

tail, possibly inflicted by another turtle during aggressive interactions, or by a predator (crocodiles, for example, are common at the collection locality).

A general assumption of reptilian tail regeneration is that the skeleton of the regenerate is a cartilaginous tube or rod without segments and articulations. The regenerated muscles provide some mobility to the regenerated tail, although its flexibility is reduced. In some species the cartilage tube may become calcified or perhaps even ossified in mature, old regenerates, which may lead to complete rigidity (Bellairs and Bryant, 1985). A surprising finding is that the accessory tail regenerate of the turtle described here did not have a single elongated rod of cartilage as its skeleton, but rather an axis formed by several dense tissue segments that are separated by spaces reminiscent of intervertebral spaces. Even though these segments are wider and longer than the vertebrae of the original tail, the regenerating turtle tail may not grow a single tube or rod as skeleton, but produce several segments. After breakage or amputation of a regenerated lizard tail, the base of the new cartilage tube that subsequently forms is wider than the severed end of the old one (Bellairs and Bryant, 1985). The fact that some tissue segments in the present case are wider and longer than a typical turtle tail vertebra may reflect a similar relationship.

The shell of chelonians has considerable regenerative capacity (Kuchling, 1997). The bifid tail described here demonstrates that the tail of chelonians, too, has some regenerative capability. The results of this study suggest that further, more detailed investigations of tail regeneration in chelonians might reveal many features of interest.

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## Thermoregulation in Captive Indian Ocean Giant Tortoises

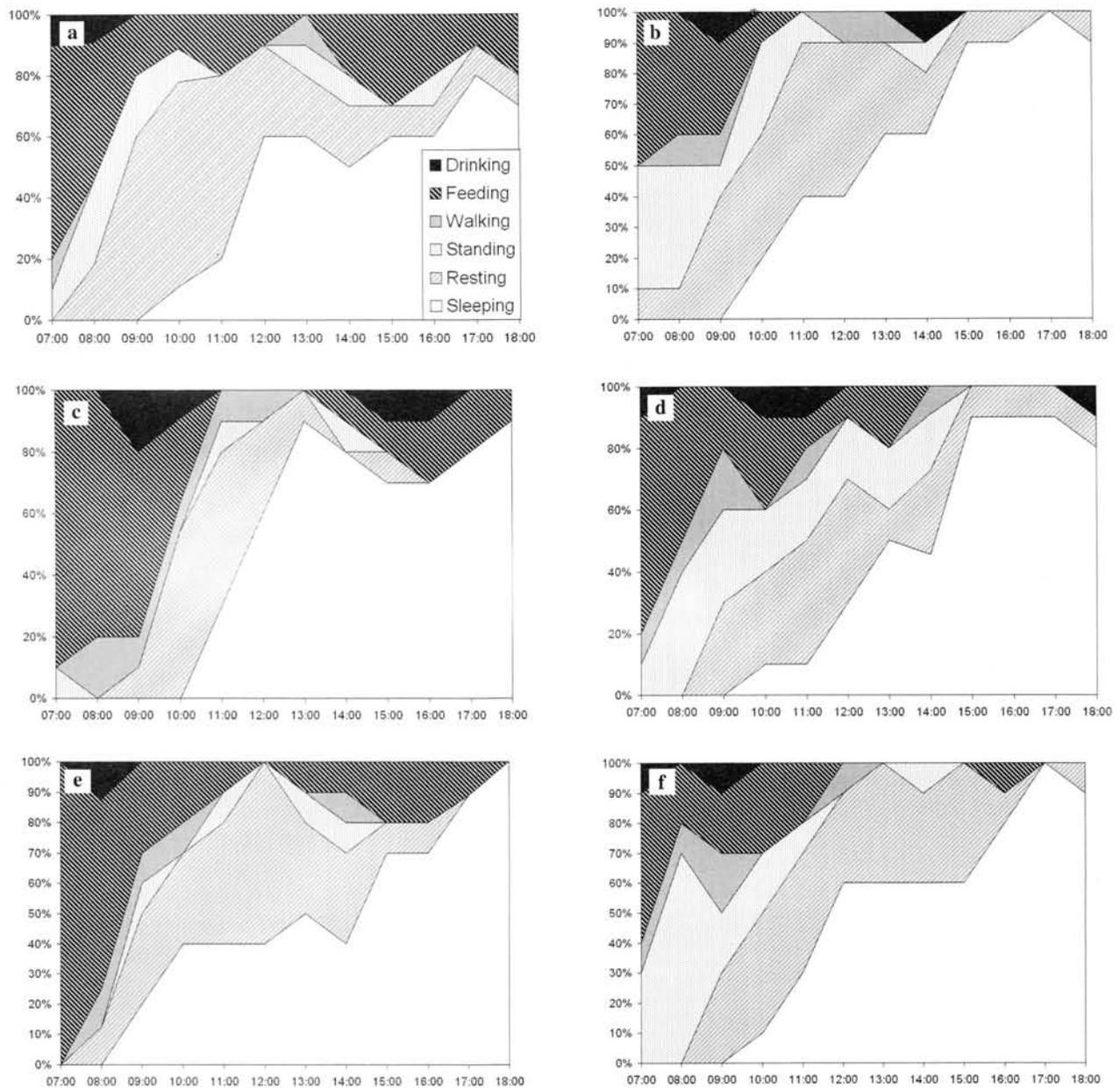
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**ABSTRACT.** — Thermoregulation in captive Indian Ocean giant tortoises *Dipsochelys dussumieri*, *D. arnoldi*, and *D. hololissa* was investigated in the Seychelles, recording behaviors and temperatures. Cloacal temperatures were 27–33°C; moving into the shade or into water prevented this range being exceeded. Males of the saddle-backed form *D. arnoldi* exhibited basking behavior during the cooler months of the year; this is interpreted as a strategy to compensate for increased heat loss caused by carapace morphology.

Thermoregulation in ectothermic reptiles is a combination of physiological and behavioral adaptations to maintain body temperature within an optimum range or to adjust physiology when this is not possible (Avery, 1982; Huey, 1982). Behavioral thermoregulation takes the form of adjusting activity patterns to maximize heat uptake and avoid over-heating or chilling, through basking, aestivation, or hibernation (Bradshaw, 1986). Among chelonians basking occurs in many freshwater species (Sexton, 1959; Boyer, 1965; Ernst, 1972; Moll and Legler, 1971; Sajwaj and Lang, 2000) and some marine turtles (Boyer, 1965; Swimmer, 1997). It has only rarely been reported for terrestrial tortoises (occasionally in *Testudo* spp. and *Gopherus* spp.; Boyer, 1965). Avoidance of heat is recorded in many tortoises (*Chelonoidis nigra* [McKay, 1964, as *Geochelone elephantopus*]; *Gopherus* spp. [McGinnis and Voigt, 1971]; *Dipsochelys dussumieri* [Frazier, 1973, as *Geochelone gigantea*]) and aestivation in *Gopherus* tortoises (Voigt and Johnson, 1976). Deliberate orientation to minimize overheating occurs in all these taxa and probably occurs in all tortoise species.

The western Indian Ocean giant tortoises of the genus *Dipsochelys* are known to time active behavior to cool parts of the day, becoming less active with increasing temperature and using body orientation to minimize the risk of over-heating (Frazier, 1973). Furthermore, over-heating may be reduced by wallowing in water to cool the body (Lewis et al., 1992). All these observations are derived from Aldabran tortoises *D. dussumieri* (the nomenclature of this species remains contentious, the most frequent recent usage is followed here; other recent names are *Geochelone gigantea*, *D. elephantina*, and *Aldabrachelys gigantea*). Observations



**Figure 1.** Behavior patterns in *Dipsosaurus* giant tortoises. Graphs show means frequencies for all behaviors throughout the year. **a)** male *D. hololissa*, **b)** female *D. hololissa*, **c)** male *D. dussumieri*, **d)** female *D. dussumieri*, **e)** male *D. arnoldi*, **f)** female *D. arnoldi*.

of captive tortoises suggest that other thermoregulatory behaviors may be exhibited by other *Dipsosaurus* taxa (presently attributed to the species *D. hololissa* and *D. arnoldi* from the granitic Seychelles islands) (pers. obs.). The suggestion that basking effectiveness relates to carapace shape (Boyer, 1965) would imply that the *Dipsosaurus* species would exhibit significant inter-specific differences in thermal budgets due to the morphological differences between these species. These differences were investigated in an attempt to explain behavioral differences between species and individuals.

**Methods.** — Three captive groups of tortoises were studied at the Seychelles Giant Tortoise Conservation Project on the island of Silhouette, Seychelles. This project was

established in 1997 by the Nature Protection Trust of Seychelles with three species, *D. dussumieri*, *D. hololissa*, and *D. arnoldi* kept in separate enclosures. The enclosures are large (each approximately 600 m<sup>2</sup>) and contain natural vegetation, trees, and landscape features. Water is provided ad-libitum and pools of water are maintained for wallowing throughout the year. The enclosures contain 5 (2.3) adult and 1 (1.0) subadult *D. dussumieri*, 5 (3.2) adult and 1 (1.0) subadult *D. hololissa*, and 6 (3.3) adult *D. arnoldi*.

Since 1997 records have been kept of the behavior of all these tortoises, changes in day-to-day behavior have been noted and in 1998–2000 detailed behavioral studies were carried out at 3-month intervals. Each behavioral study covered 10 days of observations in each of 8 time periods,



Figure 2. *Dipsoschelys arnoldi* males basking during the cool season.

recording the activity of each tortoise hourly from 0600–1800 hrs. Behaviors were categorized as sleeping (inactive, eyes closed), resting (inactive, lying down, eyes open), standing (inactive but supported on extended legs), walking, eating, drinking, climbing (walking over raised ground), wallowing (present in one of the wallows), scraping (moving soil with front legs), and digging (moving soil with hind legs).

These behavioral notes were supplemented with hourly temperature records of the air temperature (digital temperature probe exposed to air and shaded from direct sun and with no air movement), wind temperature (shaded from the sun but exposed to air movement), ground temperature (probe lying on the ground exposed to the sun, but with the temperature probe shaded from direct sun), wallow water temperature (at 20 cm depth), and leaf-pile temperature (probe inserted 30 cm into the leaf-pile). The temperature of each tortoise was monitored by recording the shell temperature (placing the probe flat on the carapace, shaded from direct sun), skin temperature (placing the probe in a fold of skin on the underside of the base of the neck), and cloacal temperature (inserting the probe into the cloaca for a distance of 10

cm in adults and sub-adults, 2 cm in juveniles). All temperatures were recorded with a digital thermometer recording to 0.1°C accuracy. There is significant variation in internal temperatures from different parts of the body in tortoises (Webb and Johnson, 1972) and the use of deep-body temperature records from the gut is preferred by some workers. Cloacal temperature was used in the present study due to its convenience and the limitations of available equipment.

**Results.** — All tortoises exhibited similar behavior patterns as indicated by the monitoring summarized in Fig. 1, and no seasonal patterns were identified. There were two exceptions to this; a male *D. arnoldi* and a male *D. hololissa*. The *D. arnoldi* remained inactive in a pile of dead vegetation 26 August – 18 September 1998 and the *D. hololissa* remained in a wallow for 8–13 January 1998 and retreated into a pile of dead vegetation during 21–23 September 1998 and 29 May – 21 September 1999. These behaviors were not repeated in subsequent years. No differences were observed between adults and subadults.

Wallowing behavior was observed in all 3 species, with both sexes of *D. dussumieri* and *D. hololissa* entering wallows at a variety of times. In *D. dussumieri* the frequency of wallowing was positively correlated with air temperature ( $r = 0.65, p < 0.05, n = 10$ ). In the other two species there was no clear correlation with air temperature although there was an increased frequency of this behavior when air temperatures exceeded 30°C. For *D. arnoldi* only males were observed wallowing and only when temperatures exceeded 29°C.

Basking (Fig. 2) was observed in *D. arnoldi* only. Following feeding all adults lay in the open with necks and limbs extended, with the carapace angled perpendicular to the sun. This activity was apparent on every sunny day in May to October; these are the cooler months of the year and the frequency of basking was related to air temperature (Fig. 3). A subadult male *D. hololissa* was observed sleeping in the sun occasionally for periods of up to 20 minutes.

Daily variations in air temperatures are shown in Fig. 4. During the study period wind cooling had the effect of

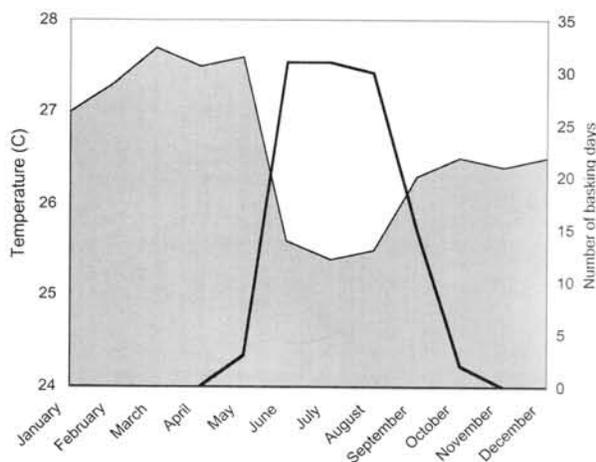
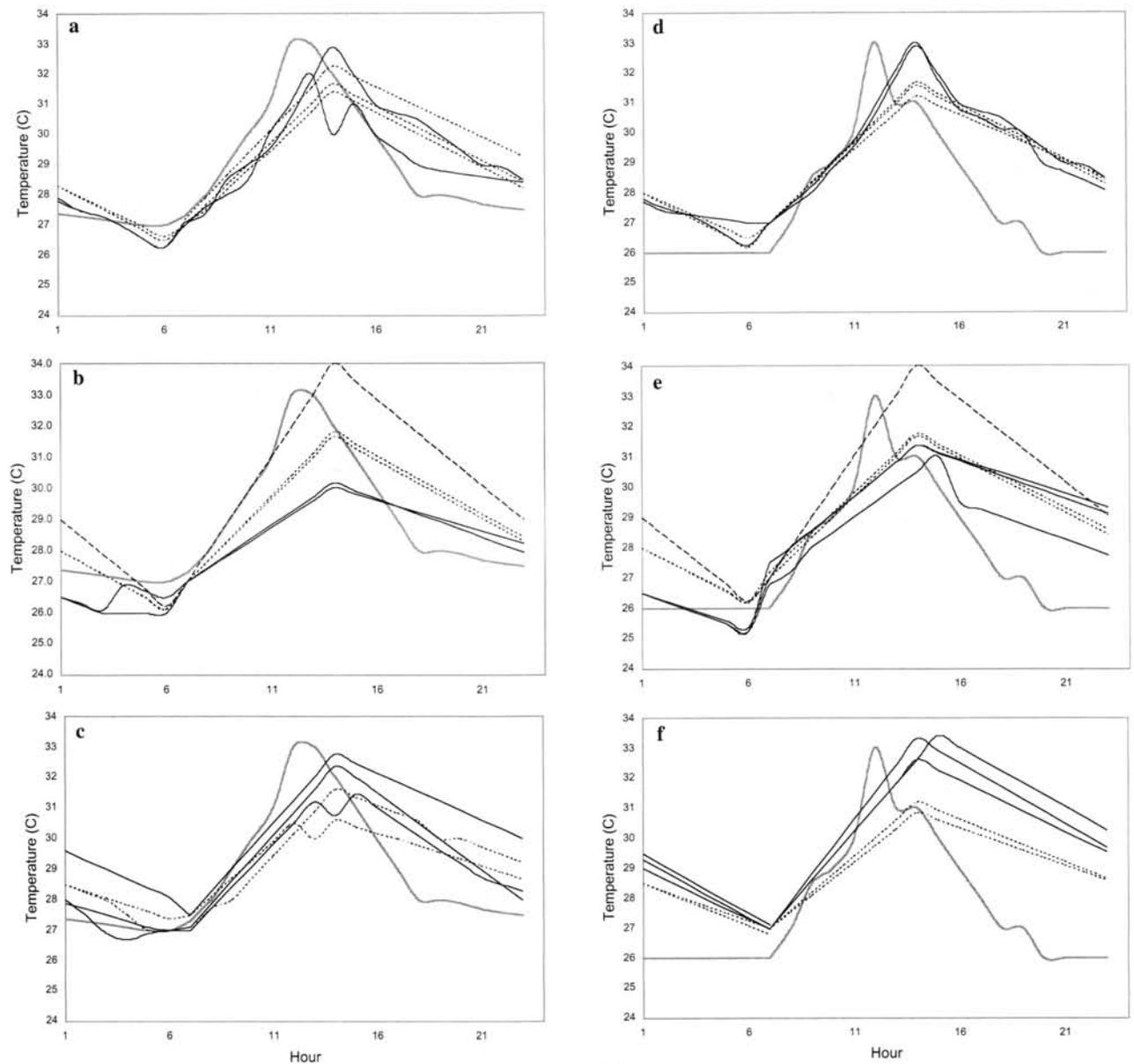


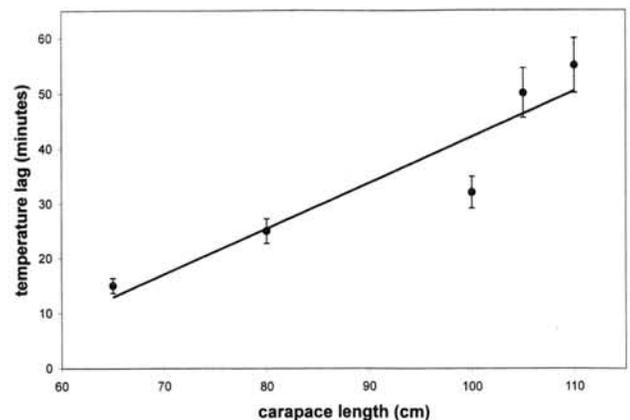
Figure 3. Frequency of basking in male *Dipsoschelys arnoldi*. Shaded area = air temperature; line = basking days (means) for all males.



**Figure 4.** Cloacal temperatures patterns. Mean temperatures recorded during two observation periods. Gray line = air temperature; solid line = males; dashed line = subadult males; dotted line = females. **a-c** hot season (January) temperatures, **d-f** cool season (July) temperatures. **a)** *D. dussumieri*, **b)** *D. hololissa*, **c)** *D. arnoldi*, **d)** *D. dussumieri*, **e)** *D. hololissa*, **f)** *D. arnoldi*.

reducing air temperature by 7%. Mid-day water temperatures were 4% lower than the air temperature but higher than the wind temperature (1°C or 4%). Temperature in the leaf-pile was constant, remaining at 25°C (7-19% lower than air temperature).

For *D. hololissa* the recorded cloacal temperature range was 27–33°C. There was a temperature rise in the sun ( $0.82 \pm 0.15^\circ\text{C/hr}$ ). Temperature increase had a 0–1 hour lag (the lag time being correlated with body size) (Fig. 5), with temperatures reaching 31–33°C. The lag results primarily from the thermal inertia of the shell, which had a corresponding lag, skin temperature followed changes in shell temperature although at only 50–60% of the temperature value. Cooling rates were higher for the shell surface ( $1.31 \pm 0.02^\circ\text{C/hr}$ ) compared to the cloacal temperature ( $0.45 \pm 0.03^\circ\text{C/hr}$ ).



**Figure 5.** Temperature increase and body size in *Dipsoschelys hololissa*.

For *D. dussumieri* the cloacal temperature range was 27.5–33°C. There was a rise in temperature in the sun ( $0.90 \pm 0.05^\circ\text{C/hr}$ ). Temperature increase had a 1 hour lag in adults (Fig. 4), with temperatures reaching 32–33°C. Cooling rates for the internal temperature were  $0.40 \pm 0.10^\circ\text{C/hr}$  in the air and slightly higher in wallows ( $0.46 \pm 0.04^\circ\text{C/hr}$ ).

For *D. arnoldi* the recorded cloacal temperature range was 27–33°C, reaching 30–32°C without basking and 31–33°C with basking. Without basking cloacal body temperature rose slowly, following the rise in air temperature ( $0.5 \pm 0.05^\circ\text{C/hr}$ ) with a 3 hour lag (Fig. 4). With basking, temperature increased with the air temperature at  $1.07 \pm 0.02^\circ\text{C/hr}$ . Temperature remained high until 3–8 hrs after air temperature fell below the cloacal temperature. Internal temperatures fell at  $0.43 \pm 0.02^\circ\text{C/hr}$  with the rate being negatively correlated with body size (measured as straight carapace length) ( $r=0.76, p<0.001, n=38$ ). Cooling rates for the shell were  $1.34 \pm 0.01^\circ\text{C/hr}$ .

**Discussion.** — General behavior patterns and cloacal temperatures of tortoises in the present study were comparable to the behavior and gut temperatures of 27.6–34.5°C recorded in wild *D. dussumieri* on Aldabra and Curieuse (Frazier, 1973; Lewis et al., 1992). They were also similar to those recorded for Galapagos tortoises, *Chelonoidis nigra* (Mackay, 1964). In these species and populations similar patterns of body temperature increase lagging behind air temperature are seen, corresponding to 'heat flow through a limited region having a high resistance compared with that of the material absorbing the heat' (Mackay, 1964), with a 'stirring' effect of blood flow.

The differences in thermoregulatory behavior between the three species of *Dipsoschelys* can be related to differences in morphology. *Dipsoschelys dussumieri* and *D. hololissa* are both typically domed and exhibit broadly similar behavior patterns. The domed shape absorbs and releases heat in a relatively even manner over the exposed dorsal surface and may reduce heat uptake as the shell acts as a thermal barrier (Boyer, 1965). Consequently a simple pattern of heating and cooling is observed, with behaviors adapted to minimizing the risks of over-heating. In contrast, the saddle-backed morphology of *D. arnoldi* (Gerlach, 1999) results in a higher rate of heat transfer. The tortoises gain heat more rapidly but also lose it faster than the domed species. The higher rate of carapace temperature rise in this species may be related to the thin shell which may be expected to heat up faster than the thicker shells of *D. dussumieri* and *D. hololissa*.

The behavioral strategy of *D. arnoldi* reflects these differences in thermal budgets; this is most pronounced in the adoption of basking behavior by the males in the cooler months of the year. That this basking results in elevation of body temperature would be expected; such thermophily has been recorded in other reptiles (e.g., Dorcas et al., 1997). In chelonians it is exhibited after feeding in some freshwater species where it may aid digestion (Gatten, 1977; Sajwaj and Lang, 2000). Such a digestive component is unlikely in *D. arnoldi* given the lack of temperature elevation in other *Dipsoschelys* species. In *D. arnoldi* it results in temperatures

being elevated in the late morning and then falling over the afternoon and night when they are largely inactive, allowing a 27°C early morning temperature to be maintained. In the absence of basking it is probable that during the cooler months of the year *D. arnoldi* male cloacal temperatures would fall below this level. The basking behavior can be seen as a mechanism to compensate for the high rate of heat loss caused by their extreme morphology.

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