Furthermore, whereas younger animals preferred saturated soil to saturated sand, adults displayed no preference.

In a previous paper, Griffiths (1983) described how the response to light changes during ontogeny in the common newt *Triturus vulgaris*. In order to evaluate some of the factors involved in microhabitat selection, the present study set out to determine the effect of substrate moisture on phototactic behaviour in adult newts, *T. vulgaris*, *T. cristatus* and the salamander *S. salamandra*. Observations were made throughout both phases of a light–dark cycle to account for any diel changes in behaviour.

MATERIALS AND METHODS

T. cristatus and *S. salamandra* were obtained from a dealer and *T. vulgaris* were collected from the vicinity of local ponds. All animals used in the experiments were terrestrial adults, and were fed earthworms, crickets and slugs in the laboratory. No feeding took place on test days. *T. vulgaris* and *T. cristatus* were tested in standard choice chamber apparatus (200 mm diameter × 35 mm deep) using the lighting cabinet described by Griffiths (1983), at 25 ± 2°C. Due to their larger size and slightly lower temperature requirements, *S. salamandra* were tested in deeper chambers (200 mm diameter × 70 mm deep) at 15°C, in a darkened room. These choice chambers were placed behind black screens and observations made through small holes. Both newts and salamanders were placed individually in choice chambers which were half-darkened by a black cover.

Lighting was provided by fluorescent tubes which yielded a "daytime" light intensity of 800 lux (*T. vulgaris* and *T. cristatus*) or 500 lux (*S. salamandra*) on the uncovered halves of each chamber. Light intensities in the covered sections were 0.5 lux and 0.2 lux for newts and salamanders respectively. Dim "night-time" lighting was provided for in both newts and salamanders by further partially foil-covered tubes which gave intensity readings of 6 lux in uncovered, and 0 lux in covered choice chamber sections respectively. All light measurements were made using an EEL photoelectric photometer. Visual contact between experimental animals was prevented by cardboard partitions.

---

* Present address: *Department of Applied Biology, UWIST, Llysdinam Field Centre, Newbridge-on-Wye, Llandrindod Wells, Wales.*

PHOTOTAXIS UNDER MOIST CONDITIONS

Adults of all three species were initially tested to determine their reaction to a light–dark choice under moist conditions. A moist substrate was provided in both covered and uncovered sections of each chamber using 10 mm thick pieces of damp foam overlain by filter paper. Animals were placed individually in choice chambers under LD 12:12 for several days. Observations were then made on their selected positions at hourly intervals for the duration of the light phase, which was from 0800–2000 hr. (*i.e.* 12 observations per animal). The experiment was then repeated under reversed LD such that observations were made throughout the dark (dimly lit) phase.

PHOTOTAXIS UNDER MOIST–DRY CONDITIONS

Initially, newts and salamanders were placed individually in uniformly moist choice chambers under LD 12:12, as described above. After several days under these conditions animals were transferred to identical containers giving either (1) light moist–dark dry, or (2) light dry–dark moist choices. The day following transfer to these conditions observations were made on the selected positions of animals for the duration of either light or dark (dim) phases, as described previously.

A dry substrate was provided using dehydrated silica gel, both moist and dry substrates being overlain by filter paper in order to ensure a uniform surface texture. Due to the hydration of silica gel over several days from the moist section it was considered inadvisable to entrain amphibians under moist-dry conditions. The relative humidities in such a moist-dry choice chamber as measured using cobalt thiocyanate paper are shown in Fig. 1.

RESULTS

In contrast to the predominantly photopositive *T. vulgaris*, *T. cristatus* and *S. salamandra* were photonegative during the light phase of LD under moist conditions. Under moist conditions in dim light, however, *T. vulgaris* and *T. cristatus* were photopositive whereas *S. salamandra* displayed no apparent preference (Table 1). Whereas the phototactic response of *T. vulgaris* during the light phase was not significantly different from that during the dark phase ($\chi^2 = 0.4$, $P > 0.05$), in *T. cristatus* and *S. salamandra* phototaxis was very much dependent upon the light intensities used during the two phases (*T. cristatus*: $\chi^2 = 40.8$, $P < 0.001$; *S. salamandra*: $\chi^2 = 8.2$, $P < 0.005$). There were no marked changes in the response to light across each phase of the diel cycle in any of the three species (Fig. 2).

With moist versus dry conditions, phototaxis was outweighed by the response to moisture in all three species, and an overriding preference for light moist rather than dark dry, and dark moist rather than light dry was evident during both phases of LD in all three species (Table 1).

Table 1. Summary of phototactic responses in newts and salamanders. Ratios in the first row of each section represent the number of animals on the light (uncovered) half of the chamber: the number on the dark (covered) half of the chamber, using 8 animals in each test (intermediate positions were scored according to the position of the head). The second row represents the same ratio expressed as a percentage for easier comparison of results. Original scores were tested for deviation from a 1:1 result using chi-squared, assuming 1 d.f. *from Griffiths (1983).

	light dark moist:moist*	light dark dry:moist	light dark moist:dry
Triturus vulgaris			
Light phase (800 lux)			
no. +:no. −	69:27*	0:96	89:7
% +:% −	72:28	0:100	93:7
chi squared	18.4	96.0	70.0
P	<0.001	<0.001	<0.001
Dark phase (6 lux)			
no. +:no. −	65:31*	0:96	96:0
% +:% −	68:32	0:100	100:0
chi squared	12.0	96.0	96.0
P	<0.001	<0.001	<0.001
Triturus cristatus			
Light phase (800 lux)			
no. +:no. −	21:75	1:95	78:18
% +:% −	22:78	1:99	81:19
chi squared	30.4	92.0	37.5
P	<0.001	<0.001	<0.001
Dark phase (6 lux)			
no. +:no. −	65:31	0:96	96:0
% +:% −	68:32	0:100	100:0
chi squared	12.0	96.0	96.0
P	<0.001	<0.001	<0.001
Salamandra salamandra			
Light phase (500 lux)			
no. +:no. −	25:71	0:96	92:4
% +:% −	26:74	0:100	96:4
chi squared	22.0	96.0	80.7
P	<0.001	<0.001	<0.001
Dark phase (6 lux)			
no. +:no. −	44:52	0:96	96:0
% +:% −	46:54	0:100	100:0
chi squared	0.7	96.0	96.0
P	>0.1	<0.001	<0.001

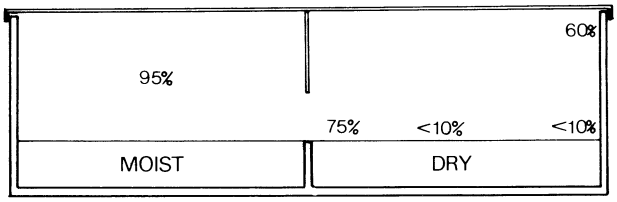


FIG. 1. Relative humidities in a moist–dry choice chamber.

DISCUSSION

The photopositive response of *T. vulgaris* and photonegative responses of *T. cristatus* and *S.*

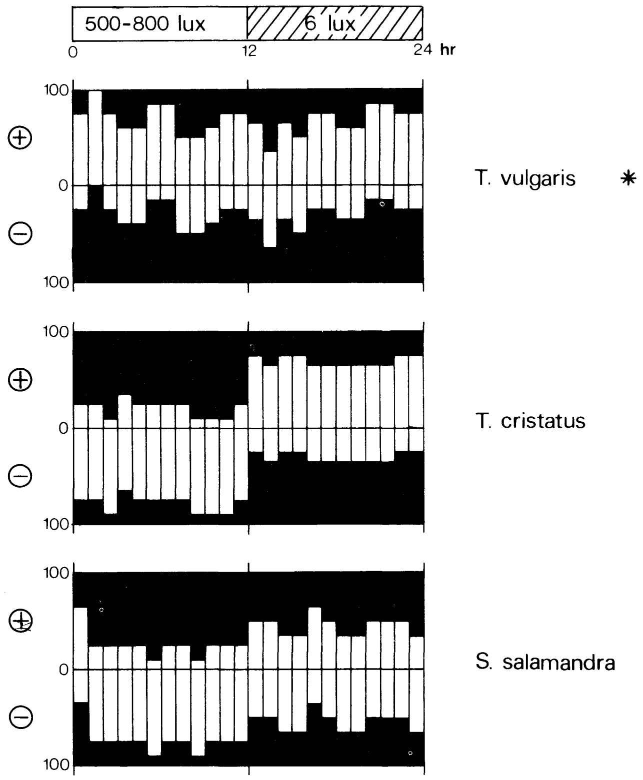


FIG. 2. Distribution of responses to ambient light conditions across a diel cycle. Photoperiod is indicated by the bar at the top of the Figure. Number of photopositive and photonegative scores were summated separately for each hour of the LD cycle and each expressed as a percentage of the total number of responses. Responses are indicated by percentages photopositive (+) and photonegative (−). * from Griffiths (1983).

salamandra under moist conditions and 500/800 lux are consistent with observations made on both retinal structure (Möller, 1951; Himstedt & Fischerleitner, 1975) and diel activity of these species (Himstedt, 1971; Dolmen, 1976; 1983). Grüsser-Cornehls & Himstedt (1976) point out that as the percentage of rods in the retina increases so does the degree of nocturnal activity, and the present results confirm that photonegativity increases in the same order, *i.e. T. vulgaris, T. cristatus, S. salamandra.* Muntz (1963), assuming that the retina of *S. salamandra* lacked green rods, found this species to be less sensitive to blue light than *T. cristatus.* Whilst confirming that the eye of *S. salamandra* is better adapted for vision in dim light, Grüsser-Cornehls & Himstedt (1976) state that there are no marked differences in the response to blue light between this species and *Triturus* spp. The assumption that the retina of *S. salamandra* contains no green rods is considered to be questionable by these authors, and they estimate that one-tenth of rods may be of this type.

In chambers offering a choice of dry or moist conditions the behaviour of all three species was similar—moist areas were selected whatever the ambient light intensity or phase of the diel cycle. As far as microhabitat selection is concerned, moisture is therefore a more significant factor than light. Testing several animals together, Anderson (1972) found that *Ambystoma macrodactylum* was strongly photonegative on both uniformly moist or dry substrates and that the response was retained, possibly to the deteriment of the salamander, even in a light moist–dark dry choice chamber. When kept in groups, however, salamanders may reduce desiccation by forming aggregations and this may affect phototactic responses.

Although both visual and olfactory stimuli may be employed by newts and salamanders in orientation (*e.g.* Czeloth, 1931; Himstedt & Plasa, 1979; Plasa, 1979), moisture gradients appear to play an important role in microhabitat selection. Under conditions of optimum moisture, phototaxis may be important in seeking terrestrial refugia and timing daily activity cycles, but under dry conditions moisture-seeking behaviour becomes all-important and overrides other behavioural responses.

ACKNOWLEDGEMENTS

I would like to thank Professor J. L. Cloudsley-Thompson and Dr S. P. Gittins for their comments on the original manuscript. The work was carried out whilst in receipt of a SERC research studentship.

REFERENCES

Anderson, J. D. (1972). Phototactic behavior of larvae and adults of two subspecies of *Ambystoma macrodactylum. Herpetologica* **28,** 222–226.

Cole, W. H. (1922). The effect of temperature on the phototropic response of *Necturus. Journal of General Physiology* **4,** 569–572.

Czeloth, H. (1931). Untersuchungen über die Raumorientierung von *Triton. Zeitschrift für Vergleichende Physiologie* **13,** 74–163.

Degani, G. & Warburg, M. R. (1980). The response to substrate moisture of juvenile and adult *Salamandra salamandra* (L.) (Amphibia; Urodela). *Biology of Behaviour* **5,** 281–290.

Dolmen, D. (1976). Diel rhythm of *Triturus vulgaris.* In *Proceedings of the 1st Nordic Symposium on Herpetology* (ed: Hagstrom, T.). *Norwegian Journal of Zoology* **24,** 234.

Dolmen, D. (1983). Diel rhythms of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) in Central Norway. *Gunneria* **42,** 1–34.

Griffiths, R. A. (1983). Ontogenetic changes in phototaxis in the smooth newt, *Triturus vulgaris* (L.). *British Journal of Herpetology* **6,** 301–305.

Grüsser-Cornehls, U. & Himstedt, W. (1976). The urodele visual system. In *The amphibian visual system—a multidisciplinary approach,* 203–266. Fite, K. V. Ed. New York: Academic Press.

Heatwole, H. (1962). Environmental factors influencing local distribution and activity of the salamander *Plethodon cinereus. Ecology* **43,** 460–472.

Himstedt, W. (1971). Die Tagesperiodik von Salamandriden. *Oecologia* (*Berlin*) **8,** 194–208.

Himstedt, W. & Fischerleitner, E. (1975). Die Antworten von Retinaneuronen auf Farbreize bei Urodelen. *Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **79,** 128–147.

Himstedt, W. & Plasa, L. (1979). Home site orientation by visual cues in salamanders. *Naturwissenschaften* **66,** 372.

Jaeger, R. G. (1971). Moisture as a factor influencing the distribution of two species of terrestrial salamanders. *Oecologia* (*Berlin*) **6**, 191–207.

Keen, W. H. (1982). Habitat selection and interspecific competition in two species of Plethodontid salamanders. *Ecology* **63**, 94–102.

Marangio, M. S. & Anderson, J. D. (1977). Soil moisture preference and water relations of the marbled salamander, *Ambystoma opacum* (Amphibia, Urodela, Ambystomatidae). *Journal of Herpetology* **11**, 169–176.

Möller, A. (1951). Die Struktur des Auges bei Urodelen verschiedener Körpergröbe. *Zoologische Jarhbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **62**, 138–182.

Muntz, W. R. (1963). Phototaxis and green rods in urodeles. *Nature, London* **199**, 620.

Pearse, A. S. (1910). The reactions of amphibians to light. *Proceedings of the American Academy of Arts and Sciences* **45**, 159–208.

Plasa, L. (1979). Heimfindeverhalten bei *Salamandra salamandra* (L.). *Zeitschrift für Tierpsychologie* **51**, 113–125.

Stier, T. J. B. (1926). Reversal of phototropism in *Diemyctylus viridescens*. *Journal of General Physiology* **9**, 521–523.

Taub, F. B. (1961). The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. *Ecology* **42**, 681–698.

Test, F. H. (1946). Relations of the red-backed salamander (*Plethodon cinereus*) to light and contact. *Ecology* **27**, 246–254.

Vernberg, F. J. (1953). Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata*. *Ecology* **34**, 55–62.

Vernberg, F. J. (1955). Correlation of physiological and behavior indexes of activity in the study of *Plethodon cinereus* (Green) and *Plethodon glutinosus* (Green). *American Midland Naturalist* **54**, 382–393.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 378–380 (1984)

FECUNDITY OF THE COMMON TOAD (*BUFO BUFO*) AT A LAKE IN MID-WALES

S. P. Gittins, R. I. Kennedy and R. Williams

Department of Applied Biology, UWISY, King Edward VII Avenue, Cardiff CF1 3NU

(*Received* 24 *October* 1983)

SUMMARY

1. The mean fecundity of toads at a lake in mid-Wales was 1344 eggs per female, with a range from 425 to 4796. 2. There was a poor relationship between fecundity and body length. The data suggest, however, that there may be a maximum fecundity for any given body length, and a minimum fecundity of about 450 eggs. Females which might produce fewer eggs than this apparently do not breed. 3. There was no significant relationship between fecundity and age. 4. There were no functional relationships between egg size and body length, age or fecundity.

INTRODUCTION

During the course of an intensive study of the population dynamics of the common toad (*Bufo bufo*) at a lake in mid-Wales (Gittins, Parker & Slater, 1980; Gittins, Steeds & Williams, 1982; Gittins, 1983) aspects of the fecundity of females coming to breed were investigated. Fecundity was studied in relation to body length, age and egg quality.

METHODS

The toads used in this study were collected as road casualties during their breeding migration to Llandrindod Wells Lake, Powys (SO 063605). They were stored deep frozen and before processing, thawed and kept in 70% alcohol at room temperature. Each specimen was given a coded label for individual identification, and a sample of 36 obtained by pooling females collected from 1978 to 1982.

Eggs were obtained via an incision in the body wall of the ventral surface from the cloaca to the base of the rib cage. The ovary was extracted with blunt forceps, and the body cavity washed with tap water to remove any remaining eggs. The eggs were placed in Gilson's fluid (Simpson, 1951) for a minimum of seven days, with intermittent agitation, after which the eggs were counted manually.

Since egg size can be taken as one measure of egg quality (Blaxter & Hempel, 1963), the diameters of samples of 17 eggs from each of 34 females were measured by a Quantimet 800 Image Analyser (Cambridge Instruments). The egg sizes obtained must be treated with some caution as the storage conditions would have influenced their size. However, as the measurements are used to compare samples that were stored under identical conditions the data should be adequate for this purpose.

The dorsal snout–urostyle length was measured for each female and their ages determined as part of a complementary study (Gittins, Kennedy & Williams, in press).

RESULTS

The mean fecundity of the 36 individuals examined was 1344 eggs per female (SD = 808), with a range from 425 to 4796.

There was a significant relationship between fecundity and body length (Fig. 1); however, one point exerts a considerable influence on the regression, and if this point is omitted, the relationship breaks down. There appears to be a maximum limit to the fecundity of a female of a given size, and this maximum limit was calculated by taking the maximum fecundity of a given length but ignoring those that were less than a previous maximum for a smaller size. A plot of maximum fecundities for given lengths (solid circles in Fig. 1) gave a significant regression ($P < 0.01$)

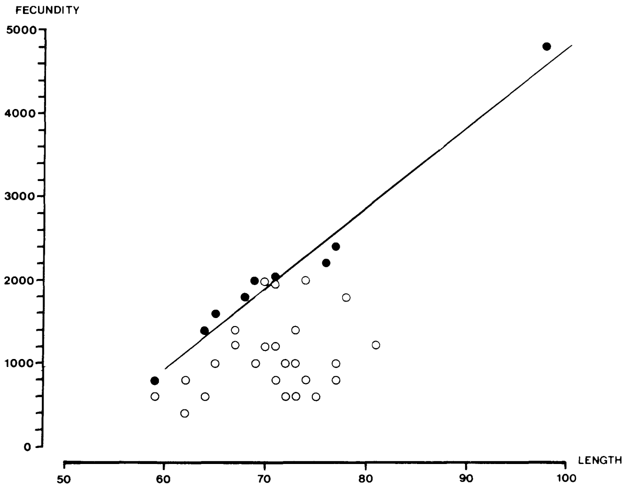


FIG. 1. Plot of fecundity against length. There is a significant relationship between fecundity and length if the unusually large female is included ($r^2 = 0.36$, $F_{1,34} = 20.70$, $P < 0.01$), but the relationship breaks down if this point is omitted ($r^2 = 0.06$, $F_{1,33} = 2.97$, $P > 0.05$). The upper limit of the fecundity for a given sized female is shown as the solid line. The points were selected as described in the text and the regression was significant ($r^2 = 0.97$, $n = 9$, $F_{1,7} = 251.5$, $P < 0.01$).

$$F = 96.7L - 4802$$

where F is fecundity and L is length in mm. There was a minimum fecundity of about 450 eggs. No significant relationship was found between fecundity and age (Fig. 2).

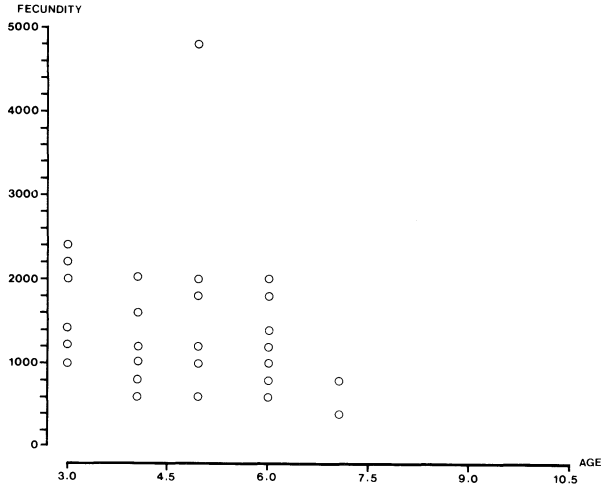


FIG. 2. Plot of fecundity against age. No significant relationship was found between fecundity and age ($r^2 = 0.01$, $F_{1,34} = 1.50$, $P > 0.05$).

Mean egg diameter was 2.1 mm (SD = 0.15 mm) and there was a significant difference between the mean egg diameters of a random subsample of five females ($F_{4,80} = 9.82$, $P < 0.01$). However, there was no significant relationship between egg diameter and body length ($F_{1,32} = 0.040$, $P < 0.05$), age ($F_{1,32} = 1.47$, $P < 0.05$) or fecundity ($F_{1,32} = 0.034$, $P < 0.05$).

DISCUSSION

In many species of fish a curvilinear relationship of the form

$$F = aL^b \quad \text{or} \quad \log F = \log a + b \log L$$

has been found which over a small range approximates to a straight line of the form

$$F = a + bL.$$

A relationship of fecundity against length has been proposed for the toad of the form

$$F = 67.5L - 3317$$

although the relationship was not strong ($r = 0.67$; Davis & Halliday, 1977). On closer inspection of their data it can be seen that two points exert a great deal of influence on the regression and that the other points do not appear to be in a particularly linear form; this would be a similar situation to the findings reported here.

It was postulated earlier that a maximum fecundity depending on the size of the toad existed, probably representing the maximum number of eggs that can be fitted into the body cavity. However, this maximum was not always attained and fecundity for a given size could vary down to a minimum of about 450 eggs. This minimum is probably a result of females which do not obtain sufficient resources to produce the minimum number refraining from breeding, as the risks of dying during the breeding migration outway the benefits of producing only a small number of offspring. Thus, from this study it appears that female fecundity in the toad is best described by a triangular zone (Fig. 1) rather than a straight line or a curve.

Egg quality as well as egg number must be taken into account when considering reproductive ability. Egg size can be taken as one measure of egg quality, and egg size was found to differ between female toads. These differences, however, could not be explained in terms of the size of the female, her age or her fecundity, so other factors must be sought.

Toads have a high fecundity and show a typical '*r*' strategy of high egg numbers with no parental care. When conditions are favourable toad numbers should increase rapidly, but the population at the lake has remained constant over a five year period (Gittins, 1983). The potential for increase is kept in check by high larval mortality, which is in the region of 94% at the lake (Gittins, unpublished data). Also many females appear to breed submaximally, possibly because of intra-specific competition for resources that could limit fecundity in a density-dependent way.

ACKNOWLEDGEMENTS

This project was sponsored by the Natural Environment Research Council. We would like to acknowledge the support of the Llysdinam Charitable Trust, Powys County Council and the following for their help in collecting the samples: J. D. Harrison, J. R. Langford, R. S. Key, P. H. Kirkland, A. Parker, L. M. Paull, C. Saxon and P. J. Wisniewski. Dr J. Fry demonstrated how to use the Quantimet Image Analyser.

REFERENCES

Blaxter, J. H. S. & Hempel, G. (1963). The influence of egg size on herring larvae (*Clupea harengus* L.). *Journal du Conseil Permanent International pour l'Exploration de la Mer* **28,** 211–240.

Davis, N. B. & Halliday, T. R. (1977). Optimal mate selection in the toad *Bufo bufo*. *Nature, London* **269,** 56–58.

Gittins, S. P. (1983). Population dynamics of the common toad (*Bufo bufo*) at a lake in mid-Wales. *Journal of Animal Ecology* **52,** 981–988.

Gittins, S. P., Parker, A. G. & Slater, F. M. (1980). Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in mid-Wales. *Journal of Animal Ecology* **49,** 161–173.

Gittins, S. P., Steeds, J. E. & Williams, R. (1982). Population age-structure of the common toad (*Bufo bufo*) at a lake in mid-Wales determined from annual growth rings in the phalanges. *British Journal of Herpetology* **6,** 249–252.

Gittins, S. P., Kennedy, R. I. & Williams, R. (in press). Aspects of the population age-structure of the common toad (*Bufo bufo*) at a lake in mid-Wales. *British Journal of Hepetology.*

Ryan, T. A., Joiner, B. L. & Ryan, B. F. (1981). *Minitab Reference Manual.* Pennsylvania: State University.

Simpson, A. C. (1951). The fecundity of the plaice. *Fishery Investigations, London. Series* 2, **17,** 5.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 380–382 (1984)

NOTES ON THE COMBAT BEHAVIOUR OF THE CALIFORNIA KINGSNAKE, *LAMPROPELTIS GETULUS CALIFORNIAE*, IN CAPTIVITY

D. L. Clark, J. C. Gillingham and A. Rebischke

Department of Biology, Central Michigan University, Mt. Pleasant, Michigan 48859, *U.S.A.*

(*Received* 21 *November* 1983)

SUMMARY

Two male California kingsnakes (*Lampropeltis getulus californiae*) were paired each spring over a three-year-period. Combat behaviour was observed in each instance, and dominance was always established. The *dorsal pin* motor pattern was not predictive of combat bout outcome but the duration of time spent in a superior position was. Subsequent combat episodes at intervals of up to five months resulted in progressively shorter durations.

INTRODUCTION

The highly ritualized combat behaviour of snakes has been well-described (Shaw, 1975; Bogert & Roth, 1966; Carpenter, Gillingham & Murphy, 1976; Gillingham, 1980). Although correlations have been made between the specific incidence of such behaviours and sexual dimorphism (Shine, 1978) its adaptive value has not been established.

Evidence has been presented recently (Gillingham, Carpenter & Murphy, 1983) suggesting that male–

male combat outcome (dominance or subordination) may have an effect on subsequent male–female interactions, *i.e.* successful mating. Therefore, the factors determining dominance may be well worth investigating. We present data here that compare motor pattern frequency with combat outcome.

RESULTS AND DISCUSSION

Two adult (Table I) male California kingsnakes (*Lampropeltis getulus californiae*), purchased locally, were paired and observed each spring between 1980 and 1982. The snakes were otherwise maintained individually in wooden glass-fronted cages (40 × 30 × 31 cm) with incandescent lighting and an LD 12:12 photoregime. Water was always available and the snakes were offered white laboratory mice weekly. Pairings for behavioural observations were made in an indoor wooden enclosure (2.5 × 2.5 × 0.5 m) with pea gravel substrate under incandescent lighting. All combat episodes were recorded on videotape for later analysis using an Esterline–Angus event recorder.

TABLE I. Snout-vent length and mass of experimental animals as measured in March 1981

Snake number	Snout-vent length (mm)	Mass (g)
LGC1	1160	526
LGC2	1070	514

The following motor patterns were observed and their descriptions either closely follow or are modifications of those of Carpenter & Gillingham (1977) for the speckled kingsnake, *Lampropeltis getulus holbrooki*:

1. *Dorsal pin*—head and neck of one individual is slightly curved, lifted above and brought down against opponent's head and trunk region.
2. *Stiffening*—one or both individuals suddenly straighten the trunk and tail while entwined, usually resulting in body separation.
3. *Biting*—one individual would rapidly bite and release the other in the head, neck or trunk.
4. *Inferior position*—individual shows no other motor pattern other than being in a position beneath opponent.
5. *Superior position*—individual shows no other motor pattern other than being in a position above opponent.

The progression of the eight combat episodes observed over the three-year period was similar to that described by Carpenter & Gillingham (1977). Following initial

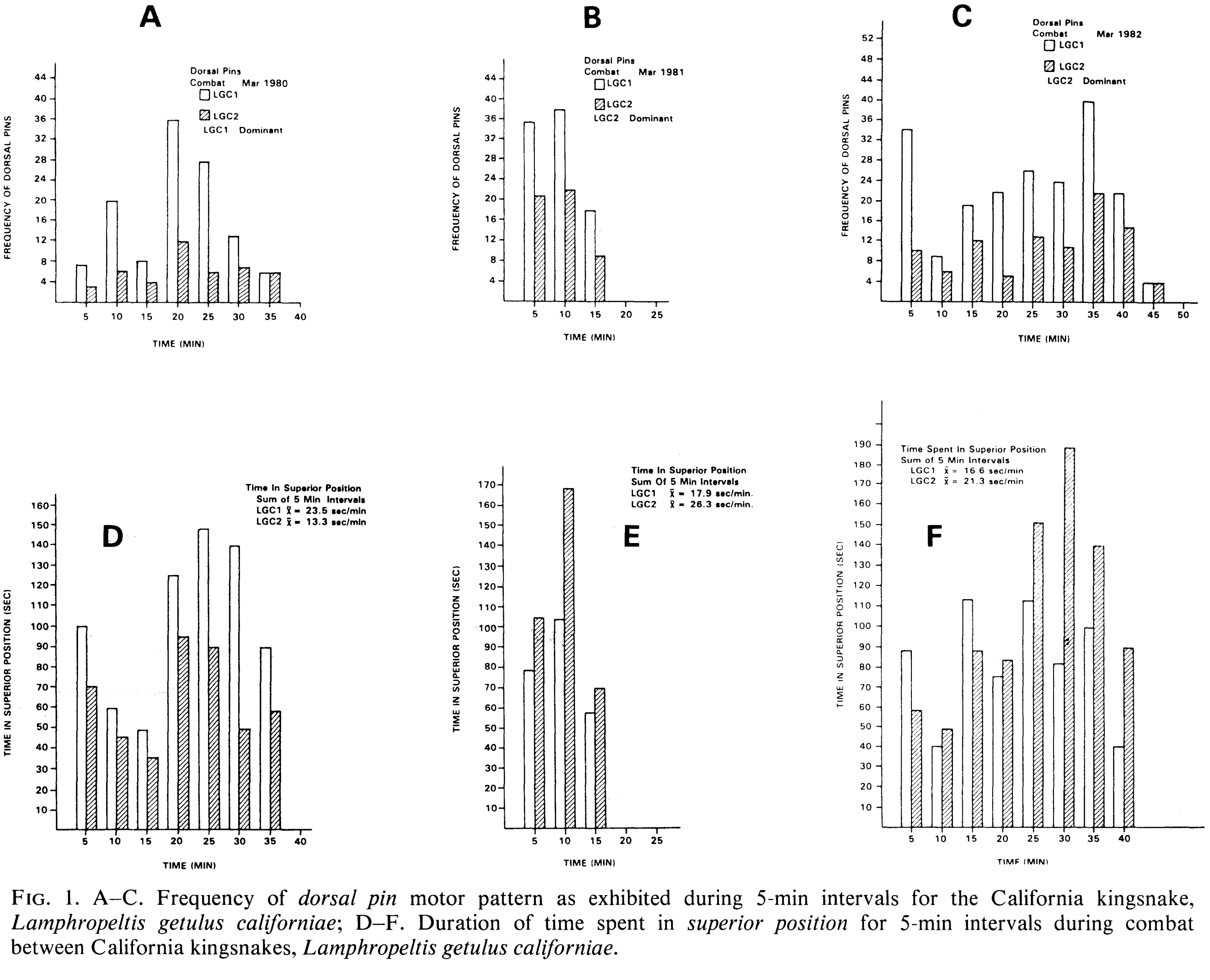


FIG. 1. A–C. Frequency of *dorsal pin* motor pattern as exhibited during 5-min intervals for the California kingsnake, *Lamphropeltis getulus californiae*; D–F. Duration of time spent in *superior position* for 5-min intervals during combat between California kingsnakes, *Lamphropeltis getulus californiae.*

contact the snakes proceeded to interact with a series of reciprocal *dorsal pins* resulting in an intertwining of their trunks. Periodically, following a sudden stiffening by one or both individuals simultaneously, they separated and began anew. Combat behaviour was observed until one individual exhibited a rapid retreat, followed by some pursuit by its opponent. No further combat-typical motor patterns were then observed. The combat interactions averaged 24.8 min in duration (range = 8.0–55.0, $N = 8$, SE = 16.1). Snake LGC1 emerged as the dominant in 1980 while LGC2 established dominance in 1981 and 1982.

A comparison of the motor pattern frequency exhibited by the dominant and the subordinate individual was quite revealing. Regardless of outcome it appeared that the exhibition of the *dorsal pin* motor pattern is dependent on the individual. Snake LGC1 showed a consistently higher frequency of the *dorsal pin* in each combat episode recorded over the three-year period (Fig. 1A–C). The use of this aggressive motor pattern by a particular snake may only be a reflection of individual variation. Although our sample is too small for statistical analysis, the *dorsal pin* frequency is certainly not predictive of combat outcome.

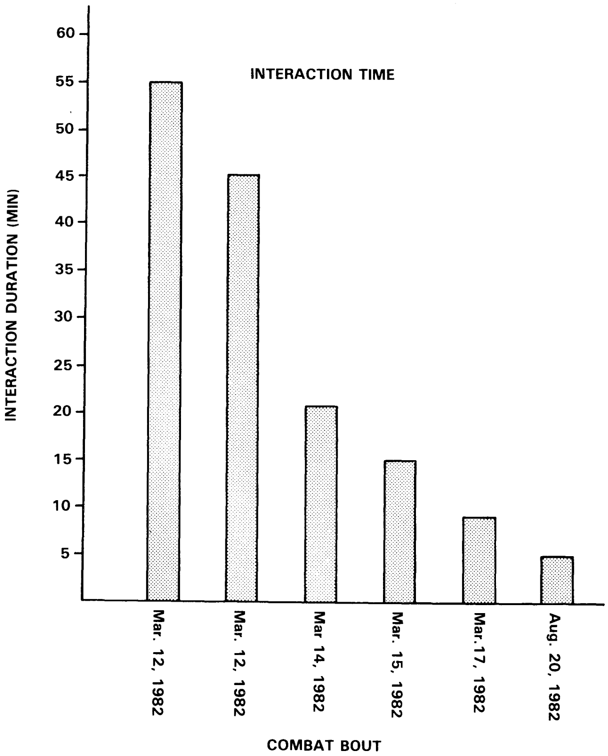


FIG. 2. Combat bout duration as measured in six consecutive pairings during 1982.

On the other hand, the relative amount of time spent in a *superior position* was predictive of combat outcome. Consistently, in all combat episodes analysed, the individual showing the greater duration of time in a *superior position* was the resulting dominant (Fig. 1D–F). Again, although the sample is small, greater competitive ability may be expressed by a snake's efficacy at maintaining this position.

A series of snake pairings were conducted following the first (March 12) interaction of 1982, all leading to the establishment of dominance. The first was 6 hr later on the same day and four more at various intervals thereafter (Fig. 2). Interestingly, each subsequent combat bout was shorter than its predecessor. An abbreviated bout even occurred after a five-month interval. Although certainly not confirmed by the sample herein, this may indicate that the two snakes were familiar with one another and perhaps recognized each other as individuals.

Although further study is definitely in order, our preliminary data indicate that certain motor patterns may be highly variable across individuals and others may communicate more information between individuals and perhaps be predictive of combat behaviour outcome. Finally, individual recognition is certainly a possibility in this species.

REFERENCES

Bogert, C. M. & Roth, V. D. (1966). Ritualistic combat of male gopher snakes, *Pituophis melanoleucus affinis* (Reptilia, Colubridae). *American Museum Novitiates* **2245,** 1–27.

Carpenter, C. C. & Gillingham, J. C. (1977). A combat ritual between two speckled kingsnakes (*Lampropeltis getulus holbrooki*: Colubridae, Serpentes) with indications of dominance. *Southwestern Naturalist* **22,** 517–524.

Carpenter, C. C., Gillingham, J. C. & Murphy, J. B. (1976). The combat ritual of the rock rattlesnake, *Crotalus lepidus*. *Copeia* **1976,** 764–780.

Gillingham, J. C. (1980). Communication and combat behavior of the black rat snake (*Elaphe obsoleta*). *Herpetologica* **36,** 120–127.

Gillingham, J. C., Carpenter, C. C. & Murphy, J. B. (1983). Courtship, male combat and dominance in the western diamondback rattlesnake, *Crotalus atrox*. *Journal of Herpetology* **17,** 265–270.

Shaw, C. E. (1951). Male combat in American colubrid snakes with remarks on combat in other colubrid and elapid snakes. *Herpetologica* **7,** 149–168.

Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia, Berlin* **33,** 269–277.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 383–384 (1984)

A NOTE ON THE CAPTIVE BREEDING OF THE BOX TURTLE *CUORA AMBOINENSIS* (DAUDIN, 1802)

RICHARD INSKEEP

26 Luxor View, Leeds LS8 5JT

(*Received* 5 *July* 1983)

SUMMARY

A description of the husbandry of two young *Cuora amboinensis* is presented. Their housing is detailed along with some notes on their behaviour, breeding, and the growth of a juvenile over a six-month period.

INTRODUCTION

Cuora amboinensis is the most common of the five species that make up this genus of Asiatic box turtles, and is also the type species. It is medium-sized, averaging 20 cm in length. The species has a wide distribution in south-east Asia (Pritchard, 1979).

STOCK

A male was purchased on 4 July 1974 from a local pet shop. At the time it was 55 mm in length (all lengths in this note refer to straight line carapace measurements). It was weighed for the first time on 1 September 1974 when it weighed 55 g and was 60 mm in length. It was kept with other small terrapins until the arrival of a female on 2 December 1976. This was purchased privately and weighed 192 g with a length of 98 mm on arrival. The two animals were kept together until 1981, sometimes on their own and sometimes with other terrapins. Figure 1 shows details of growth.

MAINTENANCE AND BEHAVIOUR

Since 1979 the pair have been kept in a 90 x 30 x 30 cm aquarium. This is divided by a glass partition 22 cm high to give a land area 28 cm wide at one end. The land area is filled with gravel which is kept dry except when the female is nesting. The aquarium is in a cabinet heated by a domestic hairdryer connected to an aquarium thermostat. The water is not heated separately. This gives a seasonal temperature variation of 18–24°C for the water and 22–28°C for the air.

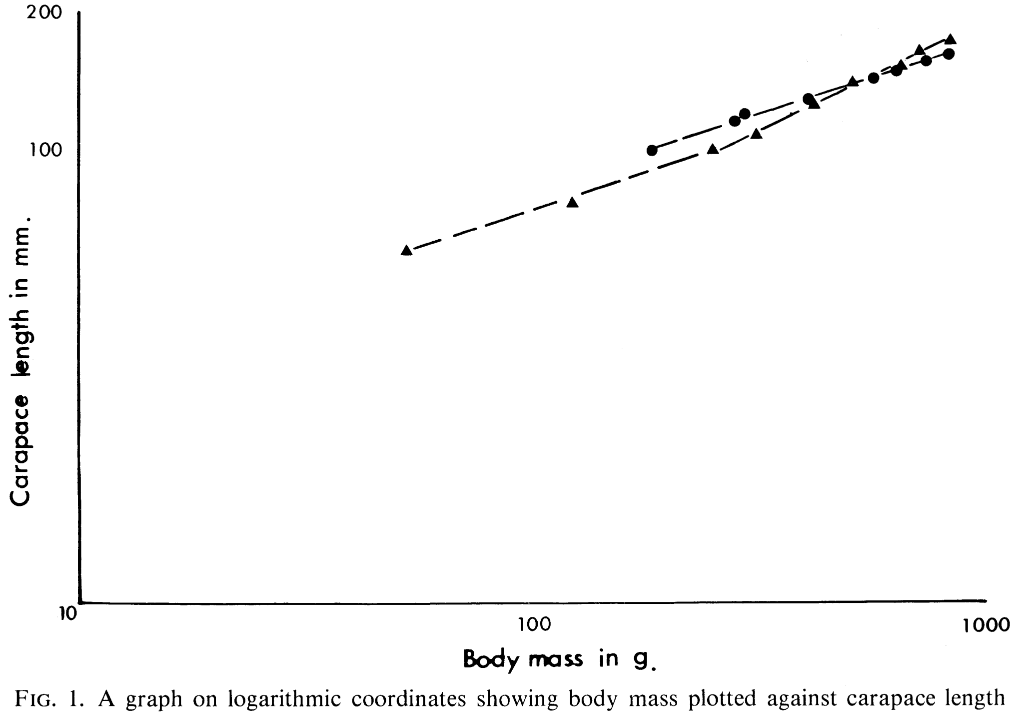


FIG. 1. A graph on logarithmic coordinates showing body mass plotted against carapace length for the two adult *Cuora amboinensis*.

There is also a smaller degree of variation on a daily cycle. It is lit by a 40W spotlamp over the land area and a 25W bulb over the water. These are on for 13 hr per day with no seasonal variation.

Smith (1931) reported this species to be entirely vegetarian in the wild. However, like others, Pritchard (1979) and Olliff (1980), I have found it to be omnivorous in captivity. My pair are fed twice per week, once with tinned dog food and once with whitebait. Lettuce is given occasionally. No supplements are added.

Although normally of mild disposition the male is often aggressive while courting. I have seen no formal courtship display. The male may circle the female a few times but then tries to mate whether she is receptive or not. If she struggles he will bite her neck until she either submits or escapes onto land. This biting has raised large sores on her neck forcing me to separate them, sometimes for months. The female first showed nesting activity during 1981, but no eggs were laid that year. Three eggs were laid in 1982, the first on 4 April and then on 4 May and the 10 June. The first two were laid just under the surface of the gravel and the third in the water.

INCUBATION AND THE HATCHLING

The eggs were incubated in saturated peat at a temperature of 28–29 °C. They were half buried in the peat as soon as they were found. Only one was measured, the third, which was 52 × 26 mm. There was no visible difference in size between any of the three eggs. The humidity in the incubator was 75–80%.

The second egg was found to be chipped on the evening of 17 July 1982. This gives an incubation period of 74 days. The hatchling did not emerge from the egg until late the next day. A brief examination showed it to be a visibly perfect specimen, with the remains of its yolk sac, approximately 5 mm diameter and 2 mm thick, firmly attached to its plastron. The egg tooth was clearly visible and wore away gradually over the next ten days.

On removal from the incubator on 19 July it weighed 11 g and the carapace measured 38 × 31 mm. The hatchling refused food for the first two days but once it started feeding it grew steadily (Table I). It is being fed four times per week on tinned dog food and whitebait.

The remaining two eggs did not hatch.

TABLE 1. Hatchling growth data taken at four-week intervals

	Weight (g)	Carapace (length × width, mm)
19.7.82	11	38 × 31
16.8.82	15	45 × 38
13.9.82	18	48 × 41
11.10.82	22	51 × 44
8.11.82	25	54 × 44
6.12.82	30	54 × 45
3.1.83	33	55 × 46

DISCUSSION

I have found little information about the reproductive biology of this species in the literature. Moll (1979) gives a clutch size of 2–4 eggs but does not say how many clutches per year are laid. Ewert (1979) gives an average egg size of 43 × 32 mm which agrees well with Smith's (1931) range of 40–46 × 30–34 mm, but makes my egg of 52 × 26 mm very untypical. Mattison (1982) states that captive breeding is unknown; however, the International Zoo Yearbook's annual list of captive-bred animals shows a total of 13 hatchings in 3 Zoos in 4 years.

ACKNOWLEDGEMENTS

I would like to thank Roger Meek and Noel Inskeep for reading the manuscript and their advice thereon.

REFERENCES

Ewert, M. A. (1979). *Turtles—perspectives and research.* Harless, M. & Morlock, H. (Eds.). New York: John Wiley and Sons.

Mattison, C. (1982). *The care of reptiles and amphibians in captivity.* Blandford Press.

Moll, J. (1979). *Turtles—perspectives and research.* Harless, M. and Morlock, H. (Eds.). New York: John Wiley and Sons.

Olliff, N. J. (1980). Observations of the Malayan box terrapin (*Cuora amboinensis*) in captivity. *Testudo* **1,** 62–69.

Pritchard, P. C. H. (1979). *Encyclopedia of turtles.* T.F.H. Publications Inc. Ltd.

Smith, M. (1931). *Fauna of British India, Vol.* 1. London: Taylor and Francis.

International Zoo Yearbook. Vol. 17–18–19–21. Zoological Society of London.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 385–386 (1984)

HERMANN'S TORTOISE (*TESTUDO HERMANNI ROBERTMERTENSI* WERMUTH) ON MINORCA, BALEARIC ISLANDS (SHORT NOTE)

C. J. Raxworthy

Department of Zoology, Bedford and Royal Holloway Colleges, University of London, Surrey TW20 0EX

(*Received* 18 *July* 1983)

The distribution of Hermann's tortoise of the western Mediterranean, *Testudo hermanni robertmertensi* Wermuth, 1952 (type locality: mountains north of Artá, Mallorca, Baleares) now only includes Mallorca and Minorca of the Balearic Islands (Lopez Jurado *et al.*, 1979). The subspecies has been recorded in the south-eastern half of Minorca and an area of maximum density delimited which includes such localities as Son Cart, Torralba d'en Salort and San Cristobal. An enclave is apparently provided by abundant vegetation cut through by numerous tracks and paths. No measurements or other observations in any detail have apparently been made on the Minorcan tortoises and those here were made during a visit to two localities in the vicinity of Mahon, the principal town, in south-eastern Minorca from late July to early August 1982.

Locality records: 1 male, 28. vii. 1982, 1 km E. of Sant Lluis, by roadside; 16 adults, 1 juv., 31. vii, 1–3, 6–8. viii. 1982, by Trepuca, 1 km S. of Mahon, in and outside villa garden.

Habitats: South-eastern Minorca is predominantly farmland. Small fields are divided up to form a patchwork by thick dry-stone walls, which probably inhibit tortoise mobility. Vegetation in mid-summer was dry with green herbaceous plants only present on roadsides and at the edges of the small fields, which may be used for animal grazing during wetter months. Local people reported often seeing tortoises, especially after rain. The enclosed garden of the Trepuca villa was 30 × 15 m (450 m^2) without normal human access. Half of the area was covered by thick vegetation consisting of *Opuntia* cactus scrub up to 3 m high and the remainder of fruit trees, shrubs, vines, small herbaceous plants and coarse grass tufts. A somewhat neglected garden, human building and other debris was also present.

Within the Trepuca garden habitat, the Moorish gecko, *Tarentola mauritanica* (L.), and Italian wall lizard, *Podarcis sicula* (Rafinesque), were also observed.

Behaviour: The tortoise near Sant Lluis (carapace length 140 mm) was observed feeding at 07.30 hr, moving along the roadside until 09.00 hr when refuge from sunshine was sought in the verge undergrowth and the tortoise remained immobile until at least 16.00 hr. The origin of the tortoises in the Trepuca villa garden was unclear, but they were probably present in this area of habitat before a dry-stone wall was built around them. With shade provided by the dense vegetation of *Opuntia*, the tortoises remained active throughout the day in contrast to those in the fields in which refuge from sunshine was sought during the hottest hours. Two dried-up corpses were observed in the fields, and two live tortoises recorded outside the garden were in the shade of an orchard and a large patch of *Opuntia* in a nearby field. The tortoises sought refuge at night in two chambers within the dry-stone walls. Fourteen adults were removed from them one evening with the females towards the rear and males by the entrance, perhaps indicating that evening refuge is sought earlier by females than males. Two nights of cool, damp weather after evening thunderstorms on 7 and 8 August 1982, caused the tortoises to vacate the chambers and seek refuge deep in the undergrowth of the *Opuntia* scrub. Bite marks indicated that the tortoises ate the soft fleshy pads of *Opuntia*; unripe grapes within their reach were also seen to be eaten, but many other herbaceous plants were also probably fed upon. Attempts at mating by the males were observed on 6 August 1982 between about 10.00 and 11.00 hr and the one juvenile tortoise found (carapace length 60 mm) with four scute growth annuli indicated some breeding.

Colour and appearance: The carapaces of the tortoises found in the fields were of the typical yellow or beige background colour, but those in the enclosed villa garden were lime green and, the tortoises probably being old, abraded smooth from probable rubbing against the dry-stone walls.

Measurements: The weight and carapace length, sex and maturity were recorded in nine of the tortoises in the Trepuca garden population (Table I). Weights in males were up to 1250 g (carapace length 170 mm) and females 1400 g (carapace length 180 mm). Individuals outside the garden included a female (carapace length 170 mm) trapped in a walled orchard and weighing only 980 g.

TABLE 1. Size/weight frequency of enclosed Trepuca garden tortoises, near Mahon. Juveniles (juv.), males (m) and females (f) are indicated.

Carapace length (mm)	Weight (g)					
	< 500	< 750	< 1000	< 1250	< 1500	Totals
< 100	1 juv.					1
< 125						0
< 150		2 m				2
< 175			2 m	1 f	1 m	4
< 200					2 f	2
Totals	1	2	2	1	3	

Within the week of observations, about half of the Trepuca garden tortoises were probably observed and the population estimated at perhaps 30, *i.e.* a density equivalent to approximately 667 ha^{-1}.

DISCUSSION

It is possible that the size of *Testudo hermanni* Gmelin increases from west to east. In the Albérès of NE Spain, of a total of five tortoises measured (A. V. Vroom, unpublished), the carapace length of the largest female was 150 mm (weight 760 g) and largest (only) male 125 mm (weight 400 g); in Mallorca, 165 mm and 140 mm, respectively (Kramer & Vickers, 1983); in the Maures (Var) of southern France, 171 mm and 148 mm, and on Corsica and Sardinia, 245 mm and 180 mm, respectively (Cheylan, 1981). In the present work, the two largest females had a carapace length of 180 mm (weights 1280 and 1400 g, respectively) and the largest male 170 mm. In *T. h. hermanni*, Stubbs *et al.* (1981) recorded the largest female (total 175) to be 200 mm (greatest weight 1650 g) and male (total 455) 188 mm (greatest weight 1400 g) at Alyki in NE Greece, and a Rumanian female of 270 mm and male of 242 mm are given by Cheylan (1981).

A mean density of 55.7 ha^{-1} in *T. h. hermanni* at Alyki in NE Greece was estimated by Stubbs *et al.* (1981) with perhaps over 150 ha^{-1} in the optimal habitat. The roughly estimated density of the Trepuca garden tortoises exceeded this, but a remarkable density, equivalent to ca. 637 ha^{-1} and comparable with the Trepuca garden population, has been recorded in a highly localized population of *Testudo graeca ibera* Pallas in far-eastern Turkey (Lambert, 1981 after D. M. Keith-Lucas, pers. comm.).

The wild populations of tortoises on Minorca are present in a habitat which to date has remained relatively unexploited. Populations of *T. h. robertmertensi* elsewhere in the western Mediterranean are small or severely threatened (Cheylan, in press). Land is inexpensive and areas of habitat could perhaps now be acquired to provide a sanctuary for this subspecies and enable more detailed studies on the population, especially with regard to the increasing threat of tourism and other commercial interests in Minorca.

ACKNOWLEDGEMENTS

Thanks are due to Dr M. R. K. Lambert, member of the IUCN Species Survival Commission Tortoise Group, for commenting on the manuscript.

REFERENCES

Cheylan, M. (1981). Biologie et ecologie de la tortue d'Hermann *Testudo hermanni* Gmelin, 1789. Contribution de l'espece a la connaissance des climats quarternaires de la France. *Memoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes*, no. 13, 1–404.

Cheylan, M. (in press). The true status and future of Hermann's tortoise *Testudo hermanni robertmertensi* Wermuth, 1952 in western Europe. *Proceedings A of the 2nd European Chelonian Symposium* (*II. Symposium Chelontologicum Europaeum*), *Oxford 1981. Amphibia-Reptilia Supplement.* In press.

Kramer, T. & Vickers, B. R. (1983). *Testudo hermanni robertmertensi* Wermuth on Mallorca (Balearic Is.). In *Proceedings B of the 2nd European Chelonian Symposium* (*II. Symposium Cheloniologicum Europaeum*), *Oxford 1981. Testudo* **2**, 7–11.

Lambert, M. R. K. (1981). The Mediterranean spur-thighed tortoise, *Testudo graeca*, in the wild and in trade. In *Proceedings of the European Herpetological Symposium, Oxford 1980*, 17–23. Coborn, J. (Ed.). Burford: Cotswold Wild Life Park.

Lopez Jurado, L. F., Talavera Torralba, P. A., Ibanez Gonzales, J. M., Macivor, J. A. & Garcia Alcazar, A. (1979). *Las tortugas terrestres* Testudo graeca *y* Testudo hermanni *en Espana*. Naturalia Hispanica no. 17. Madrid: I.C.O.N.A.

Stubbs, D., Hailey, A., Tyler, W. & Pulford, E. (1981). *Expedition to Greece 1980: A Report.* London: University of London Union Natural History Society.