

MINI-REVIEW: THERMOREGULATION IN CHELONIANS

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INTRODUCTION

Temperature is a major factor in the ecology and physiology of reptiles and since the early pioneering studies of Strelnikov (1934), Sergeev (1939) and Cowles and Bogert (1944) which demonstrated that reptiles do not passively respond to environmental heat distribution but have the ability to behaviourally regulate their body temperatures, there has been a wealth of information published on the subject. There have also been numerous reviews of these studies. One of the earliest (Brattstrom, 1965) described the body temperatures of approximately 160 species of reptiles. The most recent and extensive (Avery, 1982) discussed the thermal relations of over 500 species; however much of this information concerned lizards, and relatively few of the cited papers dealt with chelonians. Yet the thermal relations of chelonians are of interest for several reasons. The animals are often approximately hemispherical in shape which means a relatively small surface to volume geometry compared to other groups of reptiles with similar mass, and thus they experience slower overall rates of heating and cooling. Some species also grow to a very large size. This may provide them with some degree of inertial homeothermy but may also impose excessive heat loads through difficulties of finding adequate shade (Swingland and Frazier, 1979). The terrestrial forms move only very slowly (Jayes and Alexander, 1980; Williams, 1981) and this may also present difficulties from overheating even in small species which at certain times of the year have to restrict movement through areas with limited shade (Meek, 1984; Branch, 1984). The semi-aquatic forms invariably live in habitats with a wide range of thermal conditions. In the Spring and Autumn in temperate zones, a terrapin that has been basking on a log beside a pool and achieved a high body temperature may suddenly be exposed to very cool conditions when entering water. Therefore mechanisms for conserving body heat could have selective advantages for aquatic species (Bartholomew, 1982).

In this paper we review recent work on the thermal relations of chelonians — mainly those papers which have been published since the reviews by Hutchison (1979), Mrosovsky (1980: sea turtles only), Sturbaum (1982) and Avery (1982). There has been much progress in understanding chelonian thermoregulation in the past 10 years. This has been along three broad fronts:

- i. An increase in the number of species for which thermoregulatory data are available, together with the provision of more information relating to some of the well-studied species.
- ii. An increasing understanding of the mechanisms of behavioural thermoregulation, although as we shall show, progress in this area has been disappointingly slow.
- iii. An increased understanding of the physiological mechanisms which increase the efficiency of thermoregulatory processes, together with the physiological and other consequences of adaptations of this kind.

BEHAVIOURAL THERMOREGULATION

Thermoregulatory behaviour in reptiles is a mechanism which has evolved to satisfy physiological thermal requirements by exploiting thermally diverse microenvironments in the habitat. In chelonians, thermoregulatory behaviour has been observed in all of the three major life forms: terrestrial, semi-aquatic and marine (Avery, 1982).

TERRESTRIAL CHELONIANS

The first descriptions of the thermal relations of chelonians were in terrestrial species which were shown to be diurnal heliotherms maintaining body temperatures above 30°C (Sergeev, 1939; Bogert and Cowles, 1947; Woodbury and Hardy, 1948; review in Avery, 1982). Recent studies have reinforced these findings. In North African *Testudo graeca*, early morning basking enables the animals to attain body temperatures up to 35°C (Lambert, 1981; Meek and Jayes, 1982) after which locomotor activity, feeding and mating take place. If the skies are overcast, however, there is prolonged basking through the middle of the day (Lambert, 1981), as there is in coastal areas which are subjected to sea mists (Meek and Jayes, 1982). Behavioural thermoregulation enables *T. graeca* in North Africa to maintain relatively high and relatively constant body temperatures for most of the daily period following initial basking (Lambert, 1981; Meek and Jayes, 1982).

This ability has been observed in other species. The South African *Chersina angulata* maintains body temperatures which are on average 4-6°C higher than air temperatures by movement in and out of sunlit and shaded areas (Branch, 1984). In scrubland areas in

Terrestrial chelonians

<i>Chersina angulata</i>	Branch, 1984
* <i>Gopherus flavomarginatus</i>	Aguirre Leon <i>et al.</i> , 1980
<i>Testudo graeca</i>	Lambert, 1981 Meek and Jayes, 1982 Wright <i>et al.</i> , in press
<i>Testudo hermanni</i>	Meek and Inskoop, 1981 Meek, 1984, in press a, b Hailey <i>et al.</i> , 1984 Pulford <i>et al.</i> , 1984 Chelazzi and Calzolari, 1986 Wright <i>et al.</i> , in press

Semi-aquatic chelonians

<i>Chelydra serpentina</i>	Obbard and Brooks, 1981
<i>Chrysemys picta</i>	Graham and Hutchison, 1979 (laboratory) Peterson, 1986 (hibernation)
<i>Clemmys guttata</i>	Graham and Hutchison, 1979 (laboratory) Ernst, 1982
* <i>Mauremys caspica</i>	Meek, 1983
* <i>Mauremys japonica</i>	Ishihara, 1979
* <i>Pelomedusa subrufa</i>	Miller, 1979
<i>Pseudemys scripta</i>	Crawshaw <i>et al.</i> , 1980 Crawford <i>et al.</i> , 1983 Jarling <i>et al.</i> , 1984 Spotila <i>et al.</i> , 1984
<i>Sternotherus odoratus</i>	Graham and Hutchison, 1979 (laboratory) Ernst, 1986b
<i>Terrapene carolina</i>	Erskine and Hutchison, 1981 (laboratory)
* <i>Trionyx sinensis</i>	Khosatsky, 1981

Marine chelonians

<i>Caretta caretta</i>	Spotila and Standora, 1985
<i>Chelonia mydas</i>	Standora <i>et al.</i> , 1982 Spotila and Standora, 1985
<i>Dermochelys coriacea</i>	Standora <i>et al.</i> , 1984 Spotila and Standora, 1985

TABLE I: A list of species for which data on body temperature has been published between 1981 and 1987, together with references. The Table also lists references prior to 1981 which were inadvertently omitted from Avery's (1982) comprehensive review. Species for which data are recorded for the first time are indicated by an asterisk (*). All studies were carried out in the field unless the citation is marked 'laboratory'.

Yugoslavia *T. hermanni* basks in Spring throughout the morning, elevating body temperatures to around 34°C (Meek and Inskoop, 1981; Meek, 1984) with feeding, mating and locomotor activity during the middle and later periods of the day. In hot weather individuals of this species avoid moving extensive distances onto open clearings to reduce the risk of overheating (Meek, 1984) and this has also been observed in *Chersina angulata* (Branch, 1984). In the Autumn when the weather is cooler, basking intensity in *T. hermanni* increases, and the body temperatures at which feeding and locomotor activity take place are lower (Meek, 1988). In France *T. hermanni* occurs in woodland habitat with limited areas of sunlight, and although it may attain high body temperatures it has not been observed basking and appears for a large part

of the day to operate as a thermoconformer. In the afternoon body temperatures may exceed air temperatures by 4°C but it is not certain if the animals do indeed bask or whether the difference is due to metabolic heat production (Pulford *et al.*, 1984; see below).

The patterns of activity in *T. hermanni* vary between regions and with season. In Yugoslavia during Spring and Autumn activity is unimodal (Meek, 1984, 1988) but in Summer, both in Yugoslavia and at a coastal heathland in Greece, basking and activity are bimodal (Hailey *et al.*, 1984; Meek, 1988). In woodland populations in southern France summer activity is unimodal perhaps reflecting the lower heat loads in this habitat (Pulford *et al.*, 1984). Nevertheless it is interesting that maximum body temperatures of 34-

35°C have been measured in all of the populations studied so far, except during cooler Autumn weather. In areas of Greece where *T. hermanni* and *T. graeca* are sympatric, body temperatures of *T. hermanni* are on average lower than those of *T. graeca*; this is a reflection of differences in habitat utilisation (Wright *et al.*, in press).

A recent paper has demonstrated an unexpected element of subtlety in the thermoregulatory relationships of *T. hermanni* with its environment. Chelazzi and Calzolari (1986) have shown that in Italian tortoises thermoregulatory efficiency is dependent on habitat familiarity. This was demonstrated by introducing tortoises into an area alongside resident animals and monitoring their temperature and behaviour. Resident tortoises were found to reach maximum body temperatures on average two hours each day earlier than introduced animals and their body temperatures were less dependent on environmental temperatures; introduced animals behaved as thermoconformers with body temperatures closely tracking air temperatures. It was suggested that this thermal lag could have important ecological consequences for non-residents by reducing daily activity time and in females by affecting the maturation of ova. Clearly it would be of interest to know the length of time involved for a tortoise to familiarise itself with a new habitat and become a proficient thermoregulator. Such information could be important in conservation projects, for example when reintroducing captive-reared tortoises into areas where populations have been depleted through collection or habitat deterioration.

The work of Chelazzi and Calzolari also illustrates a need for investigation of the *mechanisms* by which chelonians respond with appropriate behaviour patterns to the thermal environment. What cues do they use? Experiments have shown that the lizard *Lacerta vivipara* may use light intensity, direction and distribution as cues (Avery and D'Eath, 1986; D'Eath, 1987). It is not known whether chelonians determine the distribution of heat in the environment in similar ways. This is an important gap in knowledge. Many observations and experimental results could be more readily interpreted if this information was available, for example nest site selection in *Testudo hermanni* and *Emydoidea blandingii*, which is believed to be governed by choice of substrates and temperatures which will optimise environmental sex determination (Swingland and Stubbs, 1985) — but see Meek (in press) for an alternative view — or embryological development (Gutzke and Packard, 1987).

The importance of environmental temperatures for successful incubation as a factor which influences the distribution of species is emphasised in a study of *Testudo graeca* in Morocco by Lambert (1983). This study shows that rainfall is also a contributory factor. In our opinion this promising approach could be extended even further to include the constraints imposed by thermoregulatory behaviour on the remaining activity patterns of the animals.

The results described above may give the impression that thermoregulatory considerations are always a major determinant of behaviour patterns in terrestrial

chelonians. This is not always the case, however; water balances appear to be of primary importance in the desert tortoise *Gopherus agassizii* (Nagy and Medica, 1986).

SEMI-AQUATIC CHELONIANS

It can be seen that the terrestrial chelonians which have been studied conform to the classic paradigm of diurnal heliothermy which has been investigated most thoroughly in lizards (Avery, 1982; Huey, 1982). The thermoregulatory behaviour of semi-aquatic chelonians is more variable and less easy to understand. Avery (1982) has discussed the complexities of thermoregulatory behaviour in these animals, drawing attention to studies which suggest that whilst the primary function of basking is to increase body temperature, it may have other functions.

Recent work has supported the view that the primary function of basking is thermoregulatory. The African terrapin *Pelomedusa subrufa* does not bask on non-sunny days or in a laboratory thermal gradient if the heat lamps are not switched on, but on sunny days it shuttles on and off basking sites, elevating body temperatures to around 37°C. The body temperatures of dead *P. subrufa* on basking areas may reach 54°C (Miller, 1979), which far exceeds the critical maximum of any chelonian (Hutchison *et al.*, 1966) demonstrating that thermoregulation whilst basking must involve a balance between heat losses and heat gains. Relationships between the frequency of terrestrial basking and weather conditions have been shown in *Pseudemys scripta* (Spotila *et al.*, 1984), *Chrysemys picta* (Bury *et al.*, 1979; Schwarzkopf and Brooks, 1985), *Pelomedusa subrufa* (Miller, 1979) and *Chelydra serpentina* (Ewert, 1976). These relationships have been analysed from a partly theoretical standpoint by Crawford *et al.*, (1983).

Two species which operate over a particularly wide range of body temperatures (3-32°C and 7.5-30°C respectively), are *Clemmys guttata* and *C. insculpta*; to a certain extent they are thermoconformers (Ernst, 1982, 1986a). Basking nevertheless occurs in both species; it is more frequently observed in females in late May and early June (Ernst, 1986a). Many species show latitudinal or seasonal differences in thermoregulatory behaviour, e.g. *Pseudemys scripta*, although in this case Spotila *et al.* (1984) have shown that it is the timing of behaviour which changes with latitude; the responses of the animals to the same environmental stimuli are similar in different parts of the range. The differences in timing are clearly adaptive.

There has been much debate about the functions of basking in semi-aquatic chelonians. It has frequently been shown that the frequency or duration of basking increase after feeding (see reviews and discussion in Huey, 1982 and Avery, 1982), but this does not always occur — basking in *Chrysemys concinna* for example, did not increase significantly after feeding (Henneman, 1979).

The thermal strategies of terrapins are clearly opportunistic. This is well illustrated by the study of *Pseudemys scripta* (which is the most extensively-studied terrapin species) by Spotila *et al.*, (1984), which

demonstrates aquatic basking (raising body temperatures to 1-3°C above ambient water temperature) and selection of heated areas of water in the outflow from a nuclear reactor. Thermoregulation in *P. scripta* is further discussed in an environmental context by Spotila and Standora (1985b). Crawford *et al.* (1983) suggested that terrapins might be able to reduce the amount of time thermoregulating by selecting basking areas with high operative environmental temperatures (these are rather complex measures of the heat which is available in the environment) and would therefore shift basking sites as the day progressed.

Other factors which may influence thermoregulatory behaviour have also been examined, for example the substrates of basking areas may determine bask duration (Boyer, 1965). Concrete has a high thermal conductivity and this may explain why Meek (1983) observed only limited basking by *Mauremys caspica* at a concrete irrigation channel in North Africa, although those individuals which did bask attained body temperatures of around 29.5°C. *Pseudemys scripta* thermoregulate to a selected temperature range when in a thermal gradient (Crawford *et al.*, 1980) and Jarling *et al.* (1984) have shown that there is a diel rhythmicity underlying this temperature selection with differing thermoregulatory behaviour between morning and afternoon.

The work of Erskine and Hutchison (1981) demonstrates that the pineal hormone melatonin may play a role in setting the temperature around which terrapins, like other reptiles (Firth and Turner, 1982), may thermoregulate. This is likely to become an active area for research in the next few years.

Hibernating terrapins do not appear to thermoregulate, despite some earlier reports that they might do so (work on *Chrysemys picta* by Peterson, 1986). Peterson also provides an important discussion of the problems in defining 'environmental temperature' in situations where radiant heat sources are negligible or absent.

MARINE CHELONIANS

Most of the recent studies of marine turtle thermoregulation have concentrated on physiological aspects (see below); there has been no major advance in understanding behaviour since Avery (1982) wrote 'Marine turtles may also absorb solar radiation whilst floating at the surface. Considerable elevation of shell temperature, and rather smaller elevation of deep body temperature, was reported in *Chelonia mydas* floating in shallow sea water in captivity (McGinnis, 1968). Under these conditions, a radiotelemetered 42 kg *Caretta caretta* maintained differentials between body and sea of up to 3.75°C when the sun was shining; it failed to do so on an overcast day (Sapsford and van der Riet, 1979). Further work is clearly needed to determine the significance of solar radiation for these animals'.

PHYSIOLOGICAL ASPECTS OF THERMOREGULATION

Ever since the discovery that sea turtles might exhibit some degree of endothermy there has been

intense interest in their thermoregulatory physiology (reviews in Bartholomew, 1982; Spotila and Standora, 1985a). It is perhaps not surprising, therefore, that this is the aspect of chelonian thermoregulation which has received most attention during the past 10 years. Standora *et al.* (1982), in a careful study of the distribution of heat in *Chelonia mydas* using sonic transmitters, radiotransmitters and implanted thermistors, showed that body temperatures of inactive adult turtles were rarely more than 1-2°C above the temperature of the surrounding water. Vigorously-swimming turtles, on the other hand, had temperatures in the pectoral region raised by as much as 7-8°C. It was only in the actively-moving parts of the body that temperatures were raised, however; calculations showed that the metabolically-derived heat would be unable to warm the whole body faster than about 1°C h⁻¹. Similar, although less detailed, experiments with *Dermochelys coriacea* gave essentially similar results (Standora *et al.*, 1984). Experiments on heat exchange rates suggest that larger turtles have a greater ability to thermoregulate than smaller specimens (Smith *et al.*, 1986).

Similar experiments on the heat exchange rates of terrapins have shown interesting differences between species. Soft-shelled turtles *Trionyx spinifer* heated faster than they cooled in water (by as much as a factor of two in small (<0.5kg) animals) but cooled faster than they heated in still air. Heart rates during heating exceeded heart rates during cooling at the same body temperatures in both media. This difference, called hysteresis, is particularly large in the marine turtle *Chelonia mydas* (Smith *et al.*, 1986). The ability of *Trionyx* to alter heat exchange rates is greater than that of any previously reported ectotherm in the same size range (Smith *et al.*, 1981; see also Khosatzky, 1981). *Terrapene ornata*, by contrast, showed no differences in thermal time constants (which are a measure of heat exchange rates) or heart rates when heated or cooled in water; their ability to adjust physiological control is clearly limited, and these animals must rely on behavioural mechanisms to thermoregulate (Adams and deCarvalho, 1984). How much this species actually does thermoregulate in nature is unclear, however (Fitch, 1956; Legler, 1960).

It is disappointing that physiological aspects of thermoregulation in terrestrial chelonians have not recently been studied, particularly in view of the relatively large size of some species and the insulating properties of the shell (Standora *et al.*, 1982). Spotila and Standora (1985) have shown how in a large *Chelonia mydas* walking on land along a beach in Costa Rica under the hot sun, deep body temperature rose by 7.8°C h⁻¹ (over 23 minutes), carapace surface temperature by 50.4°C h⁻¹ to reach 53.8°C, and plastron surface temperature by 16.7°C h⁻¹ to reach 42.9°C. They demonstrated that a nesting turtle would experience severe heat stress, even during overcast weather, and that if it attempted to nest during the day it would probably need to return to the water to prevent overheating before nesting was completed. Meek (in press) has reported on the rates of heat gain by a nesting *Testudo hermanni* under both hazy sunshine and when the sky was overcast. The data

suggest that during hot sunny weather nesting female tortoises too would run the risk of dangerously overheating, even at the latitude of 42° where this study was carried out.

The analysis of Spotila and Standora (1985) also demonstrates conditions which would enable sea turtles to bask on land (as they sometimes do, e.g. in the north western Hawaiian Islands, Whittow and Balazs, 1982), mainly when there is a sea breeze, relatively low levels of solar radiation, and using cooling strategies such as flipping sand onto their carapace and rear legs. These kinds of analyses could with profit be extended to terrestrial chelonians.

GENERAL CONSIDERATIONS: THE IMPORTANCE OF INTEGRATED STUDIES

It will have become apparent in this review that in those areas of chelonian thermoregulation where interest has been greatest — endothermy in marine turtles, the functions of basking, the ecological and behavioural constraints imposed by thermal limitations and requirements — a number of investigators have been active in publishing the results of experiments and observations. Progress in overall understanding has been slow, however. The reason for this has in our opinion been a lack of *integrative* studies in which physiological, ecological and behavioural factors have been investigated simultaneously, and considered as essential components in the complex of factors which has shaped natural selection in chelonians. Detailed studies, and especially those taking advantage of technological advances such as those in radioisotopes (e.g. Ward *et al.*, 1976), telemetry (e.g. Standora, 1982; Standora *et al.*, 1984) and infra-red thermography (e.g. Avery and D'Eath, 1986) must continue. Synthetic, integrative studies should however now be given a higher priority for further research.

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HYPOTHESIS:

A GEOLOGICAL BASIS FOR SOME HERPETOFAUNAL DISJUNCTIONS IN THE SOUTHWEST PACIFIC, WITH SPECIAL REFERENCE TO VANUATU

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INTRODUCTION

Vanuatu is generally considered to form part of the Outer Melanesian Arc, which runs from New Guinea through the Solomons and eventually to Fiji and Tonga (Holloway, 1979). Within the arc, however, Vanuatu is relatively isolated by the surrounding Johnson Trough, Vitiac Trench and Vanuatu Trench (Coleman, 1970). A spreading ridge is present to the east of the group. Recent work (Chase, 1971) indicates that until 6-8 mybp Vanuatu lay north of Fiji and Tonga, along the border of a wider arc, adjacent to the Vitiac Arc (Carney and MacFarlane, 1982). Until the Miocene Vanuatu maintained its position relative to Fiji. At that time it began to drift. Subsequent arc bending and counterclockwise rotation has resulted in its present position (Gibbons, 1985). This theory is consistent with the current thought that many orogenic belts are actually composites of smaller blocks (terrane) of varied origins (Craw, 1982). In general, support for the terrane accretion origin of

composite regions comes from magnetic anomalies, heat flow studies, bathymetry and stratigraphy. Terranes of the North American Cordillera (Irving, 1979; Coney *et al.*, 1980) and the central Philippines (McCabe *et al.*, 1982, 1985) have been particularly well documented. Terranes of the former have been used in an attempt to explain the biogeography of bolitoglossine salamanders (Hendrickson, 1986) and it is possible that some of the peculiarities of animal distribution in Vanuatu may also be explained by its past fragmentation and movement.

THE VANUATUAN FAUNA AND ITS AFFINITIES

The herpetofauna of Vanuatu has traditionally been regarded as depauperate Paupuan (Baker, 1928, 1929; Darlington, 1948), having suffered attrition through filter effects that have reduced diversity away from the New Guinea source area. This 'impoverished' fauna has, however, been supplemented by species of