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Basking Is Not of Thermoregulatory Significance in the "Basking" Freshwater Turtle Emydura signata

BEN MANNING AND GORDON C. GRIGG

We measured body temperatures of free-ranging Brisbane River Turtles, *Emydura* signata with radiotelemetry. These and other species of freshwater turtle are commonly observed "basking" on logs or other elevated sites, a behavior which is usually interpreted as thermoregulatory. However, body temperatures of eight *E. signata* monitored for more than 112 turtle days in winter, spring, and summer showed a striking thermoconformity with the water and provided no data showing that this species routinely elevates its body temperature above water temperature. The biological significance of basking is obscure in this population of *E. signata*, and the study highlights the need for direct measurements of body temperature in free-ranging individuals of other freshwater turtle species.

EPTILES are very diverse, both morpholog-**K** ically and ecologically, yet the present understanding of reptilian thermal relations has been derived primarily from studies of terrestrial Squamata, especially desert lizards (Avery, 1982). From these studies has grown the idea that reptiles that bask in the sun are behavioral thermoregulators that maintain high and reasonably stable body temperatures during diurnal periods of activity (Templeton, 1970). It is not surprising that, by extrapolation, basking behavior is thought to be of thermoregulatory significance in all reptiles, including the many freshwater turtles that emerge from the water onto logs or other elevated sites (Hutchison, 1979). In several species of cryptodiran freshwater turtles, basking occurs most frequently in warm, sunny, and windless weather and at times of the day that suggest basking would raise body temperature (e.g., Boyer, 1965; Auth, 1975; Crawford et al., 1983). However, the thermoregulatory interpretation is weak, having been inferred from circumstantial behavioral data (e.g., Spotila et al., 1984, 1990; Crawford et al., 1983) plus a small amount of body temperature data obtained either by direct measurement (Chelydra serpentina; Obbard and Brooks, 1979) or by telemetry from captive individuals (Pseudemys [= Trachemys] scripta; Auth, 1975). Standora (1982, unpubl.) also studied P. scripta by telemetry, but under natural conditions, and concluded that basking in that species was of thermoregulatory significance. Certainly he presented data that showed deep body temperatures rose during basking events. However, his summary graphs emphasize a pattern of thermoconformity with water temperature for most of the time, rather than being uncoupled from it for significant periods. This is to be expected in small to moderate-sized aquatic reptiles, because the

high specific heat of water dictates that they will lose heat quickly once they return to the water (Grigg et al., 1979). The functional significance of irregular warming events of short duration is not easily explainable. Moll and Legler (1971), working in the tropical end of the range of P. scripta, were sceptical about the thermoregulatory significance of "atmospheric basking" and provided a useful discussion. There seems to be agreement that freshwater turtles thermoregulate routinely by using warmer surface waters (Moll and Legler, 1971) and that "aquatic basking" may occur when opportunities present (Spotila et al., 1984). Missing, however, are long-term radiotelemetric studies of free-ranging turtles to determine whether or not body temperatures are uncoupled from water temperature by basking events sufficiently frequently and for long enough periods of time to be of thermoregulatory significance.

Species of the Australian pleurodiran genus Emydura have been observed to "bask" both terrestrially and aquatically (Webb, 1978; Legler and Georges, 1993), and Chessman (1987) reported high cloacal temperatures from E. macquarii caught while basking. (Note: Emydura macquarii and E. signata may not be distinct taxonomically. Georges and Adams [1992], using allozyme electrophoresis and making comparisons at 54 independent loci, were unable to separate them from each other or from E. krefftii.) Although consistent with expectations, these data do not provide an adequate evaluation of the role of basking in the species. There are, for example, no data on the frequency of basking, yet frequent basking could be expected if the significance is thermoregulatory. Also, there are very few direct measurements of body temperatures in any freshwater turtles under natural conditions.

We decided to conduct an intensive radiotelemetry study of thermal relations in *E. signata*, working on animals in the field where they would have opportunities to pursue their normal lifestyle, free from artifacts introduced by captivity (Moll and Legler, 1971; Balasz, 1974) and less likely to be suffering from infections (Monagas and Gatten, 1983).

One of us (BM) was quite familiar from the outset with this species at the chosen study site, a small river with shallow rapids connecting pools typically 1–1.5 m deep, with steep grassy banks and overhung in places with riparian vegetation. We know from experience that, if the pools are approached stealthily, small numbers of turtles would often be seen out of the water on exposed logs and rocks, as if basking. We expected that long-term monitoring of a number of turtles by radiotelemetry would allow us to describe the pattern and extent of thermoregulation and would disclose the extent to which thermoregulatory basking was a routine event in the life of an individual.

MATERIALS AND METHODS

We collected eight adult *E. signata* from the study area in the headwaters of the Albert River, Queensland $(28^{\circ}11'S, 153^{\circ}02'E)$ in autumn 1993, to monitor body temperatures by telemetry until the following summer. Animals ranged in body mass from 1200–1470 g and in curved carapace length from 24–26 cm. All but one were male.

We implanted a calibrated, temperature-sensitive radio transmitter (Sirtrack, NZ) into each animal under sterile conditions using halothane-in-oxygen anesthesia delivered by a 1.5 mm o.d. tube placed into the trachea. The lungs were inflated manually, under positive pressure from the anesthetic machine, every 2-3 min during the procedure, which took approximately 60 min, including 15 min or so to induce anaesthesia. In the implantation procedure, an anaesthetized turtle was held right side down in a custom made frame, with the left hind leg taped out of the way posteriorly. The transmitter was placed inside the peritoneal cavity through an incision made in the flank anterior to the left hind leg and left to float freely within. We closed the incision with an inner row of dissolving sutures and an outer row of surgical silk. Individuals recovered from the anesthetic within an hour or so. The procedure caused no apparent side effects, because all turtles resumed feeding the day after the surgical procedure. They were released in a large pool central to the study site either immediately or a

few days later. Descriptions of our general procedures for preparing, implanting, and monitoring radio transmitters can be found in Grigg et al. (1990, 1992). Briefly, we covered transmitters in wax (Paraffin and Elvax 80:20) and calibrated them in a water bath against a certified thermometer over a temperature range from 4-45 C with calibration steps of 1.5-2.0 C. They measured approximately $3 \times 2 \times 2$ cm, weighed < 2% of body mass, and had a longevity of more than one year.

Fieldwork took place in winter (May-July 1993), spring (September-October) and summer (November-January, 1993-1994). Weather was typically cool clear days in winter and warm clear/cloudy days in spring and summer. Signals from the transmitters were recorded either manually, with a Telonics TR-2 receiver and a stopwatch, or remotely, with a recording receiver recorder system using a Telonics TR-2 receiver-scanner and tape recorder turned on at predetermined time intervals by a specially built electronic timer (Grigg et al., 1990). Typically, we could detect a signal 200 m away from a turtle in the water, 300 m at a maximum. Basking E. signata dive into the water at the slightest disturbance, so we resolved to rely primarily on data collection using the remote sampling system, avoiding the possibility of artifacts being introduced by the presence of observers during manual sampling. About 98% of the measurements were collected in this way. The recording system was often on a small knoll overlooking the study site, from which several transmitters could be heard. However, turtles moved between pools along the river (one moved 15 km), and we sometimes set up the system elsewhere to collect data from as many individuals as possible. The system's timer was usually set to collect data hourly. We changed recording tapes and the batteries of recording systems quietly and under the cover of darkness so as not to disturb the turtles. Precalibrated thermistor probes connected to a chart recorder (Grant Instruments) measured shaded air temperature beside the river and water temperatures at depths of 10 cm (surface), 40, 90, and 120 cm (bottom). These measurements were synchronized with the times of sampling body temperatures whenever possible.

RESULTS

We made almost 3000 measurements of body temperature, approximately 70% of them in winter, the remainder in spring and summer. Data were collected in all three seasons from six of the eight animals; two were sampled only in

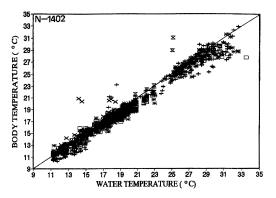


Fig. 1. Body temperatures of *Emydura signata* measured in daytime (dawn to dusk), plotted against corresponding water temperatures at 40 cm depth, all seasons pooled. Different symbols represent data from different turtles. The solid line represents Tb = Tw.

summer. Average water temperatures ranged from 13 C in winter to 27 C in summer.

Data indicated that *E. signata* at this location did not routinely uncouple their body temperature from that of the water. Indeed, they showed remarkable thermoconformity with it. Most body temperatures, by both day and night (Figs. 1–2), were within 2 C of water temperature at 40 cm depth and not discrepant from temperatures that would have been available to them within the water column (Fig. 3). Of the measurements of body temperature collected in daytime, only 10 (from three individuals) of 1402 in all seasons suggested that turtles were out of the water (Fig. 1), suggesting that basking to the extent that body temperatures are raised is a very rare occurrence. Concerning the pos-

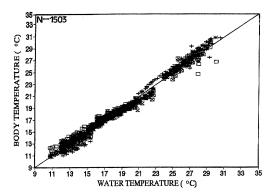


Fig. 2. Body temperatures of *Emydura signata* measured at night time (dusk to dawn), plotted against corresponding water temperatures at 40 cm depth, all seasons pooled. Different symbols represent data from different turtles. The solid line represents Tb = Tw.

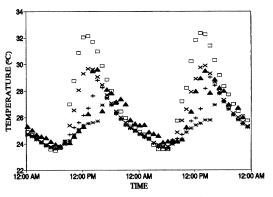


Fig. 3. A series of measurements taken over two consecutive days in January (summer), showing a typical pattern (turtle 330 in this case) of body temperatures (\blacktriangle) and water temperatures at the surface (\Box) and at depths of 40 cm (×), 90 cm (+) and 120 cm (*).

sibility of aquatic basking, the degree of variation in body temperature around the line of equality is higher by day (Fig. 1) than by night (Fig. 2), reflecting the greater range of water temperatures available by day, as thermoclines develop (Fig. 3). However, turtles apparently took no particular advantage of warmer water at the surface, with body temperatures being lower than rather than equal to surface water temperatures during the day (Fig. 4).

DISCUSSION

The results of the study provide no data to suggest that E. signata commonly elevates its body temperature by emerging from the water to bask. The term basking, with its thermoreg-

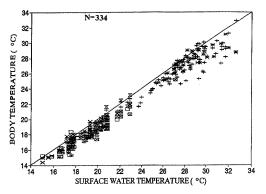


Fig. 4. Body temperatures of *Emydura signata* measured on days when surface water was distinctly warmer, plotted against corresponding surface water temperature, all seasons pooled. Different symbols represent data from different turtles. The solid line represents Tb = Tw.

ulatory implications, may be inappropriate to apply to the emergence behavior of this species. Its occurrence for periods of time long enough to result in a raised body temperature is apparently so rare that it can hardly be considered to be of routine thermoregulatory significance. The 10 observations we do have of "warm" turtles deserve comment. One possibility is that they were the result of a "behavioral fever," sensu Monagas and Gatten (1983). Another possibility is that they are the result of chance events, from turtles happening to remain in the sun for a long enough period to become warm. However, the turtles are clearly thermoconformers with only very rare exception and, indeed, seem very tolerant of low temperatures. As winter advanced and water temperatures fell, so did body temperatures, yet turtles remained active yearround. In addition, they showed little tendency to select the warmer water temperatures available, in contrast to observations made on P. scripta (Moll and Legler, 1971; Spotila et al., 1984).

There is another possible, but unlikely, interpretation of these data, which is that the telemetered individuals were affected in some way by the implantation and remained in the water as a consequence of that. However, the behavior of telemetered individuals in captivity prior to their release appeared totally normal, with vigorous response to offered food and energetic swimming to compete with their colleagues for it. Also, recaptured individuals showed healed incisions and good health, so we think that this interpretation is most unlikely.

The contrasting thermal properties of aquatic and terrestrial environments may explain why E. signata does not thermoregulate by basking. The high specific heat of water gives aquatic habitats a cooling power 50-100 times that of terrestrial environments (Schmidt-Nielsen, 1988) and confers also much higher thermal stability (Clapham, 1983). Accordingly, the costs (Huey and Slatkin, 1976) of maintaining body temperatures significantly above water temperature would be very high in terms of time lost in foraging and longer exposure to predation. Indeed, there are numerous precedents for thermoconformity among Chelonia and other primarily aquatic reptiles. Small marine turtles mostly show thermoconformity (Read et al., 1996). Crocodilians at smaller sizes are primarily thermoconformers (Grigg and Gans, 1993). Even though they may emerge during the day to bask on land, they spend most of the time in the water with body temperature at or close to water temperature. Indeed, Seebacher and Grigg (1997) have proposed, based upon observed seasonal changes in the preferred body temperature range seen in thermoregulating individuals, that *Crocodylus johnstoni* may show metabolic acclimatization in response to seasonal changes in water temperature. Given the marked seasonal changes in water temperature, their thermoconformity, and their year-round activity, *E. signata* too are likely to show an ability to undergo thermal metabolic acclimatization.

Because this species of turtle is frequently seen out of the water, apparently basking, and because a thermoregulatory interpretation of turtle basking behavior is embedded firmly in the literature, we were surprised at our results. However, conclusions about the thermoregulatory significance of basking in other species have been inferred mostly from observations of a coincidence between basking activity and the occurrence of sunny conditions or high ambient or operative temperatures (e.g., Auth, 1975; Obbard and Brooks, 1979; Crawford et al., 1983). There have been few telemetry studies. Auth (1975) telemetered body temperature from a single captive individual measured over three days and found elevated body temperatures on the two days that were sunny. It is difficult to extrapolate this finding to a whole freeranging population, a point apparently recognized by Auth because he drew attention to the need for a more extended study of unrestrained individuals. Obbard and Brooks (1979) measured cloacal temperatures of 12 of 246 Chelydra serpentina seen basking and found them to be, on average, 4.2 C warmer than air temperature. Basking frequency, even at this high latitude study site (Algonquin Park, Ontario, Canada, 46°N) was quite low, about one day in four (on four radio-tagged individuals). Schwartzkopf and Brooks (1985), studying a population in the same area, found that most basking events lasted less than one hour, so the proportion of time with body temperatures significantly above water temperature would seem to be quite low in this species too. Standora (1982) used radiotelemetry to monitor body temperatures in freeranging P. scripta and described basking events that led to increased body temperature, especially in spring. He concluded that basking is of thermoregulatory significance in this species, yet his summary figures emphasize the turtles overall thermoconformity with water temperatures, rather than their being uncoupled from it for significant periods. This, really, is what would be expected in an aquatic reptile of small to moderate body size. Grigg et al. (1979) presented generalizations that describe relationships between body mass and thermal time constants for lizard-shaped reptiles heating and cooling in water and in air. Some data for Chelonia were presented, also, from which it can be concluded that thermal time constants (τ) of between 600 and 1200 sec would be expected for 500-2500 g P. scripta cooling in water. Standora's data are not at variance with this prediction. It is clear that heat gained by small and moderate-sized turtles in bouts of atmospheric basking would be lost rapidly upon their return to the water and that their body temperature in a 24-h period will be dictated overwhelmingly by water temperature unless they remain out of water for most of the time. What, if any, benefit accrues from short, occasional periods at a higher body temperature remains to be determined, and it is possible that the higher body temperatures accompanying atmospheric basking in those species that employ it routinely may be a by-product of a behavior undertaken for some other benefit. One is left with the conclusion that the importance of basking in turtle thermal relations may have been overemphasized.

What then may be the significance of basking in *E. signata*, in southeast Queensland at least? Two other advantages suggested to accrue from atmospheric basking are the retardation of algal or fungal skin infestations (Moll and Legler, 1971), which are fatal in their advanced stages (Neill and Allen, 1954), and the synthesis of vitamin D (Pritchard and Greenhood, 1968). Neither requires that body temperature be raised, so both can be regarded as plausible hypotheses to explain the basking behavior in *E. signata* and perhaps other species as well. These ideas require further evaluation.

In short, we consider that atmospheric basking by *Emydura* is unlikely to be of thermoregulatory significance. Further, we believe that conclusions about the thermoregulatory significance of this behavior in other species of freshwater turtles are premature, based on present data. More information is needed about the frequency, extent, and duration of basking events that lead to body temperatures being significantly uncoupled from water temperature. In any species where significant uncoupling occurs routinely, a more critical approach will be needed to discriminate between thermoregulatory or other significance.

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