BRITISH JOURNAL OF HERPETOLOGY

Volume 5, No. 9 December 1977

Published by

THE BRITISH HERPETOLOGICAL SOCIETY

and edited on behalf of the Society by

H. Fox and M. Peaker

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The *British Journal of Herpetology* is published twice a year and is issued free to members. Applications to purchase copies and/or for details of membership should be made to the Hon. Secretary, British Herpetological Society, c/o The Zoological Society of London, Regent's Park, London NW1. Instructions to authors are printed on the back cover; contributions should be addressed to the Editor, Dr M. Peaker, A.R.C. Institute of Animal Physiology, Babraham, Cambridge.

CORRIGENDUM

On page 598, Vol 5 (8), the names of the present joint secretaries of the Society should be shown as P. A. W. Bennett and M. R. K. Lambert.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 641–647

THERMAL BALANCE IN THE TORTOISE AND ITS RELEVANCE TO DINOSAUR EXTINCTION*

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(*Received* 15 *October* 1976)

INTRODUCTION AND REVIEW

Extinction is one of the great evolutionary processes, but it is a baffling phenomenon to analyse and comprehend. It is not difficult to imagine how the driving force of natural selection may result in adaptation and radiation, but is is less easy to understand how changes can be sufficiently extreme to cause the extinction of major taxa, while other co-existing forms are able to survive and respond to the challenge. Of all such problems, that of the extinction of the dinosaurs at the end of the Cretaceous period is undoubtedly one of the most complex and fascinating. The dinosaurs did not all disappear at precisely the same moment, of course, but, from a peak of about 120 genera near the middle of the period, numbers dwindled down to the end of the Mesozoic era, at which time the remaining dinosaurs vanished in company with a number of other major taxa, both terrestrial and marine (Worsley, 1971).

At least a score of different hypotheses have been invoked to explain dinosaur extinction. These include: climatic changes; food problems; disease; parasites; internecine fights; anatomical inadequacy; changes in the composition or pressure of the atmosphere; racial senility; predation by mammals on dinosaur eggs; extermination of herbivorous forms by carnivores which, themselves, then starved; fatal mutations caused by increased cosmic radiation—perhaps resulting from the explosion of a supernova; mountain building; shifts of the pole; changes in the rotation of the earth; floods; draining of the swamps; the smallness of dinosaur brains; gigantism; and suicidal psychoses, etc. (Kurtén, 1968; Swinton, 1970).

During early Cretaceous times the gymnosperms, which had been the dominant form of land vegetation, were gradually superseded by the angiosperms, especially deciduous trees and shrubs. While the suggestion that consequent dietary changes may have resulted in herbivorous reptilian species dying from chronic constipation due to diminution in the number of ferns (Baldwin, 1964) does not require serious consideration, Swain (1974) has suggested that early flowering plants probably contained tannins which the herbivorous dinosaurs found unpalatable. Thus they were forced to range far afield to obtain food palatable enough for them to survive. Like modern reptiles, however, dinosaurs were unable to detect the bitter and poisonous alkaloids which occur in more highly evolved flowering plants and may, consequently, have eaten sufficient either to poison themselves or, at least, to cause the thinning of their egg shells—as DDT has been implicated in the thinning of bird egg shells. The serious flaws in the argument have been exposed by Desmond (1976).

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* An account of this work was given at the Annual General Meeting of the British Herpetological Society on 24 March 1977.

This suggestion is also contradicted by the hypothesis that the bright colours of flowers are warning colours (Hinton, 1973). Mammalian herbivores lack colour vision but, during the Cretaceous, the dominant groups of herbivores were iguanodons and ceratopsian reptiles and, so far as is known, all reptiles possess good colour vision. It is therefore possible that one of the chief selective pressures for the evolution of brightly coloured flowers may have come from herbivorous dinosaurs, and this could scarcely have occurred if they had been unable to detect the poisonous chemicals concerned.

Most of the hypotheses listed above are obviously untenable, and the phenomenon of extinction was so widespread that it must surely have been associated with some global change, probably of a climatic nature (Axelrod and Bailey, 1968).

The disappearance of the dinosaurs at the end of Mesozoic era has been explained by a general rise in the temperature of the world (Wieland, 1942). This may not have been of sufficient magnitude to appear in the geological record; nevertheless, it could have brought about the end of numerous lines of reptilian evolution, possibly through heat-induced sterility (Cowles, 1945) or the destruction of young of intermediate sizes (Cowles, 1949). According to Bellairs (1957) the early therapsid reptiles, vacillating between reptilian ectothermic and mammalian endothermal control, had not yet acquired effective cooling devices, such as sweat glands, and were therefore unable to withstand prolonged high temperatures.

Other authorities feel that extinction is a complex phenomenon hardly to be explained by temperature alone. Additional factors, such as increased aridity, changes in food supply, competition caused by the increase of the mammals and so on, should also be taken into account (Colbert, Cowles and Bogert, 1946; Colbert, 1962). Nevertheless, temperature must have played a very important part in directing the course of evolution.

The "sail" of the extinct Pelycosauria (Synapsida) may have been a device for absorbing solar heat in the Permian mornings and for radiating it again when the animals became overheated; the numerous grooves in the spines suggest that the skin covering it may have been well supplied with blood vessels (Bellairs and Attridge, 1975; Rodbard, 1949; Romer, 1948). This hypothesis has recently been supported by the calculations of Bramwell and Fellgett (1973) which showed not only that the "sail" could have enhanced heat gain, but it would also have been capable of radiating heat. Similarly, the dorsal plates of the dinosaur *Stegosaurus* probably served as forced convection fins (Farlow *et al.*, 1976).

Many authors have argued that the dinosaurs were probably homoiothermic (Bakker, 1971, 1972; Desmond, 1975; Heath, 1968; Ostrom, 1969; Ricqlès, 1972) while others have disputed their arguments, or claimed that the dinosaurs were ectothermal (Bennett and Dalzell, 1973; Feduccia, 1973; Thulborn, 1973). Certainly, they were not very speedy (Alexander, 1976), but bulk, alone, is quite sufficient to retard the dissipation of environmentally acquired heat (Colbert *et al.*, 1946; Spotila *et al.*, 1973).

For over 100 million years before their demise, the dinosaurs enjoyed equable climatic conditions. At the end of the Cretaceous, however, the seasons became accentuated, as indicated by the rise of the angiosperms with their deciduous foliage and over-wintering seeds. In 1965, Russell proposed that winter temperatures eventually fell low enough to kill such land animals as could not conserve their body warmth, and did not hibernate. This might explain why the dinosaurs died out, while crocodiles and other reptiles that were not warm-blooded managed to survive. The dinosaurs flourished in warm temperate conditions because they had evolved a degree of endothermicity, even though their bodies were not insulated by protective coats. Thus, they were probably betrayed by a slow climatic change which their peculiar physiology could tolerate only to a certain critical point.

This intriguing suggestion, however, fails to explain why the dinosaurs did not persist in equatorial regions or why ichthyosaurs, plesiosaurs, and pterosaurs, which are known to have been hairy (Sharov, 1971), should also have died out, while the turtles and crocodiles survived. At the end of the Cretaceous period, there was a great reduction in the abundance of marine phytoplankton (Tappan, 1968) which would have affected adversely the larger animals indirectly dependent on it, while the pterodactyls might have suffered from competition with flying dinosaurs or birds. It is often suggested that the dinosaurs died of cold (Bakker, 1972) or of heat stress (Cowles, 1945; Wieland, 1942) and the object of the research described below has been to determine which of these alternatives (Axelrod and Bailey, 1968) is the more likely to have been correct. Was it the cold winters or the hot summers that affected them more adversely when the climate of the world became seasonal?

In comparison with the dinosaurs of the Cretaceous, modern reptiles are mostly small and poikilothermic. They are therefore able to evade inclement seasons by aestivating or hibernating in secluded retreats. In addition to behavioural temperature regulation, however, they are known to utilise a number of physiological thermoregulatory processes (Cloudsley-Thompson, 1971) including the emergency cooling of the body of tortoises through salivation and urination (Cloudsley-Thompson, 1970).

The elongated shape and comparatively small size of most existing reptiles, however, renders prolonged homoiothermy uneconomical, and even the large Indian python only "shivers" when brooding its eggs (Hutchison, Dowling and Vinegar, 1966). Small mammals, such as shrews, must eat nearly all the time in order to maintain homoiothermy. Of existing reptiles, the tortoise is one of the more bulky and therefore, in relation to its mass, has a surface to volume ratio that approximates most nearly to that of a dinosaur. We have, therefore, carried out a number of experiments, during the last three years, to determine the relationship between evaporative heat loss and metabolic heat production at different ambient temperatures in the Mediterranean spur-thighed tortoise (*Testudo graeca* L.).

METHOD

Simultaneous measurements were made of metabolism and evaporation. Dry air, from which the carbon dioxide has been removed, was pumped through a sealed box containing the tortoise, at a rate of approximately 100 ml per minute: this maintained a dry atmosphere in the box. The emerging air was first passed through a U-tube containing anhydrous calcium chloride to collect the water vapour transpired, and then bubbled through two similar bottles containing 0.1 N barium hydroxide to collect the carbon dioxide. The U-tube was weighed before and after each measurement, to the nearest mg, and the barium hydroxide was titrated with 0.2 N hydrochloric acid to assay the carbon dioxide. The absolute quantity of carbon dioxide exhaled was calculated from the amounts that had reacted in the two bottles. The temperatures of the tortoises were controlled by immersing the box, together with a coil of the inlet tube, in a thermostatically-controlled water bath.

RESULTS

The masses and sexes of the three tortoises were: (a) 310 g (♀), (b) 1420 g (♂), (c) 1780 g (♀). Their metabolic heat production and evaporative heat losses were determined over a range from 16 to 35°C. The results, on suitable scales, are shown in Figs. 1a and 1b. The ordinate of Fig. 1a was based on a metabolic heat generation of 5000 cal per litre of oxygen consumed. Such a figure is the kind to be expected for a carbohydrate diet and puts the metabolic and evaporative heats in approximate equilibrium at the lower end of the temperature range for these medium-sized tortoises.

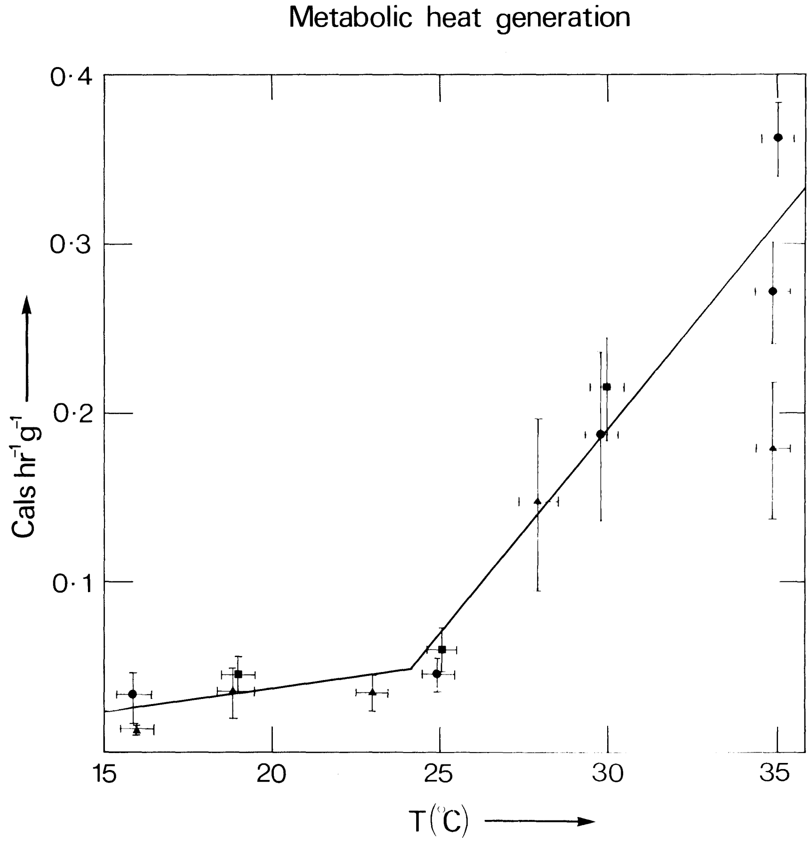

FIG. 1(a).

Because there is some indication from the results that the curve is non-linear and that there is a change of slope at about 24°C, the points were fitted by least square analyses to the two straight lines shown.

The ordinate for Fig. 1b is normalised to mass two-thirds. Such a quantity was used because if the mean density of the reptile is assumed to be constant, independent of mass, then the surface areas would be proportional to it. The distribution of the points in Fig. 1b is represented by a straight line.

The latent heat of vaporisation figures on which Fig. 1b is based were obtained from Kaye and Laby's *Tables of Physical and Chemical Constants* (1966).

From these results it can be seen that, up to about 24°C, the metabolic heat gained and evaporative heat lost approximately keep pace with one another. At temperatures above this, however, there is an excess of metabolic heat production over evaporative heat loss. At 30°C, for a 1500 g tortoise, this excess would be approximately 184 cal hr^{-1}.

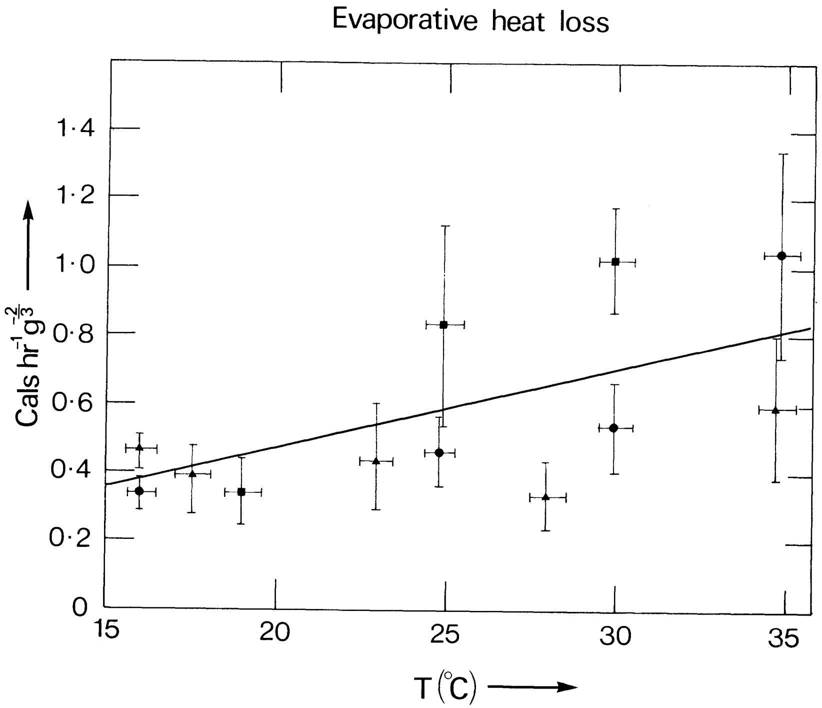

FIG. 1(b).

FIG. 1. Heat generation and loss in *T. graeca* at different temperatures. Points marked ▲ ● and ■ correspond to tortoises weighing 1780, 1420 and 310 g respectively. The vertical bars indicate the Standard Errors.

DISCUSSION

Above about 23°C, the excess heat produced by *T. graeca* must be lost to the environment by conduction and radiation. Even so, measurements of cloacal temperature have shown a mean excess above the ambient of 1.8 K at 33°C (Cloudsley-Thompson, 1974). Thermal excesses of this extent present no problem to animals as small as tortoises. Even the giant *Geochelone elephantopus* thermoregulates by behavioural means (Rodhouse *et al.*, 1975). Terrestrial forms as large as even the smallest of the Upper Cretaceous dinosaurs, however, with their extremely low surface to volume ratios, would certainly have suffered from endothermic overheating at ambient temperatures above about 35°C—even if their metabolic rates were no higher than that of a poikilothermic tortoise. Homeothermy could only have compounded the problem. It is, we believe no accident that no traces of insulating body covering have been found on fossil dinosaurs. Hair would have been disadvantageous to a large dinosaur as it would be to a modern African elephant or hippopotamus!

Calculations have shown that gigantism would be a useful strategy for reptiles in a stable, warm climate, and that thermal stress resulting from decreased equability of climate at the close of the Cretaceous could have been a primary factor in the extinction of dinosaurs (Spotila *et al.*, 1973). Our experiments suggest that the hot summers, rather than the cold winters, would have been responsible for their disappearance, whether the animals were homoiothermic (Ostrom, 1974) or poikilothermic (Feduccia, 1973). Although we subscribed to the former view, this is irrelevant in the present context, for it seems inconceivable that the metabolic rates of dinosaurs should not have been at least as high as those of a slow, solid tortoise!

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NITROGENOUS CONSTITUENTS IN THE URINARY DEPOSITS OF THE LIZARD *CALOTES VERSICOLOR*

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(*Received* 22 *September* 1975)

SUMMARY

Uric acid accounted for 89% of the total nitrogen excreted by the lizard, *Calotes versicolor*. About 1.7% of the nitrogen was in the form of allantoin suggesting the presence of uricase. Urea, ammonia, creatinine and creatine formed minor components of the urinary deposits. Allantoic acid, hippuric acid, amino acids and purines other than uric acid could not be detected.

INTRODUCTION

Many papers have been published on nitrogen excretion in lizards (Weese, 1917; Hernandez and Coulson, 1951; Khalil, 1951; Murthy, 1951, Dessauer, 1952; Seshadri, 1956, 1957; Roberts and Schmidt-Nielson, 1966; Haggag and Hassan, 1968). All these studies have consistently demonstrated that lizards excrete most of their waste nitrogen in the form of uric acid. Most of them, however, were incomplete and showed discrepancies with respect to the excretion of minor nitrogenous products like urea and hippuric acid. Although allantoin excretion has been reported in a few species of lizards (Khalil, 1951; Seshadri, 1956, 1957; Haggag and Hassan, 1968), uric acid is still considered the end-product of purine degradation in lizards (Keilin, 1959; Henderson and Patterson, 1973). This misconception is based on the earlier study of Przylecki (1925) who claimed the absence of allantoin from the urine of lizards. It is therefore necessary to conclusively demonstrate the excretion of allantoin in lizards. While working on certain aspects of nitrogen metabolism in the lizard, *Calotes versicolor*, we also felt that information on the nitrogenous excretory products might give us some clues in planning enzymic and metabolic experiments on this lizard. We therefore carried out a detailed analysis of the nitrogenous constituents in the urinary concretions of this lizard.

MATERIAL AND METHODS

The excretory pellets of the lizard, *Calotes versicolor*, were collected from cages in which these animals were kept in the laboratory, feeding on grass-hoppers. Most of the pellets used in the study were totally devoid of faecal matter. But occasionally when a pellet with faecal contamination had to be used, it was completely freed of the faecal matter before use. Nitrogenous constituents in weighed samples were extracted repeatedly in distilled water, 0.5 M perchloric acid or saturated lithium carbonate solution. The supernatants resulting from the centrifugation of the extracts were pooled and aliquots were used for analyses.

The presence of *urea* and *allantoin* was detected by paper chromatography of the extracts according to the method of Zelc (1963). *Ammonia*, *urea* and *total ninhydrin-*

positive substances were determined in perchloric acid extracts by the methods of Minari and Zilversmit (1963), Campbell, Bonner and Lee (1968) and Rosen (1957) respectively. Water extracts were used for the estimation of *creatine* and *creatinine* by the method of Taussky (1954), and *allantoin* and *allantoic acid* by the method of Young and Conway (1942). Since uric acid interferes with the colour reaction in the latter method, it was removed by boiling the extracts in the presence of 0.2 N nitric acid for 10 min (Moyle, 1949). The extracts were then neutralized and used for the allantoin analyses. Allantoic acid was tested by omitting the step in which allantoin is converted into allantoic acid. *Uric acid* was determined by the method of Steel (1958) in lithium carbonate extracts. Since uric acid is relatively unstable in lithium carbonate (Speeg and Campbell, 1968), uric acid standards were also made in lithium carbonate solution. For the estimation of *total nitrogen*, the pellets were digested at 210°C for 4 hr in the presence of selenomercuric reagent (Filipowicz, Gross and Skoczylas, 1963) in pyrex hard-glass test-tubes in a sand bath (Lang, 1958). After suitable dilution of the digests, ammonia nitrogen was determined by nesslerization (Minari and Zilversmit, 1963). The nitrogen contents determined by this method for 5, 15 and 20 mg of uric acid, which accounts for about 89% of the total weight of the pellets, were respectively 101, 107 and 101% of the theoretical values. For the presence of *hippuric acid* the method of Gaffney, Schreier, DiFerrante and Altman (1954) was used. For the detection of *purines*, lithium carbonate extracts were spotted onto Whatman No. 3 filter paper and chromatographed by the ascending one- and two-dimensional methods employing (1) 0.35 M Na_2HPO_4 saturated with *iso*-amyl alcohol, (2) *n*-butanol saturated with urea and (3) 60% *n*-propanol as the solvents (Carter, 1950; Speeg and Campbell, 1968). After drying, purines on the chromatograms were located by u.v. quenching.

RESULTS AND DISCUSSION

The u.v. absorption spectrum of lithium carbonate extracts of the pellets showed a sharp peak with the extinction maximum at 293 nm which is characteristic of uric acid. The results given in Table I also show that 89% of the total nitrogen excreted by this lizard is in the form of uric acid. Some of the uricotelic invertebrates excrete significant portions of nitrogen in the form of purine bases like guanine, adenine, xanthine and hypoxanthine (Schmidt, Liss and Thanhausser, 1955; Nation and Patton, 1961; Kanungo, Bohidar and Patnaik, 1962; Jezewska, Gorzkowski and Heller, 1963; Mitlin and Wickers, 1964; Speeg and Campbell, 1968; Horne, 1969). Urinary excretion of purines other than uric acid has been reported in lizards, but these were not identified (Khalil, 1951). However, no purine other than uric acid could be detected in the excreta of *Calotes versicolor*. Besides uric acid the only other u.v. absorbing substance detected on paper chromatograms was a bright blue spot with R_f values of about 0.015 in butanol:urea and 0.5 in Na_2HPO_4:*iso*-amyl alcohol. The identity of this substance is not known, but it may be a pterine (Hill and Dawbin, 1969).

Based on the claim of Przylecki (1925) that allantoin is absent from the urine of lizards, it is generally believed that in these animals the enzyme uricase is lacking and uric acid is the end product of purine catabolism (Keilin, 1959; Henderson and Patterson, 1973). However, paper chromatography of water extracts of the excretory pellets of *Calotes versicolor* clearly showed the presence of both allantoin and urea. Allantoin constituted about 1.7% of the total nitrogen excreted by this lizard (Table I). Allantoin excretion in lizards, which has been reported previously in a few species (Khalil, 1951; Seshadri, 1956, 1957; Haggag and Hassan, 1968), is now confirmed. The excretion of allantoin by lizards suggests the presence of uricase in their tissues. Allantoic acid could not be detected in the excreta of *Calotes versicolor*. The enzyme allantoinase is probably absent in the tissues of this lizard and allantoin appears to be the end product of purine degradation in lizards. It should be of interest to study the purinolytic enzymes in the tissues of lizards.

The lizard also excretes minor amounts of ammonia, urea, creatinine and creatine, which together can only account for less than 1.5% of the total excretory nitrogen (Table I). It might appear possible that the minor amounts of urea and ammonia owe their presence to the breakdown of uric acid by enzymes present in the faeces that contaminate the urinary excreta. This possibility, however, is extremely remote because there is not any extensive mixing of the urinary and faecal pellets and the urinary excreta chosen for the analyses were entirely free of a faecal matter. Even this remote possibility is completely ruled out by experiments in which no formation of urea or ammonia could be detected, when water extracts of the faecal matter were incubated with saturated solutions of uric acid in 0.5 M glycine-NaOH (pH 9.5) and phosphate (pH 7.0) buffers at 37°C for 1 hr.

TABLE I. Nitrogenous constituents in the urinary concretions of the lizard *Calotes versicolor*

Nitrogenous constituent	No. of samples analysed	μg nitrogen per g (mean ± S.D.)	% total nitrogen
Total nitrogen	15	332 600 ± 33 300	100.00
Uric acid	15	296 500 ± 28 610	89.19
Allantoin	10	5 513 ± 689	1.66
Ammonia	16	2834*	0.85
Urea	18	1486†	0.45
Creatinine	12	69 ± 9	0.02
Creatine	12	46 ± 6	0.01
Allantoic acid		undetectable	
Hippuric acid		undetectable	
Amino acids		undetectable	
Purines other than uric acid		undetectable	
% total nitrogen accounted for			92.18

* The values showed skewed distribution with a range of 569 to 9126. The modal value is around 3250.

† The values showed skewed distribution with a range of 193 to 4832. The modal value is around 750.

Excretion of ammonia and creatinine has been reported in other lizards (Weese, 1917; Hernandez and Coulson, 1951; Khalil, 1951; Dessauer, 1952). Urea, on the other hand, has been shown to be absent from the excreta of some lizards (Weese, 1917; Khalil, 1951; Seshadri, 1957), but present in that of others (Hernandez and Coulson, 1951; Dessauer, 1952). Our results clearly demonstrate the excretion of urea by *Calotes versicolor* (Table I). Since purine catabolism in lizards seems to go only as far as allantoin, this pathway is not likely to contribute to the formation of urea. All the urea cycle enzymes, with the exception of arginase, are absent from lizard liver (Brown and Cohen, 1960; Mora, Martuscelli, Ortiz-Pineda and Soberon, 1965; Hill and Dawbin, 1969). Hence the urea excreted by *Calotes versicolor* must result from the hydrolysis of exogenous arginine by arginase, which is present in the kidney, liver and brain tissues of this lizard (Reddy and Goel, 1973; Baby, Goel and Reddy, unpublished results).

Khalil (1951) reported the presence of amino acids in the excreta of two species of lizards. Although we could find significant quantities of ninhydrin-positive substances (Rosen, 1957) in the urine of *Calotes versicolor*, no amino acids could be detected by paper chromatography. A synthetic urine, prepared with different nitrogenous constituents in the proportions shown in Table I, accounted for 87% of the total ninhydrin-positive substances determined for the urinary deposits of this lizard (51.9 mg/g expressed as leucine). Hippuric acid also could not be detected in the excreta of this lizard. Hippuric acid was reported to be absent from the urinary pellets of *Chalcides ocellatus* (Khalil, 1951) and *Uromastix hardwickii* (Seshadri, 1957), but present in those of *Scincus officinalis* (Khalil, 1951).

ACKNOWLEDGEMENTS

We thank Prof. Leela Mulherkar, Head of the Department of Zoology, for facilities and encouragement. The facilities of the Departments of Botany and Chemistry are gratefully acknowledged. T.G.B. is the recipient of a Junior Research Fellowship from the University Grants Commission (New Delhi). We also thank Dr S. C. Goel for useful suggestions.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 655–656

THE DISTRIBUTION OF *BUFO VERTEBRALIS HOESCHI* IN THE NAMIB DESERT PARK, SOUTH WEST AFRICA

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(*Received* 1 *October* 1975)

Hoesch's toad occurs throughout South West Africa, and is one of only four anurans known from the Namib Desert Park (Channing, in press). The adults are dorso-ventrally flattened and seldom reach a snout-vent length in excess of 4 cm. Poynton (1964) recognises four subspecies of *B. vertebralis* in South West Africa. We prefer to 'lump' these as *B. v. hoeschi*, as insufficient specimens are presently available and no geographical evidence exists to warrant retaining a number of poorly known subspecies.

Hoesch's toad reaches its westernmost limit in the central Namib, where the rainfall may average less than 25 mm per year. Precipitation is concentrated in the period January to March (Schulze, 1969) with a less important winter season. We have examined the distribution of this anuran to emphasise the role played by topography in the lives of the Namib populations.

The distribution of breeding populations (sites where adults in amplexus, eggs or tadpoles were recorded) and the sites where isolated individuals were collected is presented in Fig. 1.

During dry weather this toad retreats under stones or in cracks under exfoliating granite. Breeding at Bluttkoppie, Tumasberg and Tumasberg South occurs after rains, in pools formed by runoff from large sheets of granite. The granite sheets thus effectively concentrate the minimal precipitation. The toad breeds in shallow sandy-bottomed pools which reach temperatures of 36°C. Development is relatively rapid; only 3 weeks elapse between oviposition and the emergence of young frogs. Although no breeding has yet been observed at Groot Tinkas, further collecting immediately after rains may show that toads do breed there, as the habitat and rainfall are similar to sites at Bluttkoppie where breeding was observed.

Toads in the dry Kuiseb river bed may breed either after floods caused by rains on the highlands, or after local rain. River flow is variable; in 1974 the river flowed for 102 days from 19 January, although in 1975 the river flowed for 6 days from 13 March. At Bluttkoppie, Tumasberg and Tinkas, pools are present for a short period compared to the site at the Kuiseb Bridge.

We expect populations to be found breeding to the west of the kuiseb bridge throughout the canyon bed as far as Homeb. Beyond Homeb the character of the river changes: the rocky canyon walls are replaced by sandy banks with occasional isolated granite outcrops. Less flood water reaches the lower stretches of the river from Gobabeb to the Kuiseb River delta. The record for Gobabeb is best explained either in terms of excessive river floods which are known to transport chelonians (*Pelomedusa*) and fish (*Barbus annoplus*) as well as *Xenopus* tadpoles and adults, or in terms of an escaped animal which was brought to the research station, possibly for photographic purposes, by one of the many visitors. Only one specimen has been collected there, even though one of us lives at Gobabeb.

B. v. hoeschi in the Namib desert is confined to topographic features which provide breeding pools: the bed of the Kuiseb river which drains the wetter highlands, or granite outcrops which effectively concentrate precipitation into small pools.

Isolated collecting records, unsubstantiated by evidence that the animal can and does breed at the site in question, may confuse our understanding of animals living at the extreme limits of their ranges. The use of the quarter-degree grid system, rather than pinpointing exact localities, further misleads further investigations. We recommend that more emphasis be placed on the location of known breeding populations rather than on merely extending the ranges of animals by collecting isolated individuals, especially when such individuals might have been unnaturally carried into an area where they do not occur under normal circumstances and where they cannot survive for prolonged periods.

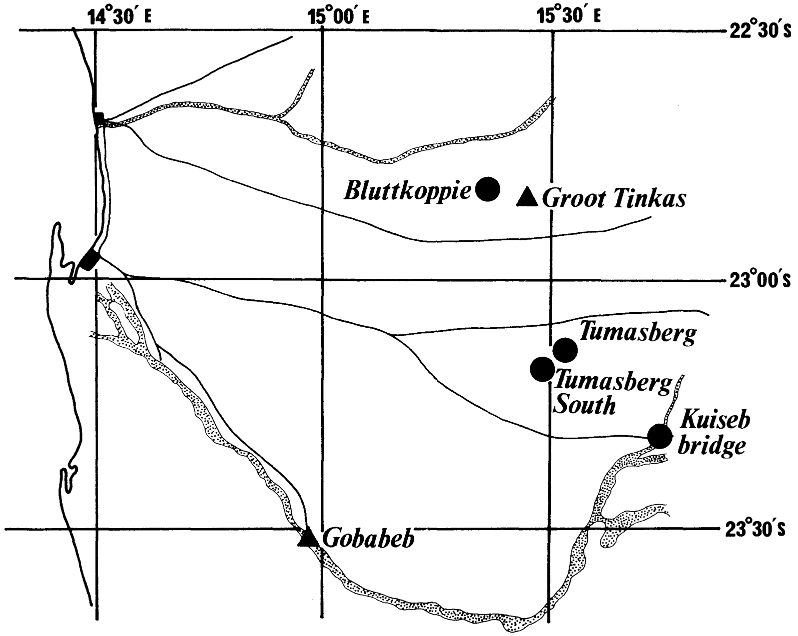

FIG. 1. Distribution of *Bufo vertebralis hoeschi* in the Namib Desert Park. Circles—breeding records; triangles—isolated individuals.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 657–659

FOAM NESTING IN LEPTODACTYLIDS: A POSSIBLE FUNCTION

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(*Received* 5 *October* 1975)

INTRODUCTION

The family Leptodactylidae is represented in Venezuela by seven genera and thirty-three species. *Engystomops pustulosus, Pleuroderma brachyops, Physalaemus enesefae* and all species of *Leptodactylus* lay their eggs in frothy foam nests. *Leptodactylus pentadactylus* makes hollows near the water's edge for the nest (Rivero and Esteves, 1969). *L. marmoratus* covers its foam nest with mud, the tadpoles escaping through a small hole in the roof (Goin and Goin, 1962). *Engystomops pustulosus* and *Pleuroderma brachyops* make foam nests in shallow pools, and *Physalaemus enesefae* lays its eggs in natural depressions at the side of the pools.

In the region of El Manteco, Estado Bolivar, the leptodactylids spawned in June 1974 at the beginning of the rainy season. It was noted that the foam nests of *P. enesefae* were flooded and disintegrated within 3 days of being laid. This paper reports the temperature of the nests of this species, and discusses the possible significance of foam nesting in leptodactylids.

MATERIALS AND METHODS

Data were gathered from a small pool in the rubbish tip of El Manteco during June 1974. The nests of *P. enesefae* were laid in small holes made by cattle and horses. All the data are from foam nests made during the previous night. The temperature was recorded for 2 days at 1400 hr, when the maximum daily air temperature is reached, from the centre of eleven foam nests, from ten adjacent hollows that did not contain eggs, and from a single egg mass of a hylid, probably *Hyla rubra*. The water temperature of the hollows was recorded at a depth of 1 cm. In order to assess the temperature of adult frogs, the air temperature was taken under pieces of wood near the pool. No specimens of *P. enesefae* were found under wood, but adults of *Leptodactylus fuscus* were found. Thus the temperature under wood was used as an indicator of the preferred ambient temperature of leptodactylids in general. Only those records from under pieces of wood that did contain frogs were considered.

RESULTS

There was no significant difference between the temperature of the foam nests (30.8 ± 0.55 S.E.) and the air temperature under pieces of wood (30.1°C ± 0.39), but both of these differed significantly ($P < 0.01$) from the temperature of the water in the hollows (35.5 ± 0.57). The water temperature on both days was slightly below the

FIG. 1. (a) foam next of *Physalaemus enesefae*, (b) eggs of a hylid.

maximum air temperatures of 38 and 37°C. The single hylid egg mass, at 35.2°C, was within the temperature range of water in the hollows. Figure 1 shows an egg mass of the hylid and a foam nest of *P. enesefae*.

DISCUSSION

There was a striking difference between the mean temperature of both the water in the hollows and the eggs of *Hyla* sp. and the temperature of the foam nests. In general, leptodactylids are nocturnal, hiding during the daytime. By contrast, hylids remain in bushes and trees. It might be inferred therefore that the average body temperature of *P. enesefae* would be lower than that of hylids. Brattstrom (1963) has shown that members of the family Leptodactylidae have a narrow body temperature range (22–28.5°C) whereas those of the non-foam nesting families Microhylidae, Ranidae, Hylidae and Bufonidae have a much wider range (15–35.5, 4–34.5, 3.5–33.5 and 3–34°C respectively). The upper values indicate that the preferred body temperatures of some species of these families are often much higher than in leptodactylids.

If leptodactylids have lower body temperatures than other anurans, how would this affect their thermal tolerance? The critical thermal maximum (CTM) of anurans depends on the temperature of acclimation. During June 1974 the ambient temperature was fairly constant from about 1800 to 0600 hr, rising after dawn to reach a maximum between 1400 and 1500 hr. If the body temperature of *P. enesefae* is similar to that of its surroundings, then for a few hours it would reach 30°C but for most of the day it would be near the minimum air temperature (mean 24.8°C in June). Brattstrom (1968) reported that in *Leptodactylus melanotus* from Mexico the CTM is 35.9°C when acclimated at 23°C but that the CTM is increased to 39.8°C when acclimated at 30°C. Since the mean temperature of water in the hollows was 35.5°C, it may be that this temperature was at or near the CTM for *P. enesefae*. Anurans acclimate to higher temperatures within 2 days (Brattstrom, 1968) and if it is assumed that the CTM of newly-laid spawn is similar to that of adult frogs, then the white foam nest, which would reflect heat, slowly disintegrating over 3 days, may serve initially to protect the embryos from thermal damage while at the same time effecting acclimation to higher ambient temperatures.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 661–662

CHANGES IN POPULATION DENSITY OF THE EYED LIZARD, *LACERTA LEPIDA*, AT THREE LOCALITIES IN PORTUGAL BETWEEN 1969 AND 1975

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(*Received* 10 *October* 1975)

Little information is available on changes in the herpetofauna of southern Europe. In this paper population changes of *Lacerta lepida* for localities in Estramadura, Portugal are presented, and an attempt is made to interpret them in relation to alterations in the environment.

The localities were: Serra de Sintra, a steep, south-facing hillside with a varied mosaic habitat of boulders and scrub, floristically rich. Lisbon, Parco Florestal de Monsanto, a shallow, south-facing slope of open grassland with occasional trees and patches of impenetrable scrub (in which sampling was not attempted), floristically poor. Cacem, an undulating area of waste ground mainly with long grass and herbs, floristically rich and located beside an expanding tower block development. At each locality total counts were measured over measured areas of 50 hectares during years between 1969 and 1975 shown in Table I.

TABLE I. Population density of *L. lepida*. Mean ± S.E.

	Locality Number of lizards (per hectare)		
Year	Sintra	Monsanto	Cacem
1969	45.3 ± 2.34	18.7 ± 1.87	35.2 ± 1.65
1971	57.9 ± 2.18	16.1 ± 1.69	37.4 ± 1.92
1973	48.5 ± 2.47	1.3	21.1 ± 1.68
1974	40.0 ± 2.79	0	13.6 ± 2.37
1975	56.8 ± 2.03	0	12.4 ± 2.53

It was found, using the χ^2-test, that the numbers at Sintra had not changed between 1969 and 1975. By contrast, the decreases at Cacem and Monsanto (Table I) were statistically significant ($P < 0.05$).

Sintra may be regarded as a control habitat; the site is remote and undisturbed with a varied habitat that might be expected to sustain high population densities. The population stability indicates that broad climatic changes are not responsible for the decreases elsewhere. Monsanto Park is a more homogeneous habitat, with a simpler structure in terms of vertical layering and plant associations; it might therefore be expected to sustain lower populations than Sintra (Pianka, 1967). Since 1969, the numbers of eyed lizards have fallen to zero (though the scrub stands offer a small potential reservoir). The population of smaller lacertids has also declined to some extent (unpublished observations). The park is a favoured leisure spot for Lisboans, and spot counts on hot July afternoons showed an increase of about thirty picnicking families between 1973 and 1975. This increased usage has caused simplification of the vegetation to a coarse mat, with a lower carrying capacity in terms of food and cover; direct disturbance of basking and food seeking has also occurred. The decreases at Cacem can be correlated with human pressure of a different kind. Tower block development has approached the site during the 6 years up to 1975. Apart from dumped rubbish, no visible changes in vegetation or in the quality of the habitat were apparent. However, the density of potential predators has increased, and feral or semi-feral dogs were seen to chase, capture and eat eyed lizards. It was estimated that the number of dogs plus cats had increased from 0.31 per hectare in 1971 to 1.16 in 1975. This was reflected in increased tail damage amongst the lizards. No decrease in the numbers of smaller lacertids was noted (unpublished) but changes in age structure were apparent. Boag (1973) recorded heavy and increasing predation of feral cats on *Lacerta muralis* in a public garden in Naples.

The eyed lizard, with its high trophic position, low population density and low fecundity, may be more susceptible to environmental changes caused by man than the smaller lacertids. The results obtained are for a limited area and are of low temporal resolution. However, the decreases warrant further investigation and it would seem that particular attention should be focused on this species.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 663–667

OBSERVATIONS ON THE FEEDING BEHAVIOUR AND MOVEMENTS OF THE SNAKES *OXYBELIS AENEUS* AND *O. FULGIDUS*

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Snakes of the colubrid genus *Oxybelis* are common in some neotropical lowland habitats, and their arboreal habits and relatively large size make them especially suitable for behavioural and ecological studies. *Oxybelis aeneus* is one of the few species of neotropical snakes whose ecology has been studied under natural conditions (Henderson, 1974). This report includes the results of observations of the behaviour of *O. aeneus* and *O. fulgidus* in captivity and new information on free-living *O. aeneus*; it permits comparisons between certain aspects of the ethoecology of captive and free-living *O. aeneus* which bear on the validity of studies utilising captive animals.

MATERIALS AND METHODS

We spent about 66 hr observing captive *O. aeneus* and about 41 hr observing captive *O. fulgidus* in a greenhouse on the roof of the Milwaukee Public Museum (see Henderson and Nickerson, 1976). Observations were made at all hours of the day and night, but primarily from about 1500 hr to 1900 hr (local time).

The snakes (13 *O. aeneus*, 4 *O. fulgidus*) were purchased from commercial dealers and were reportedly collected in Guatemala, Honduras, and Costa Rica. Additional observations on free-living *Oxybelis* in Mexico, Belize, Panama and Peru are also included.

RESULTS AND DISCUSSION

Feeding Behaviour

Prey items recorded from *O. aeneus* in the wild have been summarized by Keiser (1967) and *O. fulgidus* probably feeds primarily upon frogs, lizards, birds and, less frequently, small mammals. Both species are cryptic in colour and behaviour and we have observed *Anolis carolinensis* use *O. aeneus* as a perch on several occasions. These snakes typically do not actively forage for prey, but tend to remain more or less motionless waiting for prey movement. *Oxybelis* is visually oriented and olfactory stimuli are apparently of minor importance if indeed they function at all in the detection and location of prey. The characteristic tongue movements of *Oxybelis* were described and discussed by Keiser (1975), among others, and he called attention to the similar behaviour of the African vine snake *Thelotornis kirtlandi*, and he surmised that the trait 'may be associated with the snakes' arboreal habits.' This tongue thrusting trait, though perhaps restricted to arboreal snakes, is not widespread among them; seemingly it is associated with those that are visually oriented and, probably, have acute binocular vision. Whether similar behaviour occurs in the Asian vine snake *Ahaetulla* and the Hispaniolan *Uromacer* has not been recorded. We have made extensive observations of the feeding behaviour of members of the neotropical arboreal snake genera *Imantodes* and *Leptophis* and have never observed *Oxybelis*-like tongue movements. However, *Imantodes* is nocturnal and the snakes can seemingly locate motionless prey through olfactory stimuli (Henderson and Nickerson, 1976). *Leptophis* is primarily diurnal but feeds almost exclusively on nocturnal prey (hylid frogs). Although some of our observations suggest it is oriented to prey motion, its preference for hylids, which ordinarily are inactive by day, must necessitate active foraging, and perhaps olfactory cues are important. Leo G. Hoevers (personal communication) has observed free-living Belizean *L. mexicanus* feed on motionless prey.

After seeing the movement of a potential prey animal (usually an *Anolis* lizard), *O. aeneus* and *O. fulgidus* would begin a slow, deliberate stalk as the animal remained in motion. If the lizard stopped moving, so did the snake, and stalking behaviour resumed when the lizard again became mobile. Hunting snakes seemed unable to visually locate prey that remained immobile and perhaps the tongue movements function to monitor by olfaction prey that is unseen because it is motionless. This hunting technique was occasionally accompanied by side-to-side swaying motions of the head in a 5–10 mm plane and by forward and backward motions of the head. Both of these motions may serve to enhance binocular vision. When the snake had approached to within 150–375 mm of the anole it grabbed the lizard, whether the latter was in motion or not, with a smooth, rushing lunge that appeared almost gentle.

O. aeneus and *O. fulgidus* took prey that was above and below them on vegetation and they were also aware of prey movement on the gound. One large *O. aeneus* became aware of an alligator lizard (*Gerrhonotus*) on the ground 1.3 m below the bush into which the snake had climbed. The snake gradually descended with tongue extended straight out, until its head was 0.5 m above the lizard. The snake then dropped to the ground, catching the lizard's neck at the instant of contact. Anoles captured in bushes likewise were usually seized just behind the head, shifted to the back of the mouth, immobilised, and invariably swallowed head first. Although *Oxybelis* does descend to the ground, it might not deliberately do so to hunt, and terrestrial lizards recorded from stomachs of *Oxybelis* might have been taken while the snakes maintained their arboreal perches or which were initially observed while the snake was in a bush.

Oxybelis aeneus was observed drinking water from large plastic pools on the floor of the greenhouse while hanging in a bush, and also from water beaded on the leaves of bushes and trees.

Field observations in Belize (Henderson, 1974) and in the vicinity of Acapulco, Mexico (Henderson, unpublished) of *O. aeneus* in alert postures by day for 24–48 hr also suggest that it hunts by ambush.

MOVEMENTS

From mark and recapture of free-living *O. aeneus*, Henderson (1974) showed that the horizontal activity range is small compared to that of most other snakes for which data are available, but that if vertical movements of this scansorial snake had been included, activity range size would have increased considerably. For example, if an arboreal snake moved in an area of 3 m × 5 m its horizontal activity range, calculated as an area, would be 15 m^2. But if that same animal also moved in a 3 m vertical range its activity range involved a volume of up to 45 m^3 (this is, of course, an oversimplification). The confines of the greenhouse prevented the snakes from moving more than about 7 m in one direction. Most of the snakes were not left free in the greenhouse for more than a few hours at a time, but on two occasions we left individuals there for extended periods.

An *O. fulgidus* was released in the greenhouse at 0945 hr on 6 December and left until 1320 hr on 8 December. During the 51 hr: 35 min that the snake was free it never descended to the ground and moved in a straight-line, horizontal distance of 1–2 m. It captured and ingested at least three *Anolis carolinensis*. Its vertical movements were greater than its horizontal movements (Fig. 1). After sunset it ascended to a higher perch and descended again some time after sunrise. Henderson (1974) noted similar behaviour in the population of *O. aeneus* studied in Belize.

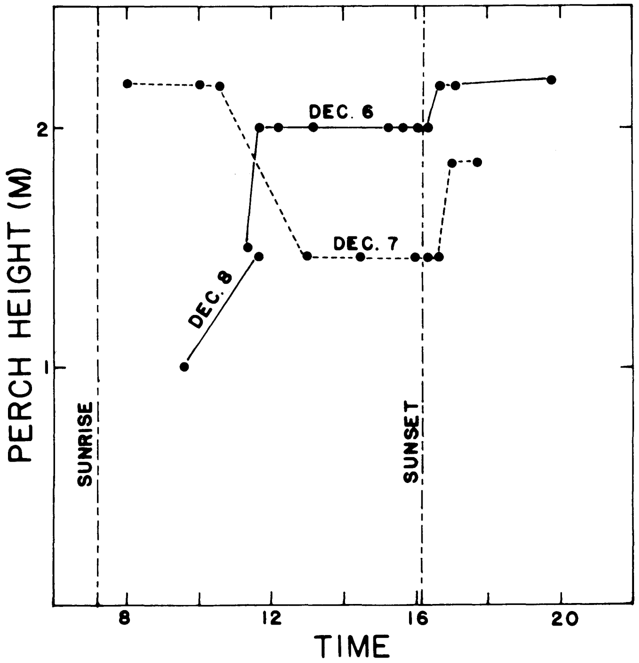

FIG. 1. The vertical position of one *Oxybelis fulgidus* at various hours of the day. See text for details.

On 29 November at 1515 hr an *O. aeneus* was released in the greenhouse. From 1525 hr to 1555 hr it remained in a bush with only slight changes in body position, but apparently it was watching several active anoles. From 1556 hr to 1608 hr it moved about at a height of 1–2 m on five different bushes, all in contact with each other or nearly so. At 1615 hr, at a light intensity of about 10 ft-c it was perched at 2.3 m. At 1630 hr, with 3 ft-c of light, it moved to an adjacent bush. At 1643 hr, with light level down to less than 1 ft-c, the snake assumed a loose-coiled, head down position at the distal end of a branch at the top of a bush (2.3 m) which Henderson (1974) described as a typical sleeping posture for the species. The snake remained in this same position until 0628 hr on 30 November when the head was raised slightly. It remained motionless except for slight movements of the head until 0810 hr (200 ft-c) when it began to slowly descend through the branches. At 0835 hr it had descended to 0.65 m and was in a typical ambush position; shortly thereafter it was removed from the greenhouse.

We have numerous additional observations of *Oxybelis aeneus* ascending to the distal portions of branches at twilight or dark, and assuming a loose-coiled head down posture as described by Henderson (1974) in free-living *O. aeneus* (Fig. 2).

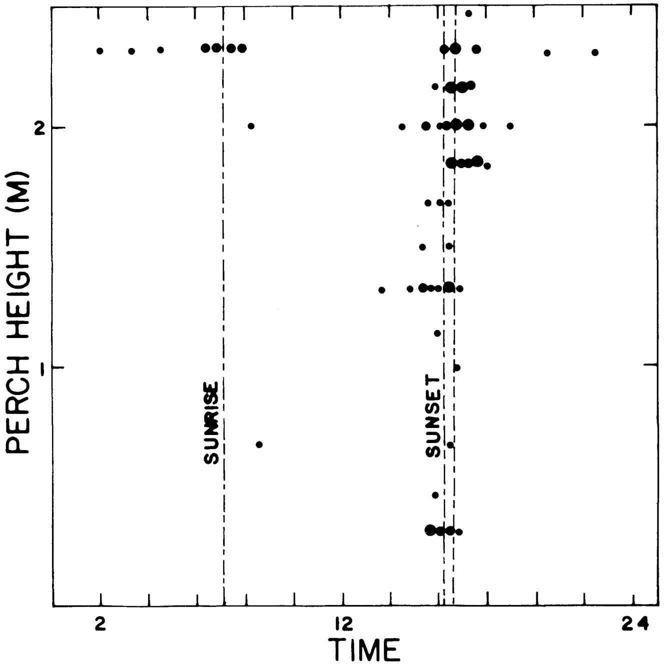

FIG. 2. The vertical position of *Oxybelis aeneus* at various times of the day. Small dots = 1 record, medium dots = 2 records, large dots = 3 records. See text for details.

The horizontal movements of *O. aeneus* are extremely limited. A mean daily movement of 0.72 m was recorded by Henderson for free-living marked individuals in Belize. The snakes probably shift to new locations in search of sites more favourable for ambush when a site occupied has failed to yield prey. Perhaps *Oxybelis* descends to the ground mainly during such shifts to new hunting sites.

Henderson (1974) speculated on the range of vertical movement in *O. aeneus* in a tropical rainforest where opportunity for such movement is great. However, extensive vertical movements are rendered unlikely by the fact that *O. aeneus* does not ordinarily occur in rainforest. Rather, it is associated with the forest periphery. For example, Harry W. Greene (personal communication) has taken a number of *O. aeneus* on Barro Colorado Island, Canal Zone, but found none in the forest which covers most of the island. Pekka Soini (personal communication), who has collected in the vicinity of Iquitos, Peru for 10 years, has never observed *O. aeneus* in the rainforest although *O. argenteus* and *O. fulgidus* were common. Thus, the range of vertical movements exhibited by the Belizean *O. aeneus* might be typical for the species regardless of habitat.

Conclusions from studies of captive animals even under simulated natural conditions have always been looked at with suspicion because it is difficult to determine how much behaviour is modified by captivity. By studying a species both in the wild and in captivity it is possible to judge the validity of data obtained from captive animals. Our observations on horizontal and vertical movements, on sleeping perches and postures of *O. aeneus* suggest that these aspects of behaviour were not significantly altered in the subnatural environment. The snakes fed readily while in the greenhouse, including individuals that would not take food in the confines of 61 × 32 × 42 cm glass enclosures. Thus captives kept in an artificial environment providing ample space and a simulation of natural conditions, such as those in the greenhouse of the present study, can yield valid data on some aspects of behaviour.

ACKNOWLEDGEMENTS

We wish to thank the same people who assisted us in our study of *Imantodes* (Henderson and Nickerson, 1976) and also Henry S. Fitch who made many valuable suggestions on an earlier draft.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 669–671

A METHOD TO IDENTIFY INDIVIDUAL YOUNG GHARIAL (*GAVIALIS GANGETICUS*)

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(*Received* 18 *December* 1975)

During 1975 the Gharial Research and Conservation Unit reared fifty-two young gharial. In order to afford proper care to individual animals and to record data from each, it was essential to be able to identify them individually. Marking, with paint or tags, these delicate young was not considered desirable, and the present paper describes a method of individual identification.

Gharial have black dorsal and lateral markings on a base of light to dark brown; as in most reptiles these markings are particularly evident in the young. The tail is laterally compressed and, on its sides, has the same colour pattern as the dorsal surface. Proximally, the tail has a double crest of projecting scutes and, distally, a single crest (Fig. 1). The black stripes on the tail in the region of the single crest extend onto the projecting scutes. In fifty-two specimens the number of scutes on the single-crested region ranged from 21 to 24. These scutes were numbered serially from the proximal end, and the location of the black stripe on each scute was noted for each specimen. It was found that no two individuals had a similar sequential pattern of black stripes, and that the stripes on the first eight scutes were sufficient for the individual identification of all fifty-two gharial. Data for ten specimens are shown in Table I and typical patterns are shown in Fig. 2.

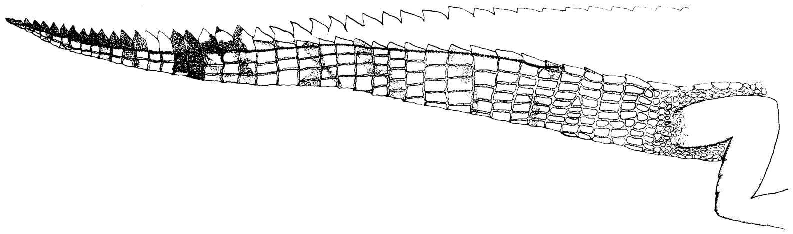

FIG. 1. The tail of the gharial showing the double- and single-crested regions.

It can be seen from Table I that examination of the first two scutes only allows separation of gharial numbers 2, 4, 7, 8, 9 and 10 from the others in the group; inclusion of the third scute separates numbers 1 and 3. Numbers 5 and 6 are unusual in not being separable until the sixth scute. All fifty-two can be separated by using 1–8 scutes.

Although the intensity of the black markings may vary at different times, the pattern, presumably genetically determined, does not change. Therefore, the method

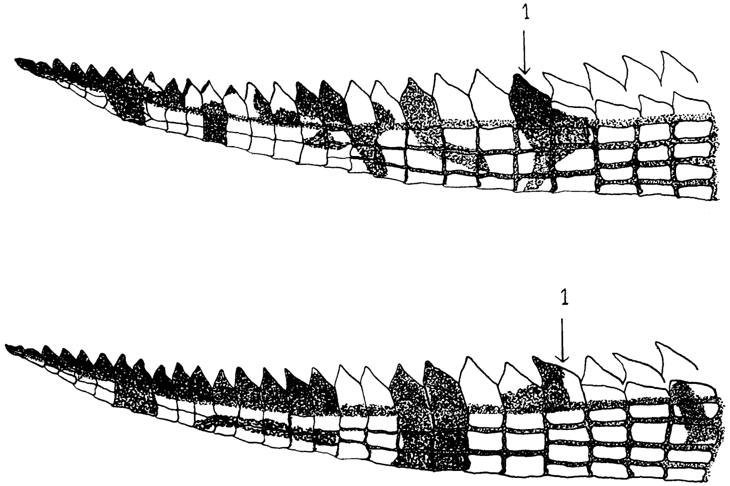

FIG. 2. Colour-pattern variations used for individual identification of gharial. Shown are specimen 1 (upper) and specimen 2 (lower) from Table I.

appears to provide an infallible key for individual identification. The technique has also been tested on a group of fifteen muggers (*Crocodylus palustris*) and, similarly, allowed individual identification. It seems likely that the technique will prove of value throughout the crocodilians since it can also be applied to wild gharial while basking, which is of immense value to field studies in that accurate recording of movements etc. can be achieved without the use of telemetry. The avoidance of telemetry is important because it can never be guaranteed that the device and the capture preceding its attachment does not interfere with natural behaviour.

TABLE I. Pattern of black stripes on the single-crested scute region of the tail in ten gharial. The letters and symbols refer to the location of the black stripe on the scutes. Key: A, anterior; B, base; F, fully black; L, left side; P, posterior; T, tip; ⏝ between the two, and **, fully black in all distal scutes; a dash indicates the absence of black markings.

Gharial number	Scute number 1	2	3	4	5	6	7	8
1	F	—	—	F	PB	—	F	F
2	P	B	—	F	F	—	—	**
3	F	—	⏝ LP ⏝		—	F	F	—
4	⏝ B ⏝		—	P	F	—	PT	F
5	F	—	P	A	—	F	F	—
6	F	—	P	A	—	P	F	—
7	F	PT	PT	F	PT	—	—	—
8	F	F	—	PT	F	F	—	**
9	—	P	A	—	—	P	**	
10	P	—	—	P	F	—	—	**

ACKNOWLEDGEMENTS

L.A.K.S. is a Ph.D. student supported by the State of Orissa (Forest Department) through the crocodile project. H.R.B. is supported by the FAO. We are grateful to both organisations and to the Government of India.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 673–676

LOCOMOTORY BEHAVIOUR DURING BASKING AND SPOOR FORMATION IN THE GHARIAL (*GAVIALIS GANGETICUS*)

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Cott (1961) reported three distinct terrestrial gaits in crocodilians—the high walk, the belly run and the gallop. In the wild none of these methods has yet been noticed for the gharial because a basking gharial is never far from water. On one occasion a basking gharial 5.5 m in length was observed to wheel about and move into the water when our boat approached it nearly 45 m away. All three terrestrial gaits have however been observed in young captive gharial studied up to 10 months of age: the high walk in relation to suspicious circumstances, and the belly run and gallop as a response to sudden fright. Zug (1974) has suggested that galloping is infrequent and has described the locomotory pattern in a single juvenile specimen of *Crocodylus porosus* in captivity. However, in addition to these methods, a slow and leisurely belly walk is seen in both captive and wild gharial during basking. This belly walk is responsible for spoor formation, which we use to estimate body size (unpublished).

All three species of Indian crocodilian—*Gavialis gangeticus*, *Crocodylus porosus* and *C. palustris*—occur in Orissa but with different habitat preferences, so all three species never occur together. Compared with the other two species, gharial move and bask frequently. The Satkoshia Gorge of the River Mahanadi in Orissa at present harbours two juvenile muggers (*C. palustris*), three adult muggers, one juvenile gharial and four adult gharial—two males and two females. Muggers are seldom seen out of the water, probably because the water is deep enough (10 m in the dry season) to keep them warm. By contrast, the gharial, particularly the juvenile and the males, bask a few hours after sunrise and sometimes during other times in the day. Basking occurs daily in the winter but rarely in the summer. The characteristic basking movements described below leave a compact, inverted U-shaped spoor.

We recognise six behavioural phases associated with basking:

(i) *Preparatory phase*. Before emerging, a wild gharial surfaces near the basking site three or more times at 10–30 min intervals and then suddenly moves onto the bank. The young captive gharial swim to a pool edge and come up for basking without the preparatory phase.

(ii) *Emergence phase*. The gharial climbs up the sand slope of the basking site with the help of the forelimbs. Then it lies on the shore with half the body or the tail remaining in the water. At this stage the body makes almost a right angle or an acute angle to the edge of the basking site. When the slope of the basking site is steeper the greater is the tendency to make a right angle (Fig. 1). The duration of the phase depends on the position of the sun. If the sun falls laterally then the gharial may remain longer in the same position; if the sun is in line with the body axis then the emergence phase is short.

(iii) *Pre-basking phase.* This involves the complete emergence of the body in the same line as in phase (ii). It is accomplished by a backward push of the fore and hind limbs against the ground with slight lifting of the body to facilitate forward movement. The paws and feet make deep impressions depending upon the ground. No good scute spoors are formed because the body and tail move in a straight line without any lateral movement.

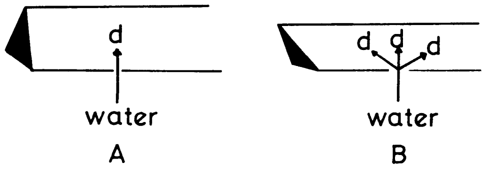

FIG. 1. Relation between the nature of the basking site and the direction of emergence. When the ground is a steep slope (A), the direction of emergence (d) makes almost a right angle with the edge of the basking site. When the ground for basking is almost flat (B), there is equal possibility for the direction of emergence to describe a right or an acute angle with the edge of the site.

(iv) *Basking phase.* Actual basking begins with the gharial turning to the side so that the body axis during basking forms an obtuse angle to the body axis upon emerging. This initial part concludes with a lateral sliding of the body and tail so that the body axis remains perpendicular to the axis upon emergence. These movements drag the tail over the sand and leave a spoor, formed by that part of the tail bearing single ventral scutes. However, spoors from this phase are not clear since during the movements the tail does not touch the ground completely due to the effect of a lifting force F_2 travelling the whole length of the tail in the form of a wave (Fig. 2).

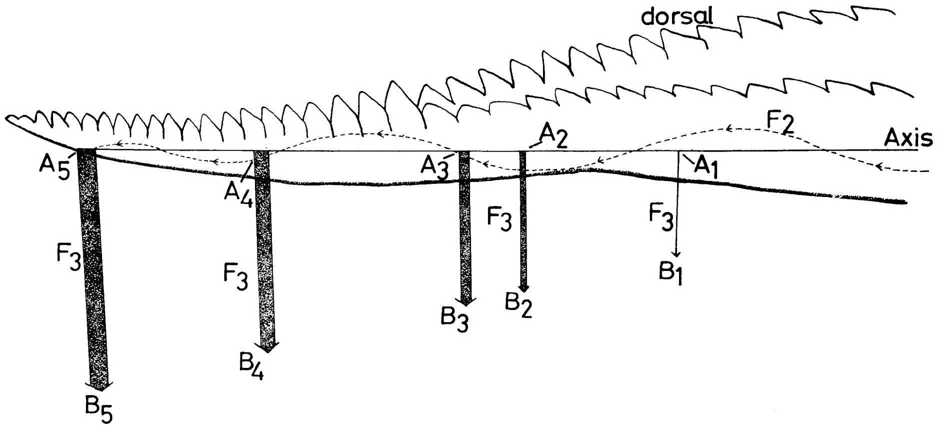

FIG. 2. Forces in action during the basking phase proper. A_5 to A_1 are imaginary points on the tail axis to demonstrate the nature of the lateral force (F_3) when it travels from these points to the respective limiting points B_5 to B_1. Play action of F_3 is limited up to a line drawn through these limiting points. F_2 is the lifting force travelling the whole length of the tail.

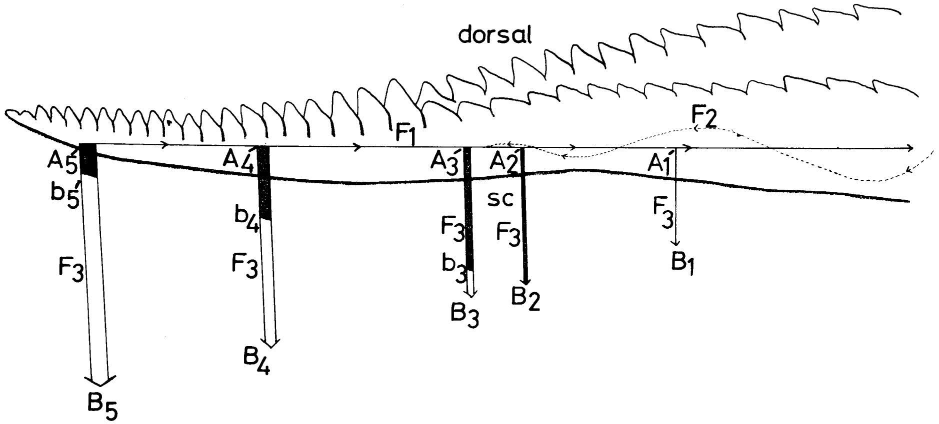

FIG. 3. Forces in action during the post-basking phase (see text for details).

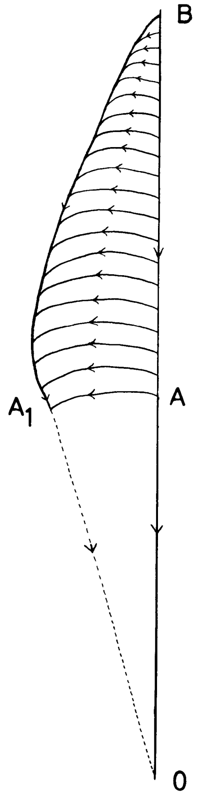

FIG. 4. Mechanism and nature of spoor formation during the post-basking phase (see text for details).

(v) *Post-basking phase*. The gharial moves forward and laterally from the position during phase (iv). In so doing three forces act concurrently (Fig. 3): (a) a forwardly-directed dragging or propulsive force (F_1) acting in a straight line to the body axis and originating from limb movements, (b) a lifting force (F_2) directed posteriorly in the form of a diminishing wave and originating from muscular movements at the base of the tail (the diminishing nature of this force is due to F_1 and the weight of the tail), (c) a lateral force (F_3) originating at the base of the tail due to muscular action. F_3 in the absence of the other forces would bring the tail to a position along B_5–B_1 from A_5–A_1. However, due to F_1 the extent of F_3 is reduced to b_5–b_4–b_3–B_2–B_1. The tail is dragged along this line producing spoor marks of the pattern shown in Fig. 4 (B to A). It should also be noted that the lifting force F_2 produces effects approximately up to A_2 which marks the region from where the tail begins to have ventral scutes arranged in a single row. In the portion of the tail anterior to A_2 all three forces are in action. Due to the action of F_2 in the anterior region the tail in this region seldom touches the ground and should it do so does not leave a spoor of the scutes because the effective strength and range of F_3 is low and F_1 is also in action. Thus even if this portion of the tail makes some lateral movement it does not leave any spoor (Fig. 4, AO). In Fig. 4, OB represents the body axis in which F_1 acts in the direction BO; BA_1O is the path in which the tail is dragged.

(vi) *Re-entry phase*. This phase is usually short although it may be prolonged by brief pauses. Usually the gharial enters the water with a single sliding movement. The extent to which the limbs are used depends on the nature of the basking site, the greater the slope the lesser is the use of the limbs. Thus there is less probability of observing good pugs at this stage, and the movements do not leave a caudal scute spoor. However, the sliding spoor is important to surveyors in detecting the basking site.

ACKNOWLEDGEMENTS

L.A.K.S. is supported by a research scholarship from the State Government of Orissa (Forest Department); H.R.B. is supported by the UNDP/FAO project on crocodile breeding. We are grateful to these organisations and to the Government of India.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 677–678

RAISING HATCHLINGS OF THE LEATHERBACK TURTLE, *DERMOCHELYS CORIACEA*

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(*Received* 29 *January* 1976)

In 1975, while tagging studies on the turtles *Caretta caretta* and *Chelonia mydas* were in progress for *Caretta Research*, a non-profit-making, privately-funded sea-turtle research group based on Sanibel Island off the west coast of Florida, a leatherback (*Dermochyls coriacea*), a rare visitor to Florida, was discovered laying eggs. After the female returned to the sea the eggs were dug up; there were 91 good eggs and 39 of irregular shape and size. Four normal eggs were removed to be hatched at home. These four eggs were placed in a small styrofoam container full of sand and later taken to Massachusetts. There the container was kept at a temperature of 29°C. Water was sprinkled onto the sand every day to simulate the rain that falls nearly every afternoon during the nesting season. The eggs were laid on 15 July and they hatched on 24 September—an incubation period of 71 days.

When the turtles hatched two were placed in a twenty-gallon tank filled with sea-water and equipped with an aerator and filter; the other two were given to Mr and Mrs Jack Campbell who have raised loggerheads for me in previous years.

Although the ideal temperature for keeping hatchlings is probably about 28°C, these were kept at about 23°C. A difficulty in keeping hatchling leatherbacks is that they continuously beat their heads against the end of the tank and usually keep this up until they die. Therefore it seemed logical that a lower temperature would slow their activity and prevent this behaviour. So far this has worked, and the only time they swim vigorously is when they are returned to the tank after feeding.

The water was brought from the sea in plastic pails and added to the tank. It is checked periodically for acidity and adjusted when necessary by the addition of sodium bicarbonate. When the water level is reduced by evaporation it is returned to the original level by adding tap water. The water has been changed only once on 10 November since 24 September 1975.

The main food of the leatherback in the wild is jelly-fish (Ross Whitham, personal communication). I first tried to feed them on Knox Gelatin with mashed chicken liver mixed in, but the gelatin liquified before they could eat it. Since then they have been fed only chicken liver cut up into small pieces. The turtles were fed in a different tank so that any food left over would not contaminate the main tank. The feeding container was filled with tap water at about the same temperature as the sea-water in the tank. Immediately after feeding the turtles were returned to the main tank. At first they would swim vigorously for 10–15 min, pushing against the glass or hitting it. This was prevented by feeding them in the evening and by turning off the light over the tank before they were returned; as soon as they settled the light was turned on again.

Spoczynaska (1970) reported that she kept leatherbacks for 21 days and that 42 days was the record. Three of our specimens have survived 249 days since they were hatched; one unfortunately choked while feeding. The only problem seems to be the

TABLE I. Growth record of a specimen of *D. coriacea* hatched on 24 September 1975

	Carapace length (cm)	Weight (g)
25 September 1975	6.0	—
24 October	8.9	—
10 November	10.3	—
3 December	12.7	255
18 December	13.3	297
1 January 1976	14.3	310
21 January	14.9	345
12 February	15.2	454
23 February	16.5	505
12 March	17.8	585
21 March	18.4	670
4 April	19.0	765
24 April	19.7	920
8 May	20.3	1010
26 May	21.6	1035

necessity for either larger or separate tanks to permit their rapid growth. It is hoped that these notes will assist those who may need to raise such hatchlings in the future; the growth of one specimen is shown in Table I.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 679–683

ON THE FORM *TRITURUS ALPESTRIS LACUSNIGRI* (SELIŠKAR AND PEHANI, 1935)

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INTRODUCTION

In 1935, Seliškar and Pehani described a new form of Alpine newt from Črno Lake in the Julian Alps, Yugoslavia. This form differed from the nominate by its very dark, almost black colouring, slender body, long tail, and rather big head which was quadratic in shape and strikingly wider than the trunk when viewed from above. According to the original description an arched lobe on either side of the upper jaw was characteristic of this subspecies. Dark dots on the belly occurred in many specimens. This form was named *Triturus alpestris lacusnigri* by the above authors. They also called attention to the fact that this form strongly resembles the subspecies *Triturus alpestris reiseri* (Werner, 1902). According to both authors, *Triturus alpestris lacusnigri* differs from *Triturus alpestris reiseri* by its square head and slender body. Compared to the nominate form the main distinguishing character of the form *reiseri* (Werner, 1902) are the extraordinarily big head, rather circular viewed from above, the breadth of which exceeds the diameter of the trunk; the form of the oral aperture (the sides of the upper jaw overlap the lower jaw), and the greater height of the tail. Werner also found small differences in the colouring.

In August 1975 I had an opportunity to visit Črno Lake and catch several specimens there. At this time females conspicuously prevailed over males in water, which is quite usual for the majority of Middle European localities of this species. This was reflected in the number of specimens caught: 6 females; 1 male.

DESCRIPTION OF THE SPECIMENS FROM ČRNO LAKE

MORPHOMETRIC CHARACTERISTICS

Seliškar and Pehani gave some absolute measurements of the form *lacusnigri*. It is therefore possible to carry out a comparison with new data on the material from this locality. Brief biometrical characteristics of the breadth of head in the form *reiseri* are given by Wolterstorff and Radovanović (1938). Calculations of relative data from absolute measurements published in the papers mentioned are given (Table I). Data on the nominate form from the Dolomites and Bavarian regions (Roček, 1974a) are also presented for the sake of comparison. The authors of both earlier papers used whole length of the body (trunk + tail) as a basic measurement to calculate the index L/LtC (L = length of body, LtC = width of head). In the present work this character is used: (i) calculated on the basis of total body length in accordance with the earlier data; (ii) calculated on the basis of trunk length minus tail, so as to compare with data by Roček (1974a).

From the data in Table I and from absolute measurements by Seliškar and Pehani (1935) and Wolterstorff and Radovanović (1938) it was established: (i) The index

L/LtC in the form *reiseri* (males and females) is on average lower than in the form *lacusnigri* (Table I). The relative width of the head in the form *reiseri* is greater. The limits of variation amplitude, however, overlap. (ii) Comparing the relative width of head L/LtC where L is the length of trunk minus the tail, Seliškar and Pehani give the lowest average values (5.01 and 5.35 for males and females respectively) while average values by the author closely approach or are indentical with values characterizing the nominate form from the Dolomites and Bavarian Alps (5.35 and 5.61 respectively).

TABLE I. Comparison of the relative width of the head (L/LtC) in some Alpine newt forms with the nominate form and with the newly obtained data from Črno Lake

Number of specimen	*T.a. lacusnigri* (Seliškar and Pehani, 1935) I	II	*T.a. reiseri* (Wolterstorff and Radovanović 1938)	Newly obtained data from Črno Lake I	II	*T.a. alpestris* (Roček, 1974a) D	BA
Males 1	9.50	5.22	7.31	9.35	5.35		
2	8.72	5.00	8.66	—	—		
3	8.25	4.84	7.91	—	—		
4	8.60	4.72	8.54	—	—		
5	9.63	5.26	8.18	—	—		
6	—	—	8.00	—	—		
7	—	—	8.08	—	—		
8	—	—	8.54	—	—		
9	—	—	7.91	—	—		
10	—	—	8.18	—	—		
Mean	8.94	5.01	8.13	9.35	5.35	5.44	5.76
Females 1	9.60	5.30	7.64	9.96	6.08		
2	9.78	5.37	8.08	9.98	5.76		
3	9.02	5.00	8.35	9.48	5.14		
4	10.14	5.48	8.31	9.90	5.62		
5	10.82	6.16	8.07	9.83	5.76		
6	10.22	5.39	8.52	11.59	5.28		
7	8.87	4.75	8.23	—	—		
8	—	—	8.17	—	—		
9	—	—	8.15	—	—		
10	—	—	8.64	—	—		
11	—	—	8.87	—	—		
12	—	—	10.00	—	—		
13	—	—	8.75	—	—		
Mean	9.78	5.35	8.44	10.12	5.61	5.61	5.90

Explanations:

I = Calculation of the character L/LtC from the whole length of body; it permits comparison with data of Seliškar and Pehani (1935) and of Wolterstorff and Radovanović (1938).

II = Calculation of the character L/LtC from the length of trunk; it permits comparison with data of Roček (1974a).

D = Dolomites.

BA = Bavarian Alps.

(iii) Smaller (mostly younger) specimens (Smirina and Roček, 1976) have a relative head width greater than the larger older specimens (Roček, 1974b).

Further morphometric characters are: Relative tail length (L/LCd): females 1.10–1.56; male 1.34. Relative fore limb length (L/PA): females 4.41–4.90; male 4.01. Relative hind limb length (L/PP): females 4.66–4.96; male 3.79. Relative distance between fore and hind limbs (L/LiE): females 1.96–2.24; male 2.09. Relation of length of fore limbs to hind limbs (PA/PP): females 0.96–1.09; male 0.94. Relation of the length of fore limbs to the distance between fore limbs and hind limbs expressed as a percentage. (PA · 100/LiE): females 41.7–50.8; male 52.2. Relation of length of hind limbs to the distance between fore and hind limbs expressed as a percentage. (PP · 100/LiE): females 39.5–48.0; male 55.0. Where: L = trunk length minus tail; LCd = tail length; PA = fore limb length; PP = hind limb length; LiE = distance between fore and hind limbs.

The data show that the values of seven characters fluctuate within the variability ranges of Middle European specimens (Roček, 1974a). One exception is the relative width of the head (L/LtC) which is at the limit of variability. On the other hand the values given by Seliškar and Pehani (1938) are markedly different in the character L/LtC from the form *reiseri*. It should be emphasised, however, that measurements were made by different methods and that in all cases only a small number of specimens was available. Nevertheless, the separate taxonomic position of the form *reiseri* is supposed to be fully justified from the morphometric point of view, whereas the values of the form *lacusnigri* are very close to those of the nominate form *Triturus alpestris alpestris*.

COLORATION

As with other amphibians this form of Alpine newt shows a highly variable colouring which in essence accords with the variability of colouring of the nominate form. The very dark coloration of the upper surface which Seliškar and Pehani claim to be one of the most important distinguishing characters of this form cannot be accepted as being diagnostic. This colouring is determined by the water temperature and the bottom colour (the darker is bottom colour, the darker is the upper surface coloration). There are also seasonal differences in the intensity of colour.

The sole important conspicuous difference refers to the black blotches on the lower body surface, i.e. the abdomen, throat and lower surface of head. Variation in the spotting is remarkable. All six females had spots on the undersurface of body (Fig. 1). The spot density fluctuates, however, grading from the standard with several imperceptible little spots, to spots of middle size and spots only on part of the area, to a condition with deep and regular spots. Spots are circular or elongated in shape with cranio-caudal orientation. Spots on the lower side of head do not correlate in number with abdominal spots. Two females with the highest number of spots on the under side of head had the abdomen entirely free of spots. In contrast a female with numerous abdominal spots had only slight spotting on the throat and only several spots at the margin of the lower jaw (Fig. 1). The only male had its under side of the body spot-free.

The subspecies *Triturus alpestris apuanus* shows similarities to the description given. *T. alpestris apuanus* is distinguished from the nominate form *T. alpestris alpestris* by the spots on the lower side of body (Wolterstorff, 1934). The occurrence, intensity and density of spots are also variable characters in this subspecies (Wolterstorff, 1934), judged also from figures given by Lanza (1972). In the case of the male with an unblotched belly Gasco (1880/81) and Wolterstorff (1934) hinted that a percentage of specimens in *apuanus* populations have an unblotched belly. The absence of blotches therefore does not indicate sexual-dimorphism.

FIG. 1. Alpine newts from Črno Lake; left the only male. Abdominal side.

CONCLUSIONS

It is evident that data at my disposal do not permit any definite conclusions on the taxonomic position of the form from Črno Lake. Primarily this is due to the small number of specimens in the sample and that older biometric data are only partly comparable with the new data. Nevertheless a tentative estimation of the systematics is proposed on the relationship of *apuanus* and *reiseri*.

The values of the critical index L/LtC fluctuate in the specimens from Črno Lake to the limit of variability values of other Middle European material. Thus, in this specific character *lacusnigri* is situated between the nominate form and the form *reiseri*, though closely approaching the nominate form. The differences between *lacusnigri* and the nominate form cannot be statistically verified. The impression that the width of the head far exceeds that of the trunk is encouraged by the fact that the trunk and the tail are slender. This is not true in many cases (Fig. 1). In most specimens the slender trunk seems to be a labile feature and modified according to the ecological conditions prevailing. Consideration of the coloration and spots on the under side of body infers a relationship to *apuanus*. Specimens possessing this character occur only rarely in nominate populations. Ernst (1952) found differences between the nominate and *apuanus* form in this character. In terms of coloration of the under side of the body the form from Črno Lake is taxonomically close to *apuanus*. The striking correspondence in coloration makes it evident that the form from Črno Lake is identical with the form *apuanus* and consequently the name *lacusnigri* is a synonym for the name *apuanus*. However, evaluation and comparison of the sample from Črno Lake with the typical *apuanus* material have to be carried out before a final decision can be made.

ACKNOWLEDGEMENTS

Thanks are due to Doc. Dr Ota Oliva CSc. for discussions on the problem and to Dr Vladimír Hanák CSc. for reading the manuscript. Both are from Department of Systematic Zoology, Charles University, Prague.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 685–686

NOTES ON THE HERPETOLOGY OF THE COSTA BLANCA IN SPRING

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(*Received* 3 *March* 1976)

These observations were made between 29 March and 11 April 1975 in the vicinity of Calpe, a small town on the Mediterranean coast of Spain about 60 km northwest of Alicante. Most of the time was spent within 3 or 4 km of the town, although a few excursions were made to Jalón, about 20 km northwest of Calpe and approximately 100 m above sea level.

The uncultivated countryside consists largely of dry, stony hillsides covered with Mediterranean scrub. There are a few watercourses, although most of them were dry. However, we did visit a large permanent river at Jalón and a marshy region covering an area of about 2 square km behind Calpe, and we found one or two freshwater ponds and a partially dry stream running through a small valley. Much of the land is cultivated; terraced vineyards are common on the hillsides and on flat ground there are fields which support a sparse growth of grass used for grazing sheep and goats.

The weather was rather mixed. The first few days were predominantly cloudy and a little rain fell. Thereafter, the sun shone for long periods, although it was rare to have a completely cloudless day. Strong winds blew on many days. The nights were cool, with the temperature falling to 7 or 8°C. During the day the highest shade temperature was only 18°C, but it was warm in the sun, and small lizards became very active within 10 or 15 minutes of coming out to bask. At Calpe in late March and early April sunrise is at 6.30 a.m. and sunset 6.45 p.m.

The species of amphibians and reptiles recorded are as follows:

AMPHIBIA

Anura

Discoglossus pictus. Single juvenile specimen found in damp sand under a rock at top of beach at Calpe.

Bufo bufo. Large adult female found in a small pool in a stream at Jalón.

Bufo calamita. Thirty or 40 specimens seen in a shallow pool (at Calpe) which had many rushes growing in it. Freshly deposited spawn of *B. calamita* seen when pool first visited on 6 April, but there were no toads in amplexus and all specimens were males. Over the next few days, the pond dried up ; most toads left and the spawn died.

Rana ridibunda. See at Jalón and in the large marsh at Calpe. Common, but more abundant at Jalón. Usually found in close association with water; seemed to prefer fairly shallow weedy water into which it retreated when disturbed.

REPTILIA

Squamata, Sauria

Tarentola mauritanica. Relatively common; some 30 specimens observed. From 8 a.m. to 10 a.m. and from 5 p.m. to 6.30 p.m. often seen basking in the sun, usually on drystone walls. Such specimens dark in colour, presumably to maximise absorption of incident radiation. Specimens seen in middle of the day more often inside disused buildings and were generally light in colour.

Podarcis hispanica. This small lacertid was fairly common on large boulders in dry riverbeds and valley sides, and on sandstone cliffs at the back of the beach at Calpe. Far more abundant on concrete walls and drystone walls on outskirts of Calpe where over a hundred specimens seen. Specimens disturbed on drystone walls retreated between stones and quickly reappeared a few inches away. If repeatedly disturbed, this pattern continued, the lizard moving a few inches further along the wall each time. However, there seemed to be a limit to the distance it would move from its original spot; once it had travelled about 2 m in one direction, it started to return. On fine days this species emerged about 8.00 a.m. and could be seen until 6.30 p.m. Mating observed several times and on 10 April we saw a female with loose folds of skin indicating recently laid eggs.

Lacerta lepida. About 12 specimens of this large lacertid seen around Calpe on south-facing drystone walls built onto the front of banks. Only walls with large, deep crevices between stones (into which lizards could retreat) were inhabited. *L. lepida* observed in the open between 9 a.m. and 4 p.m. On days when a strong wind was blowing lizards emerged later and retired earlier, or occasionally did not emerge. In spring *L. lepida* is active for shorter periods of the day than other, smaller lacertids in the same area. Of 5 adults, 4 were males and one a female. This sex ratio and the situation in which the lizards were found suggests they were just emerging from hibernation.

Psammodromus algirus. Fairly common in areas of dense scrub. Often seen basking around the base of a bush. When disturbed, they retreated into the bush and quickly reappeared at a slightly different location.

Psammodromus hispanicus. Several hundred of these small lacertids seen in fields around Calpe. Only found in fields where there were large patches of bare ground or where the ground vegetation was very low. Most common around small bushes where it could retreat when disturbed; also found on open ground where there were few places to hide. A few *Psammodromus hispanicus* occurred in scrub; not nearly as common here as in the fields. In scrub, usually found where vegetation was sparse. *Psammodromus algirus* often present nearby but generally among rather denser vegetation. *Psammodromus hispanicus* emerged about 8.30 a.m., seen until 6.15 p.m. Many females were gravid and one laid two eggs on 9 April.

Chalcides bedriagai. Four specimens of this small skink found under small stones on the very loose, dry, sandy soil in fields where *Psammodromus hispanicus* abundant.

Squamata, Serpentes

Malpolon monspessulanus. Six specimens seen in fields or among scrubby vegetation. Most were on or beside drystone walls.

Natrix maura. Common at Calpe in the large marsh and around a partially dry stream. In the marsh they generally basked on the banks of small streams in the morning and were in the water in the afternoon. Water temperature in which snakes were found varied from 15°C to 24°C. Twenty-five or 30 specimens seen in the marsh; 7 were 15 to 20 cm long and presumably had hatched the previous summer. Some disgorged tadpoles when caught.

Most specimens around the partially dry stream were under stones on damp earth in the stream bed. Of approximately 30 snakes found in this area, 3 were adults; the rest were only 15 to 20 cm long. Some of these disgorged worms.

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AMPHIBIANS AND REPTILES COLLECTED IN THE ORINOCO DELTA

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Rivero (1964) listed only two species of frogs from the Orinoco Delta: *Hyla boans* from Caño Manamo and *Pipa pipa* from the southern sector. Davey (1946) divided the delta into three sectors according to their different drainage patterns: the *North-Western*, the area west of Caño Manamo; the *Central* which includes the swampy, heavily-wooded region of tidal rivers; and the *Southern* which is less swampy and has fewer channels.

Collecting was carried out at night around the mission of San Francisco de los Guayos and near the village of Nabasanuka, both areas in the central sector. The former location is indicated in the list as SF, the latter as N. The following species were collected:

Bufo marinus marinus Linnaeus. In great numbers along banks of channels at SF and N.
Rana palmipes Spix. One in ocumo plantation at SF.
Leptodactylus mystaceus (Spix). Several at SF.
Hyla rubra Laurent. One at N.
Hyla crepitans Wied. One at N.
Plica plica (Linnaeus). One near N.
Iguana iguana iguana (Linnaeus). Several in forest near N.
Mabouya mabouya mabouya (Lacépede). One beneath house at N.
Geochelone voglii. One captive specimen seen in village of Winnikeena.

ACKNOWLEDGEMENT

This work was supported in part by CONICIT grant SI-0168.

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