# Use of Thermal Springs for Aquatic Basking by the Pig-Nosed Turtle, Carettochelys insculpta

J. SEAN DOODY<sup>1,2</sup>, RACHEL A. SIMS<sup>1</sup>, AND ARTHUR GEORGES<sup>1,2</sup>

<sup>1</sup>Applied Ecology Research Group, University of Canberra, ACT 2601, Australia [Fax: 61-26-201-5305; E-mail: doody@aerg.canberra.edu.au]; <sup>2</sup>Co-operative Research Centre for Freshwater Ecology, University of Canberra, ACT 2601, Australia

ABSTRACT. - During a three-year ecological study of the pig-nosed turtle (Carettochelys insculpta) in the wet-dry tropics of northern Australia, we documented the turtles' use of small, localized thermal springs discharging from the river bottom. Dataloggers attached to the carapace to monitor ambient water temperatures recorded the frequency and duration of thermal spring use by individuals. Turtles used the thermal springs frequently during the winter (4-6 months) when river temperatures were lower than that of the thermal springs ( $\overline{x} = 29 \pm 0.52^{\circ}$ C). Turtles often utilized thermal springs for several consecutive hours, leaving the springs only to surface for air. Thermal springs may be derived from groundwater (which maintains a temperature equivalent to the annual mean air temperature), rather than from a specific geothermal heat source. Nine of 19 radio-telemetered adult females were seen to use thermal springs, of which seven were gravid and two non-gravid. Thus, gravid turtles may seek thermal springs more than non-gravid turtles. Frequency, duration, and timing of usage collectively suggest active thermoregulation as the primary function of thermal spring use. Utilization of thermal springs probably permits turtles to be more active in cooler months, which may enhance growth rates and accumulation of energy for reproduction. Onset of nesting along river stretches with thermal springs preceded nesting in a stretch not known to have thermal springs by 24 days. Thus, we speculate that by warming themselves on thermal springs in the months prior to nesting, turtles may have accelerated follicular development and nested earlier.

KEY WORDS. - Reptilia; Testudines; Carettochelyidae; *Carettochelys insculpta*; turtle; ecology; basking; thermoregulation; thermal springs; movements; reproduction; nesting; Australia

Thermoregulatory basking behavior is widespread among aquatic turtles, spanning marine, freshwater, and semi-aquatic forms (e.g., Whittow and Balazs, 1982; Ernst, 1986; Krawchuck and Brooks, 1998). Moll and Legler (1971) recognized two forms of basking. Aquatic basking occurs when turtles float close to the surface, taking advantage of the warmth of the surface stratum of water and perhaps benefiting directly from absorption of solar radiation. Atmospheric basking occurs when turtles climb onto emergent logs, rocks, or banks to bask directly in the sun's rays. While less is known of the consequences of aquatic basking (Chessman, 1987), atmospheric basking has been shown to raise body temperatures of turtles (Moll and Legler, 1971; Standora, 1982; Crawford et al., 1983; King et al., 1998; Sajwaj and Lang, 2000), though the elevated temperatures can be quickly lost when the turtles return to the water (Manning and Grigg, 1997). Thermoregulation is thought to be the primary function of basking behavior (Crawford et al., 1983), but there could be other attendant advantages such as removal of algae (Neill and Allen, 1954; Boyer, 1965) or ectoparasites (Cagle, 1950), or promotion of Vitamin D synthesis (Cagle, 1950). In turn, thermoregulation can influence ingestion (Kepenis and McManus, 1974; Parmenter, 1980), digestion (Kepenis and McManus, 1974), retention rate (Spencer et al., 1998), intestinal motility (Studier et al., 1977), metabolism (Bennett, 1982; Jackson, 1971), activity (Gatten, 1974; Parmenter, 1981), and growth (Christy et al., 1973; King et al., 1998).

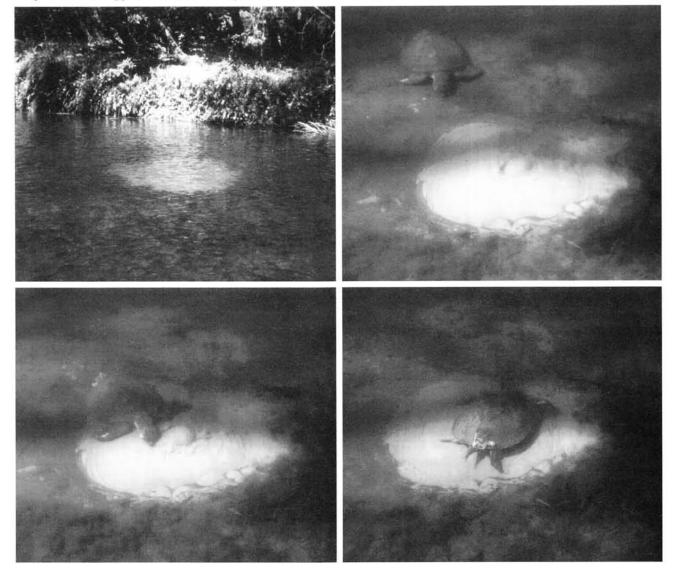
The pig-nosed turtle, Carettochelys insculpta, is a large freshwater cryptodire restricted to northern Australia and southern New Guinea (Georges and Rose, 1993). We initially observed individual C. insculpta spending much of their time resting on localized thermal springs discharging from the river bottom during the cooler months in Australia. As part of a larger study investigating the influence of reproductive condition on movements, we fitted temperature dataloggers and radio-transmitters to adult female Carettochelys (gravid and non-gravid). Our objectives were to determine how often and when turtles used thermal springs, and to determine the influence of reproductive condition on thermal spring basking in females. In some reptiles, gravid females bask more than non-gravid females (e.g., Charland and Gregory, 1990; Schwartzkopf and Shine, 1991). We also compared water temperatures of thermal springs to those in various microhabitats, and to the seasonal change in river temperature. Thus, we report a new behavior in turtles, and a rare and different form of aquatic basking. We also present evidence that access to thermal springs for thermoregulation may have influenced timing of nesting.

### MATERIALS AND METHODS

We studied *Carettochelys* in a 30 km stretch of the Daly River at Oolloo Crossing, Northern Territory, Australia (14°04'40"S, 131°15'00"E), from July to early October 1998. The Daly is a large river with moderate flow in the wetdry tropics. During the dry season, the river is mostly springfed, between 50 and 80 m wide, and averages 1.5 m deep at the study site. Following late wet season flooding in February and March, the river typically clears by May, with visibility approximately 3 m.

Turtles were captured with dipnets from boats, by diving, and with hoopnets (after Legler, 1960) baited with wallaby (*Macropus agilis*) meat. Nineteen female turtles (9 gravid, 10 non-gravid) were fitted with radio-transmitters (Sirtrack two-stage, waterproofed in epoxy). Radio-transmitters were mounted on aluminum plates bolted to the rear edge of the carapace, off-center. Neoprene was fitted between the plate and the turtle to reduce skin damage. Reproductive condition was determined in the field by radiography using a portable x-ray machine (EXCELRAY<sup>®</sup> 31-HR-100P, settings 60 KVP, 30 MA, 0.4 sec), and a makeshift darkroom. Each turtle was also equipped with a Stowaway<sup>®</sup> temperature datalogger, which was waterproofed with two balloons and attached to a cattle ear tag (Allflex<sup>®</sup>) with waterproof tape. The cattle ear tag was then fastened to the trailing edge of the carapace. Cattle ear tags were a proven marking technique in 1996–97. Datalogger packages were numbered for individual identification from a distance. Dataloggers recorded temperatures every 16 minutes for 20 days.

In most cases turtles were located during daylight hours, several times a week throughout the study, though a few were not located until after the study was completed. Two individuals were intensively tracked (up to 3 fixes per day) throughout the study. Turtles were recaptured when possible near the end of the 20-day period, and dataloggers were downloaded and re-launched for a second 20-day period. We also investigated the duration of thermal spring use by intensively monitoring a thermal spring for 2–4 continuous hours on four different days. In addition we made opportunistic observations of any turtles on thermal springs throughout the study.



**Figure 1.** Thermal springs in the Daly River, which are difficult to detect during the warmer months, become conspicuous after being used by turtles. Turtle activity around the thermal spring harrows a circular area of sand, free of algae and debris (top left). Subsequent series (top right, bottom left, bottom right) shows a male *C. insculpta* approaching and basking on a thermal spring.

Thermal springs were found by noting cleared areas of sand on the river bottom or by discovering a group of turtles concentrated in a very restricted area. The cleared areas associated with thermal springs resulted from a combination of instability in the sand through which the water was passing, which prevented algal accumulation, and the activity of turtles. We confirmed the presence of a thermal spring by snorkeling, during which time a temperature was taken with a calibrated alcohol thermometer inserted 5 cm into the sand. The thermal springs were flagged to aid in future location. Turtles were determined to be using thermal springs when they could be seen on the cleared circle, or were within 10 m of a thermal spring as determined by radiotelemetry.

To determine the overall thermal environment available to the turtles, Stowaway® dataloggers were placed in four microhabitats thought to bracket available water temperatures. These microhabitats were: (1) open, shallow pools (0.5 m deep) with low flow, (2) open bedrock flat (1 m deep) with moderate flow, (3) open sand flat (1 m deep) with fast flow, and (4) shaded deep pool (2.5 m deep) with low flow in a logjam. Dataloggers were attached to a star picket and sensors were fastened just above the river bottom, where C. insculpta spends the majority of its time (pers. obs.). Microhabitat dataloggers were calibrated and recorded temperatures once every hour for 75 days throughout the season in 1998. River temperatures were recorded every 15 minutes between May and November, 1996-98 using Datataker® Model DT500 dataloggers. River temperature data are presented as spline functions of mean daily temperatures.

Timing of nesting was determined in two ways, depending on the river stretch. In the 30 km stretch in which an intensive nesting study was being conducted, nesting surveys were conducted daily and actual nesting dates were obtained. In the other two stretches, which were adjacent and upriver, nests were located on surveys that were 8–10 days apart. Nesting beaches, as characterized by Georges (1992), were located with the aid of a motorboat. Nests were found by following tracks left by gravid turtles, by noting slight depressions in the sand, and by probing the sand.

#### RESULTS

Description of Thermal Springs. — We located 25 thermal springs in a stretch of river ca. 25 km in length. The substratum disturbance caused by emerging water in the thermal springs varied from a few to 70 cm in diameter for single springs, however, aggregations of discharge points often resulted in a sandy area clear of algal growth up to 2 m in diameter (Fig. 1). Most thermal springs were in sandy substrates. Temperatures of thermal springs at 5 cm sand depth averaged  $29.9 \pm 0.52^{\circ}$ C (range =  $29.5-31.0^{\circ}$ C; n = 10). The thermal springs may be derived from groundwater (which maintains a temperature equivalent to the mean annual temperature), rather than from some specific geothermal source of heating. Thermal springs ceased to influence water temperature 7 cm above the substrate. The

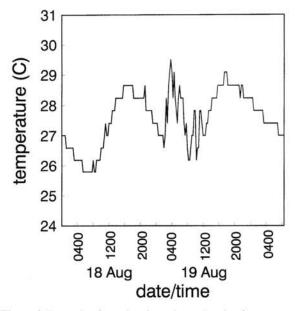


Figure 2. Example of a turtle using a thermal spring for an extended period of time between 0200 and 1100 hrs, 19 August. Data are ambient water temperatures recorded from a Stowaway<sup>®</sup> datalogger attached to the turtle's rear carapacial edge. The figure shows a background sinusoidal variation in daily river temperatures for two days, interrupted by thermal spring use causing a narrow spike in temperature.

temperature of many other springs in the river did not differ from that of the surrounding river water, and turtles were not seen to use these.

Frequency and Duration of Thermal Spring Use. — Turtles were seen resting on thermal springs (Fig.1) a total of 157 times (females = 147, males = 4, unknown = 6). Of these, 136 sightings were of 9 telemetered females. Turtles often remained on the thermal spring for several hours (Fig. 2). During 9.5 hours of intensive radio-tracking, we found two turtles to use thermal springs 79 and 85% of the time. Turtles used the thermal springs both by day and night (Figs. 2, 3).

Behavior. - Observations of turtle behavior on the thermal springs were difficult due to the turtles' wariness of approaching boats, and our diving was infrequent due to the threat of saltwater crocodiles (Crocodylus porosus). However, we made a few observations. Turtles were tolerant of one another when using thermal springs; as many as five were seen sharing a single spring. For nearly one month, two females simultaneously utilized the same thermal spring. In one case, however, a large female apparently displaced a smaller female from a thermal spring, with the displaced female immediately moving 300 m downstream to another thermal spring. One telemetered female was seen to partially bury herself in the sand of a thermal spring, flip sand over her shell with her hindlegs, then bury down into the spring. However, it is difficult to rule out the possibility that the turtle was attempting to hide from us.

Gravid vs. Non-Gravid Turtles. — Nine of the 19 telemetered females were seen using thermal springs; 7 of these turtles were gravid. While this was suggestive of an association between reproductive condition and propensity to use the thermal springs, the result was only marginally

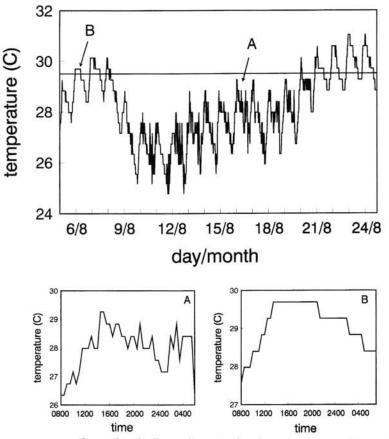


Figure 3. Top: A 20-day temperature trace from a female *C. insculpta*, showing thermal spring use. The straight line indicates the modal temperature of thermal springs in the river. Bottom: Note the spiked profile (A) indicative of thermal spring use when river/external body temperatures average below that of the thermal spring, compared to the step profile (B) exhibited when average river temperatures are similar to that of the thermal spring.

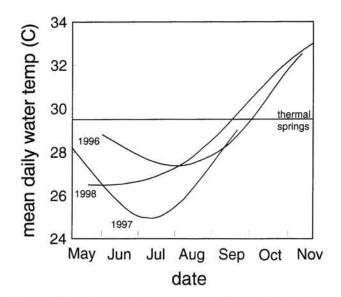
significant (p = 0.051, Fisher's Exact Test). Thirteen of 19 datalogger packages were attacked by freshwater crocodiles (*Crocodylus johnstoni*), as evidenced by teeth marks in the packages, resulting in datalogger failure, and loss of dataloggers.

Temporal Patterns. — The behavior of one turtle (Fig. 3) in August provides an example of seasonal thermal spring use. Turtles used thermal springs when river temperatures were cooler than that of the thermal spring, but not when river temperatures were warmer or averaged that of the thermal spring. Temperature traces of 3 other turtles of 9–10 days each showed a similar pattern of use. Seasonal change in water temperatures during 1996–98 (Fig. 4), compared to the modal temperature of thermal springs, indicates the seasonal periods when turtles are likely to be associated with the thermal springs. This pattern was supported by observations of turtles ceasing to use the thermal springs by 9 September in 1998.

*Microhabitat Temperatures.* — The shallow open pool exhibited the highest and most variable temperatures, while the deep shaded pool showed lower temperatures (Fig. 5). Between these two microhabitats, temperatures differed by 2–4°C. The deep pool was generally 2°C cooler than the rock and sand flats, which were nearly identical.

*Timing of Nesting.* — In 1998, nesting began significantly earlier ( $F_{1,121} = 47.62$ , p < 0.001; Fig. 6) in a 27 km

river stretch with numerous thermal springs ( $\overline{x} = 30$  July) than in a 28 km stretch where thermal springs are not known to occur ( $\overline{x} = 23$  August). A similar difference was noted in 1997 but data were confounded by sampling effort.

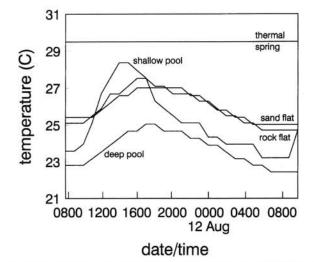


**Figure 4.** Mean daily water temperatures for the Daly River during 1996–98. The straight line represents the modal temperature of thermal springs in the river. Figure shows that *C. insculpta* could use thermal springs to thermoregulate for between 4 and 6 months a year.

## DISCUSSION

Thermal Spring Use. - The frequency (Fig. 3) and duration (Fig. 2) of thermal spring use, coupled with river temperatures during the cooler months (Fig. 4) suggest that thermal springs are important to Carettochelys for up to five months of the year. Turtles were regularly seen on thermal springs between July and September in 1996-98. Temperature profiles from four turtles provided evidence that turtles used thermal springs when river temperatures were cooler, but ceased using them when river temperatures rose (see Fig. 3). Indeed, once river temperatures exceeded those of thermal springs in September 1998, turtles were no longer seen on thermal springs, the cleared areas around them (Fig. 1) being no longer evident. A similar pattern was observed for four species of percid fish, which were attracted to a thermal effluent only during the cooler months of the year (Benda and Proffitt, 1973). We suggest that thermal spring basking is a complex behavior, as turtles would habitually seek out particular thermal springs. Some turtles were seen to use the same thermal spring for over a month, while others moved between different thermal springs. Five chelid turtle species common in the river (Chelodina rugosa, Elseya dentata, Emydura victoriae, Emydura subglobosa, Emydura tanybaraga) were not observed to use thermal springs.

Owing to datalogger failure we were unable to adequately test the hypothesis that gravid female *Carettochelys* used thermal springs more frequently than non-gravid females. However, of the 9 telemetered females recorded using thermal springs, 7 were gravid, and an additional 3 non-telemetered females seen using thermal springs were all



**Figure 5.** Example of environmental temperatures of different microhabitats available to *C. insculpta* in the Daly River on 11–12 August. Shallow pool was open, low flow, 0.5 m deep. Deep pool was shaded, low flow, 2.5 m deep. Sand flat was open, high flow, 1 m deep. Rock flat was open, moderate flow, 1 m deep. Straight line represents modal temperature of thermal springs.

gravid. Collectively, this suggests that gravid females may have used thermal springs more than non-gravid turtles, but this needs to be verified.

*Microhabitat Temperatures.* — Environmental temperatures were similar among the sand and rock flat microhabitats, but warmer and more variable in the shallow pool, and cooler in the deep shaded pool (Fig. 5). Although turtles could potentially raise their body temperatures by using the shallow pools, in our three years of fieldwork *C. insculpta* was rarely seen in this microhabitat. This is not surprising, as this shallow sandy area provided no cover or food.

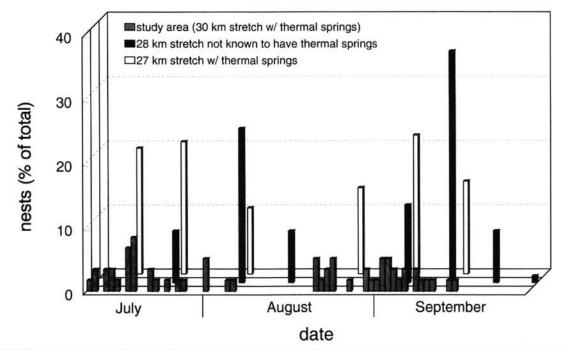


Figure 6. Differences in timing of nesting of *C. insculpta* in particular stretches of river. Gray bars represent laying dates in the study area where thermal springs are prevalent. White bars represent dates found for nests in the stretch immediately adjacent and upstream of the study area where thermal springs are also present. Black bars represent dates found for nests in the stretch adjacent to that represented by the white bars, but where no thermal springs have been observed.

*Carettochelys* is an extremely aquatic turtle, and is not known to exhibit atmospheric basking. Further, we have not seen this species engage in typical aquatic surface basking in three years of study. Turtles could, however, raise their body temperatures by resting on thermal springs.

Potential Consequences of Thermal Spring Use. — Crawford et al. (1983) reviewed potential reasons for basking behavior in turtles, and concluded that thermoregulation was the primary factor influencing basking behavior in the turtle *Trachemys scripta*. We suggest the same for thermal spring basking in *Carettochelys*, although other reasons may exist. By warming themselves on thermal springs in winter when river temperatures are cooler, turtles could maintain higher metabolic, ingestion, and digestive rates (Jackson, 1971; Kepenis and McManus, 1974; Parmenter, 1980; Bennett, 1982), intestinal motility (Studier et al., 1977), retention rates (Spencer et al., 1998), activity levels (Gatten, 1974; Parmenter, 1981), and growth rates (Christy et al., 1973; King et al., 1998).

Studies manipulating food intake found that fed turtles basked more than unfed turtles (Gatten, 1974; Hammond et al., 1988). In some stretches of the Daly River, *C. insculpta* may facilitate digestion by basking on thermal springs after feeding, but this remains speculative. Alternatively, turtles may forage after achieving a preferred body temperature, taking advantage of the inertial resistance to heat loss due to their large body size (Bartholomew and Tucker, 1964). Regardless, thermal spring basking during the cooler months probably permits turtles to be more active a greater percentage of the year (Parmenter, 1980).

Manning and Grigg (1997) questioned whether atmospheric basking in aquatic turtles was of thermoregulatory significance. Much of their argument rested on the fact that the turtles they studied (*Emydura signata*) spent only brief periods out of water raising their body temperature, only to return to the water and rapidly lose heat. They argued that the net result was that turtles were thermoconformers, their body temperatures effectively not uncoupled from water temperatures. We feel that the long periods *C. insculpta* spent basking on thermal springs during the cooler season, combined with their large body size, supports a thermoregulatory phenomenon.

Turtles inhabiting stretches of river with thermal springs nested, on average, 24 days earlier than turtles nesting in stretches not known to have thermal springs (Fig. 6). This may represent a consequence of frequent thermal spring basking. Increased basking could accelerate follicular development (Whittow and Balazs, 1982), and has been associated with earlier parturition in gravid viviparous reptiles (Shine, 1980; Schwartzkopf and Shine, 1991). Two studies found no difference in basking frequency and duration between male and female *Chrysemys picta* during extended periods prior to nesting (Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998). However, *C. picta* females basked longer than males on days just prior to and during nesting (Krawchuk and Brooks, 1998). *Chelonia mydas* basked more during the breeding season, and less as the nesting season progressed (Balazs, 1980). Gravid *Podocnemis expansa* are known to bask only 2–3 weeks prior to, and during nesting (Mosquiera Manso, 1960), a behavior presumed to play a role in egg maturation (Pritchard and Trebbau, 1984). In the laboratory *Trachemys scripta* females basked more than males in spring/summer, but not in autumn/winter (Hammond et al., 1988). *Emydoidea blandingii* females basked more than males during the fall, but not during the spring (Sajwaj and Lang, 2000).

This putative connection between thermal spring basking and timing of nesting in C. insculpta may be spurious, as we cannot be certain that thermal springs did not exist in the stretch of river where we found no thermal springs. However, once used by turtles, thermal springs are conspicuous (Fig. 1), and we did not detect thermal springs in the stretch in over 20 nest surveys in 1996-98. Although some other factor may have caused the differential timing, we can find no other differences between the stretches, except the availability of ribbonweed (Vallisneria), the preferred food of C. insculpta in the Daly (Heaphy, 1990; M. Welsh, unpubl. data). The paucity of ribbonweed in the upper stretch may have caused a delay in nesting by limiting energy uptake, thereby slowing follicular development. Christens and Bider (1987) found that the onset of nesting in the turtle Chrysemys picta was affected by mean air temperatures the previous year rather than temperatures in the current year, suggesting that productivity and food availability were implicated. Lastly, just prior to nesting, at least some gravid C. insculpta aggregate, moving from beach to beach in groups of up to 12 animals (pers. obs.). It is possible that the behavior of such a group influences the exact timing of nesting, thus affecting data independence.

In summary, the apparent importance of thermal springs to C. insculpta warrants further research. In particular, internal body temperatures, monitored by temperature-sensitive radio-transmitters, are needed to accurately characterize the thermal biology of the turtles. The present study recorded ambient water temperatures around the turtles, which are only indicative of body temperatures. Determining the ultimate importance of the thermal springs to Carettochelys would be challenging but worthwhile. For example, Christy et al. (1973) found that, compared to those in nearby natural sites, Trachemys scripta inhabiting thermal effluent areas near a fossil-fuel generating plant grew faster and attained a larger body size. However, because the thermal effluent area was extensive, observed growth differences could be due to either direct effects of temperature (i.e., increased metabolic and digestive rates) or indirect effects (increased productivity of food items). Due to their point-source nature, thermal springs would be expected to elicit only direct effects on turtles. Laboratory studies manipulating body temperature and examining its influence on digestive efficiency and growth would be revealing, while investigating effects on timing of reproduction would be logistically difficult.

#### ACKNOWLEDGMENTS

We are grateful to the following people for assistance in the field: J. Young, R. Alderman, B. Christiansen, C. Deen, M. McKenzie-Gay, M. Pauza, A. Pepper, S. Sims, A. Swindle, M. Welsh. We also thank S. Sims for designing datalogger packages, and special thanks go to B. Doyle and E. Doyle for providing accommodation. Logistical support was provided by the Applied Ecology Research Group, University of Canberra. This work was supported by an Australian Research Council Large Grant awarded to A. Georges.

## LITERATURE CITED

- BALAZS, G.H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. National Oceanographic and Aeronautics Association Technical Memo, National Marine Fisheries Section, NOAA-TM-NMFS-SWFC-7.
- BARTHOLOMEW, G.A. AND TUCKER, V.A. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. Physiol. Zool. 37:341-354.
- BENDA, R.S. AND PROFFITT, M.A. 1973. Effects of thermal effluents on fish and invertebrates. In: Gibbons, J.W. and Sharitz, R.R. (Eds.). Thermal Ecology. USAEC, Springfield, VA, pp. 438-447.
- BENNETT, A.F. 1982. The energetics of reptilian activity. In: Gans, C. and Pough, F. (Eds.). Biology of the Reptilia, Vol. 13. Academic Press, London, pp. 155-194.
- BOYER, D.R. 1965. Ecology of the basking habit in turtles. Ecology 46:99-118.
- CAGLE, F.R. 1950. The life history of the slider turtle, *Pseudemys scripta troosti* (Holbrook). Ecol. Monogr. 20:31-54.
- CHARLAND, M.B. AND GREGORY, P.T. 1990. The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. Copeia 1990:1089-1098.
- CHESSMAN, B.C. 1987. Atmospheric and aquatic basking of the Australian freshwater turtle, *Emydura macquarii*. Herpetologica 43:301-306.
- CHRISTENS, E. AND BIDER, J.R. 1987. Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in southwestern Quebec. Herpetologica 43:55-65.
- CHRISTY, E.J., FARLOW, J.O., BOURQUE, J.E., AND GIBBONS, J.W. 1973. Enhanced growth and increased body size of turtles living in thermal and post-thermal aquatic systems. In: Gibbons, J.W. and Sharitz, R.R. (Eds.). Thermal Ecology. USAEC, Springfield, VA, pp. 277-284.
- CRAWFORD, K.M., SPOTILA, J.R., AND STANDORA, E.A. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.
- ERNST, C.H. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta*. J. Herpetol. 20:22-29.
- GATTEN, R.E., JR. 1974. Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrepene* ornata. Copeia 1974:912-917.
- GEORGES, A. 1992. Thermal characteristics and sex determination in field nests of the pig-nosed turtle, *Carettochelys insculpta* (Chelonia: Carettochelydidae), from northern Australia. Austr. J. Zool. 40:511-521.
- GEORGES, A. AND ROSE, M. 1993. Conservation biology of the pignosed turtle, *Carettochelys insculpta*. Chelonian Conservation and Biology 1:3-12.
- HAMMOND, K.A., SPOTILA, J.R., AND STANDORA, E.A. 1988. Basking behavior of the turtle *Pseudemys scripta*: effects of digestive

state, acclimation temperature, sex, and season. Physiol. Zool. 61:69-77.

- HEAPHY, L. 1990. Ecology of the pig-nosed turtle *Carettochelys insculpta* in northern Australia. Ph.D. Thesis, University of New South Wales, Sydney.
- JACKSON, D.C. 1971. The effect of temperature on ventilation in the turtle, *Pseudemys scripta elegans*. Resp. Physiol. 12:131-140.
- KEPENIS, V. AND MCMANUS, J.J. 1974. Bioenergetics of young painted turtles, *Chrysemys picta*. Comp. Biochem. Physiol. 48A:309-317.
- KING, J.M., KUCHLING, G., AND BRADSHAW, S.D. 1998. Thermal environment, behavior, and body condition of wild *Pseudemydura umbrina* (Testudines: Chelidae) during late winter and early spring. Herpetologica 54:103-112.
- KRAWCHUK, M.A. AND BROOKS, R.J. 1998. Basking behavior as a measure of reproductive cost and energy allocation in the painted turtle, *Chrysemys picta*. Herpetologica 54:112-121.
- LEFEVRE, K. AND BROOKS, R.J. 1995. Effects of body size on basking behavior in a northern population of the painted turtle, *Chrysemys picta*. Herpetologica 51:217-224.
- LEGLER, J.M. 1960. A simple and inexpensive device for trapping aquatic turtles. Utah Acad. Sci. Proc. 37:63-66.
- MANNING, B. AND GRIGG, G.C. 1997. Basking is not of thermoregulatory significance in the "basking" freshwater turtle *Emydura* signata. Copeia 1997:579-584.
- MOLL, E.O. AND LEGLER, J.M. 1971. The life history of the slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles Mus. Nat. Hist. 11:1-102.
- MOSQUIERA MANSO, J.M. 1960. Las tortugas del Orinoco. Segunda edicion. Ed. Citania, Buenos Aires, 148 pp.
- NEILL, W.T. AND ALLEN, E.R. 1954. Algae on turtles, some additional considerations. Ecology 35:581-584.
- PARMENTER, R.R. 1980. Effect of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys s. scripta*). Copeia 1980:503-514.
- PARMENTER, R.R.1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. Comp. Biochem. Physiol. 70:235-238.
- PRITCHARD, P.C.H. AND TREBBAU, P. 1984. The Turtles of Venezuela. Soc. Stud. Amph. Rept. Contrib. Herpetol. No. 2, 403 pp.
- SAJWAJ, T.D. AND LANG, J.W. 2000. Thermal ecology of Blanding's turtle in central Minnesota. Chelonian Conservation and Biology 3:626-636.
- SCHWARTZKOPF, L. AND SHINE, R. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? Oecologia 88:562-569.
- SHINE, R. 1980. Costs of reproduction in reptiles. Oecologia 46:92-100.
- SPENCER, R., THOMPSON, M.B., AND HUME, I.D. 1998. The diet and digestive energetics of an Australian short-necked turtle, *Emydura* macquarii. Comp. Biochem. Physiol. 121A:341-349.
- STANDORA, E.A. 1982. A telemetric study of the thermoregulatory behavior and climate-space of free-ranging yellow-bellied turtles, *Pseudemys scripta*. Ph.D. Thesis, Univ. of Georgia, Athens.
- STUDIER, E.H., STUDIER, A.L., ESSY, A.J., AND DAPSON, R.W. 1977. Thermal sensitivity and activation energy of intrinsic intestinal motility in small vertebrates. J. Thermal Biol. 2:101-105.
- WHITTOW, G.C. AND BALAZS, G.H. 1982. Basking behavior of the Hawaiian green turtle (*Chelonia mydas*). Pac. Sci. 36:129-139.

Received: 22 August 1999

Reviewed: 4 February 2001

Revised and Accepted: 25 April 2001