QUESTIONS IN CROCODILIAN PHYSIOLOGY

CARL GANS

Division of Biological Sciences, The University of Michigan

ABSTRACT

Morphologists, physiologists, behaviourists and ecologists have traditionally asked different and often mutually exclusive questions within their different conceptual frameworks. Only the concept of natural selection and the idea that the animals have been modified for one or another mode of life history provide a common denominator or common framework for comparison.

This approach also suggests that the observed responses to disturbance and to the multiple facies of the biotope are likely to be adaptive and that such adaptation is to be looked for. Finally one can see that selection is apt to differ during the stages of ontogeny and that age-specific selection is likely to produce age-specific adaptation. Three cautions then apply to the interpretation of data now in the literature. Each reflects the need to treat the animal holistically in an adaptive context.

INTRODUCTION

The Crocodilia, which include some twenty-one species of Recent reptiles (Wermuth & Mertens 1958), are probably the unique surviving members of the radiation that gave rise to the birds. Consequently there has always been significant interest in crocodilian adaptation. This has recently increased as it became clear that the shameless and unrestrained skin trade and accelerating habitat destruction were driving many populations to extinction.

One very useful result has been that, for the first time, we are seeing extensive studies of crocodilians in the wild and of adults restrained under seminatural conditions. It is probably fair to say that the information gained over the last decade or so has doubled the fund of our previous knowledge. In analyzing this information and extrapolating perhaps to ancestral forms, reference must obviously be to the physiological studies that have been carried out, mainly in the laboratory, on circulation, ventilation, respiration and digestion.

Certain cautions are necessary when interpreting published results and extrapolating from these, and it may be useful to emphasize these. These cautions may be stated as follows: The behavioural state of the experimental animal may modify the results; enormous ontogenetic changes occur in structure and function; crocodilians respond differently to the aquatic and terrestrial facies of their biotope.

The present discussion stresses biomechanical or functional morphologic studies, as well as approaches used in my laboratory. This is not intended as another chance to tell tales; rather the aim is to document the essential unity of biology and the broad-based unity of approaches. If behavioural cautions apply to the interpretation of morphology, they probably apply as well to physiology and biochemistry. If morphologic cautions apply to physiology, they are likely to apply to behaviour and biochemistry as well.

Unfortunately, I have to base my examples mainly on experiments with a South American crocodilian, *Caiman crocodilus*. It is assumed that (within the framework here offered) this

species is fundamentally similar to African forms. We actually have some pilot experiments suggesting that this is so. However, such assumptions are apt to be wrong though the crocodilians appear to be a tightly knit group (Cohen & Gans 1970): Crocodilians do show significant ecological and other diversity (Greer 1971) and it is consequently still necessary to determine exactly the predictability from our data.

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CROCODILIAN BEHAVIOUR

When I first became interested in herpetology, reptiles were considered to be rather dull animals; they rested in cages for days on end, moving hardly at all. We all knew that snakes could not hear and responded only to visual cues or vibrations of the soil.

Some of these erroneous assumptions should have been extirpated from the literature long ago. The late Raymond L. Ditmars reported some seventy years ago that some reptiles, allowed to occupy an outdoor paddock during the summer, sometimes became very active and chased their keepers, while other species of reptiles responded in a perhaps less devastating fashion to more nearly natural circumstances.

We have now been accumulating a number of observations suggesting that crocodilians respond in a variety of qualitative and quantitative ways to disturbance. Breathing rate can be seen to increase immediately after animals are disturbed and will decrease only much later even if the animals never moved much. It is well known that such excitation is also reflected in oxygen utilization and patterns of thermoregulation. Excited animals may not feed or mate and prolonged excitement may lead to stress syndromes.

Less obvious responses to disturbance also occur in a phenomenon known as diving bradycardia (Gaunt & Gans 1969). This phenomenon is seen in crocodilians restrained on a tilting board (and probably in an excited state). For instance, these will crash their heart rate from 35 to 4 beats per minute, if their noses are forcibly pushed under water. The general phenomenon occurs in many vertebrates (Andersen 1961) and is assumed to involve autonomic mechanisms (White 1976).

We found that unrestrained animals, allowed to swim more or less freely in an aquarium, gradually decrease their heart rate over the next few hours (from 23 to 10 beats per minute). However, their heart rate does not drop during short (5–10 minute) submersions; instead, it rises slightly (1 to 2 beats per minute) during and immediately after each breath. Only when an investigator enters the room is the dive accompanied by a sharp drop (to 4 beats per minute) in heart rate.

Bradycardia puts the animal into a position of minimal utilization and conserves resources. Animals that dive voluntarily can presumably replenish their oxygen by emerging at will. They encounter no need to reduce distribution below the consumption level (and thus build up a tissue debt); such animals do go into tachycardia when they breathe, as this will accelerate oxygen

absorption and CO_2 release and will gain maximum benefit from multiple breaths. These observations have now been confirmed by telemetry of free-living animals (Smith *et al*. 1974).

A second example concerns the ventilatory mechanics (Gans & Clark 1976). We have recently been looking at pulmonary pressure and airflow in some detail. Direct recordings suggest that the pulmonary pressure in a resting caiman is almost always supra-atmospheric and that it drops when the glottis and nares open, permitting outflow of air. Pulmonary pressures below atmospheric permit the lung to fill until the glottis again closes; then the pressure returns to supra-atmospheric. Several variants of this pattern are seen. The pressure may show a peak at the beginning of exhalation and a second peak after inhalation when it first rises beyond and then returns to the baseline level. Indeed the literature contains a variety of comments suggesting that reptilian respiration typically consists of an exhalation, an inhalation and a secondary partial exhalation so that flow is in essence triphasic.

I must admit a bias against such explanations. The outflow during the third phase would presumably include the air most recently inhaled which consequently has the highest oxygen concentration. From a purely energetic viewpoint, such terminal outflow seems ineffective. Our myograms suggest that the pressures may indeed have four phases (rise, fall, rise, fall), but the flow will generally be diphastic (outflow, inflow); after all, airflow can only proceed when the glottis is open. The glottis opens either at baseline or during the first rise, and closes just about the time that the pressure in the lungs again becomes positive. Thus, the secondary peak may only be interpreted as a repositioning of the viscera. It obviously increases the muscular work per unit of gas moved, and hence decreases the efficiency.

The pressure may produce some kind of opening of the alveoli, but it is a point as yet speculative. An experiment just completed in my laboratory by Mr Brian Clark proved exceedingly suggestive. He catheterized the trachea of some animals and checked the breathing curves over a few days, rather than for a few hours only. As the animals became accustomed to the experimental procedure, they lost the pre- and post-breathing peaks and ventilated their lungs in a pattern that is diphasic, both in pressure (drop, rise) and in flow (out, in). The pressure and the flow cycles are not coincident; thus, inhalation starts before the rise in pressure. The experiment documents again the fact that excited animals behave differently.

It might be argued that animals in nature are not under 'resting' conditions. Consequently we should be studying the excited conditions and there may indeed be some merit to this. The only difficulty is to quantify which excited condition and to understand what level of excitement is actually involved. Determination of so-called physiological scope is supposed to reflect the animal's capacity to do work at levels above those reflected in the resting metabolism. Consequently the resting level must be determined on a comparable basis, and for this the animals must be calm.

For such reasons, we have modified our laboratory so that we can carry out electromyographical and general physiological experiments in isolation; the room is sealed and all signals to equipment and from the animals proceed by cables. Small closed circuit television cameras allow us to monitor both the animals and their physiological parameters, and a variety of servo-mechanisms allow us to control animal activity. This being the case, there would seem to be no reason why the animals should not achieve baseline values. However, even under these conditions, the animals still respond to the vibrations or noises apparently transmitted when janitors

clean the next room or when someone writes on a chalkboard affixed to the door. Certainly any opening of the room's door elicits a response even if it occurs in total darkness in the middle of the night.

The first lesson then is care when watching the crocodiles through the keyhole; they seem to be watching back.

THE PROBLEM OF SIZE

A number of species of adult crocodilians reach sizes over 500 kg; even juveniles of the smaller species weigh more than 150 kg at sexual maturity. In the large forms such as *Crocodilus niloticus* and *Crocodilus porosus*, sexual maturity may well be at weights greater than 100 kg. On the other hand, most observations proceed on relatively small animals. It is obviously much easier to cut serial sections through hatchlings than through adult *Crocodilus niloticus*. Museum curators have a curious (but understandable) predilection for popping hatchlings into alcohol, while preserving only the skulls and bits of skin of the adults. This kind of selection against large size also applies to other large and giant reptiles. There is scarcely a museum that has preserved material of any adult crocodilian or marine turtle. This house-keeping viewpoint might not be too bad, were it not that adult crocodilians differ from the juveniles in some significant aspects.

This difference was first brought home to me when I helped Dr Werner H. Stingelin dissect a two-metre-long alligator and compared the proportions of its brain with those of the hatchling now perpetuated in many textbooks. The olfactory bulbs of the adult were more than twice as long as the brain itself. The allometric trends in the sizes for the olfactory bulb and the rest of the brain are shown in Figure 1. It is based on the miscellaneous specimens of a short-snouted species that had been used in various experiments. The right hand limit of the graph suggests that morphologists and physiologists share the tendency decried for museum curators (after all, large animals cost more initially, require larger cages and more food, and bite more effectively). (See Dodson 1975 for more extensive data on cranial changes in another species.)

The above example refers to body proportions only. We now have an observation suggesting changes in the muscles attaching to the intercostal segment of the rib as the animal matures. Either the muscles do spread ventrally with age or the aponeurosis always contains a thin layer of fibres that later enlarge. There is clearly a gradual increase in the complexity of costal muscles with size and thus probably a change in the mechanics of the system.

Physiological data show similar size-related changes. Breathing rates for our 'unrestrained' and resting animals decrease (literature values for 'resting' animals of similar size may be five times as high as those determined on our isolated animals). We do not yet know how these changes affect oxygen consumption.

As interesting are data for the various measures of temperature preference (Diefenbach 1975a, b, c). Juveniles prefer lower rates of rise and lower temperatures at which they will feed voluntarily than do adults. This apparently reflects directly on the pH optima of the digestive juices, and retention times for food in the stomach. We still lack data that would tell us how long in ontogeny this process continues. This is obviously a matter that could be nicely documented

cronwrighti, a procedure which does not conform to the modern concept of a subspecies.

The distribution of *Psammobates* in South West Africa is still obscure, although there seems to be considerable overlap between *P. oculifer* and *P. tentorius* (Figure 4). Localities near Aus (square 2616 CB) cited by Mertens (1955, 1971), and quoted by Loveridge & Williams (1957), are perhaps open to question. Mertens lists the following tortoises from the farm 'Plateau' near Aus, collected by H. Erni; *Homopus boulengeri*, *H. signatus*, *Chersina angulata*, *Psammobates oculifer*, *P. tentorius verroxii*, and *P. tentorius trimeni*, with *Geochelone pardalis babcocki* found either at 'Plateau' or 20 km to the west of the farm. It is difficult to believe that the two very closely related *Homopus* species could co-exist on a South West African farm so far north of their recorded, and otherwise allopatric, ranges. Similarly, the apparent concurrence on one farm of two distinct subspecies of *P. tentorius*, together with such a large array of other testudinines, seems too extraordinary to accept without further confirmation. *P. tentorius verroxii*, however, can be accepted for the Aus area on the evidence of Fitzsimons (1938).

The overlap between *P. oculifer* and *P. tentorius* in the area north-west of the junction between the Orange and Vaal Rivers is well documented by Power (1932). This overlap is shown in Figure 4 as extending south of the Orange River but it should be noted that no authenticated record of *oculifer* has yet been obtained there. There seems to be no reason why it should not occur north-west of Hopetown, unless the river itself has been an effective physical barrier. Boulenger's record of *oculifer* between Richmond and Victoria West is erroneous (Loveridge & Williams 1957).

P. oculifer and the now rare *P. geometricus* have several similarities and constitute a species group. They are separated spatially by the *tentorius* complex.

Psammobates geometricus (Linnaeus, 1758)   (Figure 5)

Although apparently now much reduced in range, the recent historical distribution of this species was never extensive. It is found in the western Cape coastal area between the mountains and the sea and extends no farther northwards than the 200 mm isohyet in the Eland's Bay area (3218 AD), and possibly not as far. Rau (1971) should be consulted for a detailed analysis of the position. Although a reserve has been created for the species in a small piece of natural veld near Paarl, one or two other populations certainly survive. Destruction of natural veld for farming, and encroachment by urban sprawl, are probably the main reasons for its decline. Three of the 12 records shown have been confirmed in the current Cape survey.

Psammobates oculifer (Kuhl, 1820)   (Figure 6)

This species occurs over a large part of South West Africa, Botswana, and the northern Cape Province of South Africa. It is also found in the western part of the Orange Free State, and in the northern Transvaal. The Transvaal records, all held by the Transvaal Museum and largely collected by reliable scientists over the last 15 years, constitute a considerable range extension over that accepted by Hewitt (1933) and Loveridge & Williams (1957). It seems to occur in

because supposedly diagnostic characters proved weak in application to recently collected southern African material (Greig in preparation). There are several records of subspecies *babcocki* occurring within the range of subspecies *pardalis*; one of these, for the square 2818 AB, was collected during the present survey.

Geochelone pardalis has a wide distribution, and occurs in South Africa from sea-level to at least 2 000 m altitude, and in a variety of veld types, from Highland Sourveld in the Amatola Mountains (eastern Cape) with a rainfall of up to 1 400 mm per annum, to Namaqualand Broken Veld with a rainfall of below 100 mm (terminology from Acocks 1953). It is the only species (with perhaps *Chersina angulata*) of southern African tortoise accommodating enough in diet and environment preference, to be kept in captivity with a reasonable chance of survival and reproductive success. Its great size (up to 43 kg but averaging 10–12 kg) militates against its collection for museums, and the patchy distribution shown in Figure 2 is probably only apparent.

The mountain tortoise has been exterminated in the western Cape coastal areas, largely for food. It was eaten by all racial groups and its meat and eggs are still highly regarded in certain areas. It is frequently kept as a pet, and escapees are regularly encountered in the urban and peri-urban areas in the western Cape region. A number of unwanted pet mountain tortoises have been given sanctuary in various nature reserves, such as the Cape Point Nature Reserve and the Goukamma Nature Reserve, and records from such places must always be regarded with suspicion. South African farmers in areas from which the species has been eliminated, have been known to reintroduce it from areas such as Aberdeen District where it occurs in abundance.

Of the 188 records shown in Figure 2, 65 are represented by specimens obtained in the current Cape survey, 56 of these being previously unrecorded localities.

Genus *Psammobates* Fitzinger 1835

As Loveridge & Williams (1957) pointed out, no group of tortoises has fostered the making of so many specific and subspecific names as has *Psammobates*. To *Psammobates tentorius* and its three subspecies, they allocate the six species and 22 subspecies of Hewitt (1933, 1934) and Fitzsimons (1938). While Hewitt's excessive 'splitting' is rightly criticized, it is possible that examination of extensive series of specimens with accurate locality data will lead to a review of the taxonomy of *P. tentorius* and the revival of some of his presently discredited subspecies. Most older collections in museums, notably those of the Albany Museum in Grahamstown. on which Hewitt based most of his work, are characterized by imprecise, and in some cases erroneous, locality data.

Figure 3 displays the plethora of specific and subspecific names and their geographic distribution, largely the result of Hewitt's work. Full species are printed in upper-case, sub-species in lower-case. The ranges of the three species, *P. tentorius, P. fiski* and *P. verroxii (sensu* Hewitt) are indicated by shaded background.

It is quite clear that many of these names were rightly rejected. For example, *P. strauchi* (Lidth de Jeude) labelled 'Cape of Good Hope' and based on only one specimen, is a *P. geometricus* lacking the nuchal scute. From a large collection of tortoises from Hanover, Hewitt subjectively separated three types, which he names *P. fiski fiski, P. fiski seimundi* and *P. fiski*
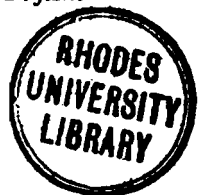
on the quarter-degree grid in the manner now generally accepted in southern Africa for zoo-cartographic display (Davis 1965).

The maps were supplemented for this paper with further unpublished museum records, mostly post-1957. Finally, in order to confirm and amplify the distribution maps thus created, a survey was undertaken throughout the Cape south of the Orange River to obtain specimens of known provenance. Tortoises were solicited from farmers by telephone and letter, great care being taken to obtain accurate locality records. Collectors were instructed to prepare sketch-maps of localities, and a telephonic interrogation with the aid of 1 : 50 000 topographical maps, yielded results of an acceptable degree of accuracy.

Few people can apparently resist the temptation to keep a tortoise found on a highway or in the veld as a 'pet', and tortoises are adept at escaping from inadequate enclosures. Thus, more than in any other group of animals, all new tortoise survey locality records have to be very carefully considered before acceptance is granted. Nevertheless, as it has been the policy in the recent Cape survey to solicit material from farmers remote from towns wherever possible, and as a query as to the naturalness of the local populations is made in every case, the survey results may be regarded as being an accurate reflection of the actual position.

When specimens were obtained from areas outside the 'expected' range of a species, these were thoroughly investigated and verified. Museum records of doubtful provenance are unfortunately more difficult to check. In the maps presented here, museum, literature, and Cape survey records have been combined; questionable localities are indicated as such.

RESULTS

Figure 1 shows collecting stations and was compiled from the records contained in Figures 2 to 14. The eastern Cape bias results from the fact that the pioneers of South African chelonian taxonomy, J. E. Duerden and J. Hewitt, were both based at the Albany Museum in Grahamstown. Duerden collected several hundreds of tortoises in 1906 (Duerden 1906, 1907) and Hewitt supplemented this collection with his own material. The bias is the more pronounced because the present writers are also stationed at Grahamstown. Nevertheless, the coverage of southern Africa is remarkably uniform, and the only major gaps are those in the Kaokoveld and Damaraland (South West Africa), the south-east Transvaal, and eastern Orange Free State. Land tortoises are almost certainly now extinct in the Transkei, and nearly so in Lesotho.

Geochelone pardalis (Bell, 1828)   (Figure 2)

This is the largest southern African species and is known as the mountain tortoise, leopard tortoise, or bergskilpad. Two subspecies are currently recognized. Loveridge & Williams (1957) attempt to justify Loveridge's establishment of the subspecies *Geochelone pardalis babcocki* (Loveridge, 1935), and assign several South West African localities to the nominate subspecies. The putative range of *G. pardalis pardalis* has been shown here, but reservations as to the validity of the differentiation are expressed – not simply because of the extensive range overlap, but