

The Behaviour and Energetics of Hatchling *Varanus rosenbergi*

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Abstract

Varanus rosenbergi is one of the several varanid species that deposit their eggs in termitaria, thereby taking advantage of the warm, humid microclimate within the termitaria for incubation. The emergence of hatchlings from the termitaria is described, along with their general behaviour. Measurements of field metabolic rate (FMR) of hatchlings indicate the importance of the microclimate of termitaria in allowing them to maintain high levels of activity at a time when adult activity is constrained by cool ambient climatic conditions.

Key words: Varanidae, *Varanus rosenbergi*, termitaria, hatchling emergence, FMR.

Introduction

A number of reptile species deposit their eggs in termitaria, including some varanids; e.g. *Varanus niloticus* (COWLES, 1930), *V. prasinus* (GREENE, 1986), *V. giganteus* (BRAITHWAITE, 1990), *V. rosenbergi* (KING & GREEN, 1993) *V. varius* (CARTER, 1999). The internal temperature of termitaria of *Nasutitermes exitiosus*, the mound species used by *V. rosenbergi*, is maintained by the termites at around 30 °C for most of the year, but shows a mid-winter decline to around 20 °C (WATSON & ABBEY, 1986). In addition, humidities are high throughout the year; thus termitaria provide a perfect microclimate for the incubation of eggs (COWLES, 1930).

WATSON and BARRETT (1981) have described the structure of termitaria as follows; there is a protective earthen outer wall that is comparatively soft and friable, but about 10 cm beneath the mound surface there is an extremely hard inner layer of material (about 14 cm thick) that is difficult to penetrate (CARTER, pers. comm.). On the inner side of this layer the warm nursery galleries are found, and these consist of a flaky material that is easily broken.

V. rosenbergi mate over a period of about 12 days in January, and in late February/early March the female spends a couple of days digging into a termitarium. After digging about 0.7 m into the termite mound she constructs a circular nest chamber within the nursery zone and lays her eggs. She then backfills the excavation and within a few days the termites totally reseal the mound.

Hatchlings first appear in spring (September/October) but the precise timing of hatching and mode of hatchling escape from termitaria has not been reported for *V. rosenbergi*. COWLES (1930) reported that hatchlings of *V. niloticus* escape from termitaria unaided, while CARTER (1999) found that adult *V. varius* dig into termitaria to release hatchlings.

While the seasonal pattern of energy and water use has been described for adult *V. rosenbergi* (GREEN et al., 1991) there is no information on the field metabolic rates (FMRs), feeding rates and water fluxes of hatchlings. These are expected to be higher than adults in mass-specific terms since:

- a) allometrics indicate that small lizards exhibit higher mass-specific FMRs than large lizards (NAGY, 1982),
- b) the mass-specific standard metabolic rates (SMRS) of hatchlings are higher than

adults (THOMPSON & WITHERS, in press)

- c) the hatchlings grow rapidly and presumably show high levels of anabolism, and
- d) the hatchlings are exposed to mound temperatures of about 30 °C throughout the night, whereas the body temperatures of adults decline substantially overnight while using cool burrows (KING, 1980; CHRISTIAN & WEAVERS, 1994).

The present study was undertaken to establish the timing of events surrounding hatching in *V. rosenbergi*, to observe the general behaviour of hatchlings and measure their use of energy, food and water.

Materials and Methods

The study was carried out on Kangaroo Island, South Australia, between 1991 and 1996. Direct observations were made of females laying eggs in termite mounds in summer, with a close watch being kept on these mounds during the following September and October (spring), when hatchlings first appear.

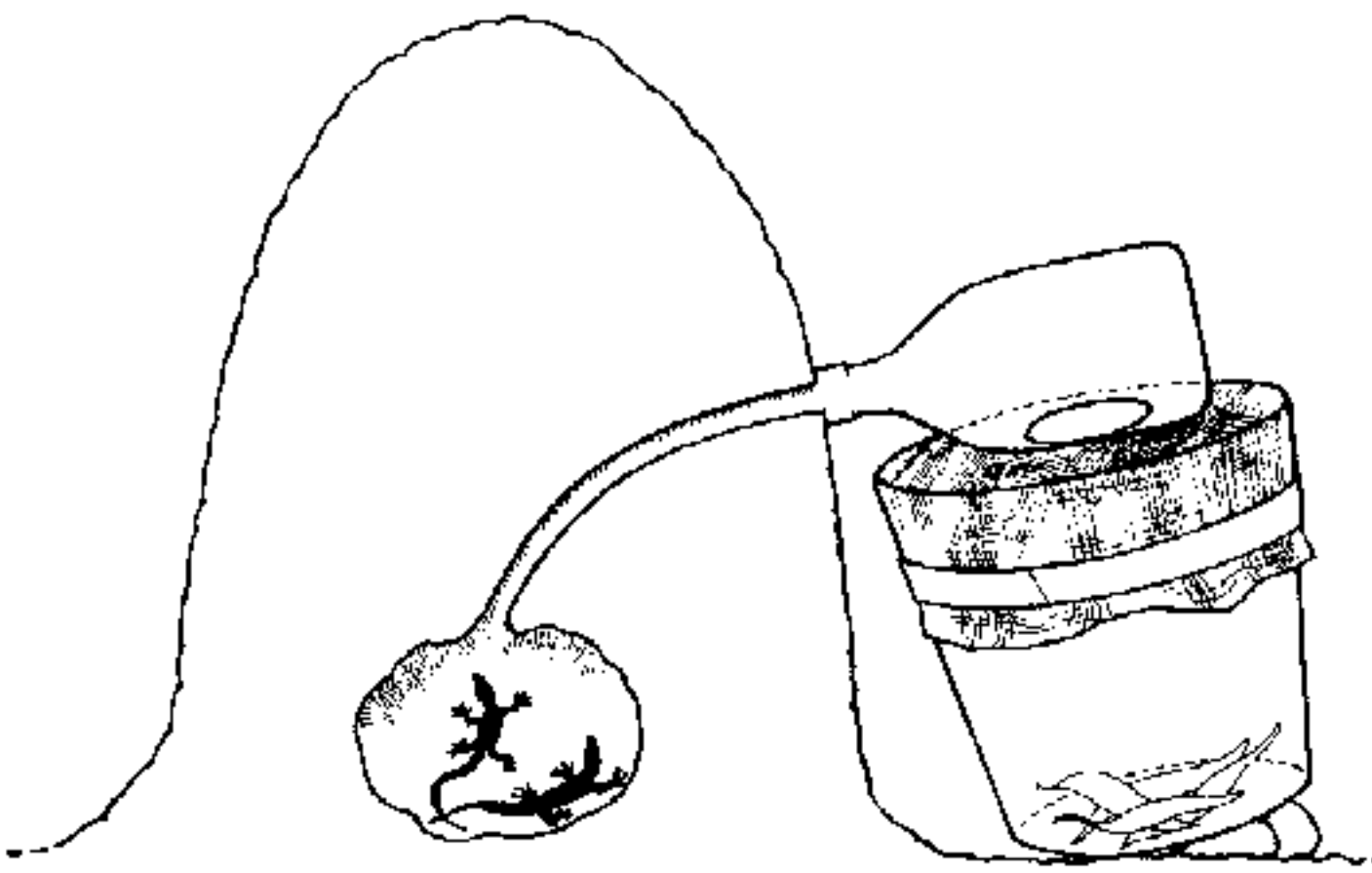


Fig. 1. Trap attached to the exit hole of a termite mound for catching hatched *V. rosenbergi*.



Fig. 2. Termitarium surface with a small hole (about 1 cm in diameter) indicating a first sign of activity by hatching *V. rosenbergi*.

Some hatchlings were caught by attaching a trap to the exit hole of each mound (Fig. 1), while other mounds were cut with a bow saw to gain access to the egg chamber which the hatchlings inhabit.

FMR and water of hatchlings influx were measured by means of the doubly-labelled water technique (LIFSON & McCLINTOCK, 1966; NAGY, 1980). Hatchlings were

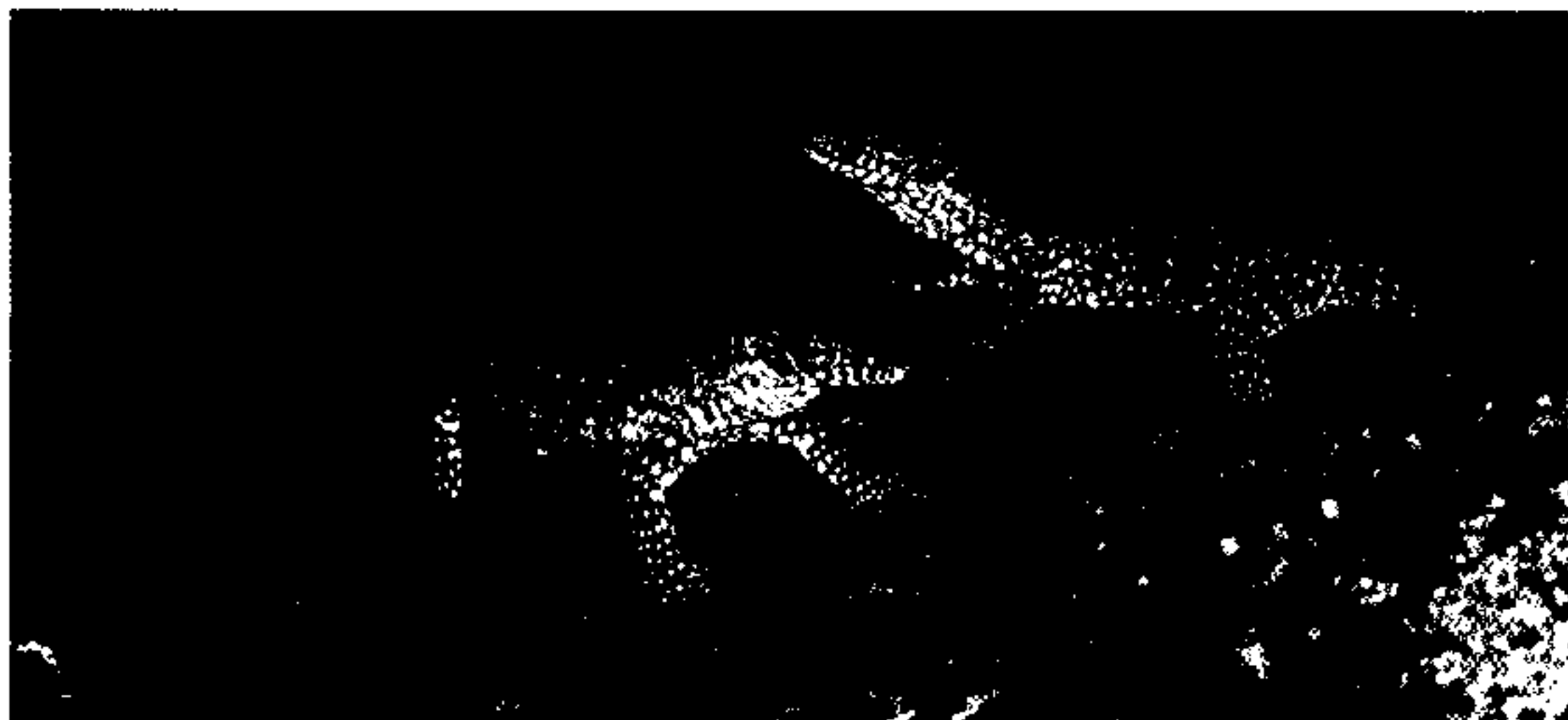


Fig. 3. Young *V. rosenbergi* recaptured at two termite mounds about four months after hatching. They have lost their bright orange coloration that is present at hatching.

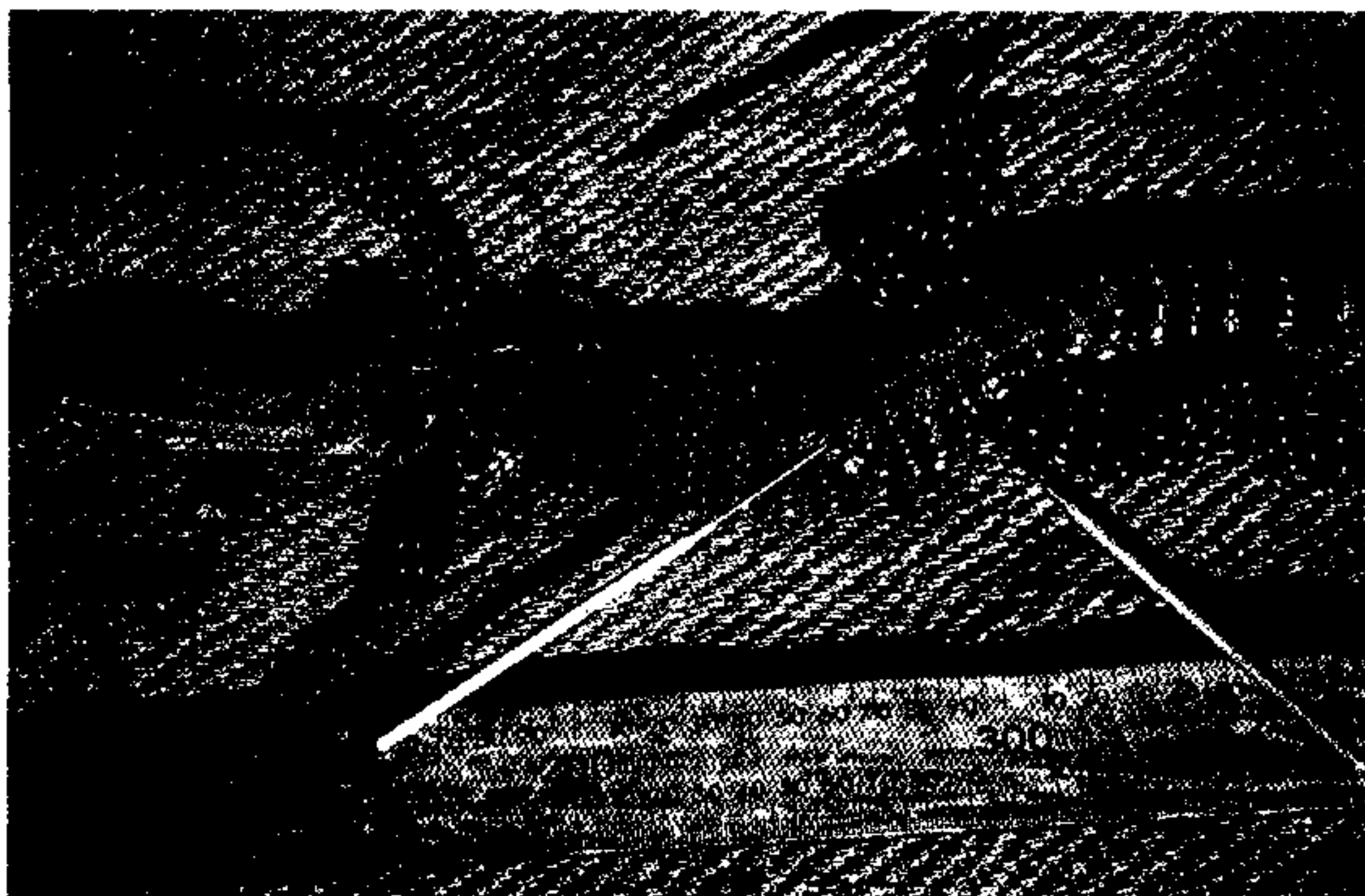


Fig. 4. *V. rosenbergi* about 23 months old killed but not eaten by an adult *V. rosenbergi* (see text).

weighed to the nearest 0.5 g with a spring balance (Pesola) and bled from the tail vein (50 μ l) before being injected in the peritoneal cavity with 50 μ l of $^2\text{H}_2^{18}\text{O}$. After 6 hours of isotope equilibration, a further blood sample (50 μ l) was taken, and the animals given individual marks of acrylic paint on the dorsum. The animals were then released back into their termitarium, and recaptured between 6 and 8 days later when they were reweighed and a final blood sample obtained. All blood samples were stored in flame-sealed haematocrit tubes and frozen until analysed.

Some hatchlings were released into a large enclosure (5.5 m \times 9.1 m) instead of their termitaria, to establish the FMR and water fluxes of hatchlings exposed to the same environmental conditions as adults. The enclosure floor was covered by native shrubs and litter, with an overstorey of trees (*Eucalyptus* spp.). These hatchlings were released for 25 to 30 days before recapture blood samples were obtained.

Water was extracted from the blood samples by heat distillation under vacuum (WOOD et al., 1975), after which 5 μ l aliquots were reduced with zinc reagent at 500 °C for 30 minutes. The hydrogen/deuterium gas generated was analysed in an isotope ratio mass spectrometer (V. G. Optima). 20 μ l aliquots of extracted water were equilibrated with standard charges of CO_2 at 60 °C, after which the equilibrated gas was drawn off and the 46/44 ratio measured by mass spectrometry (V.G. Optima). Total body water was derived from comparisons of equilibration samples with standard dilutions of the injectate. FMR and water flux were calculated from the change in isotope levels during the release periods, after background subtraction, assuming that mass-specific water pool sizes were constant during the period of measurement and that any changes in body mass were linear (LIFSON & McCLINTOCK, 1966; NAGY, 1980). Since the hatchlings are carnivorous it was assumed that each litre of CO_2 produced was equivalent to 25.7 kJ of metabolised energy (NAGY, 1982).

The carcasses of four hatchlings were weighed and then dried to constant mass in an oven at 80 °C. The dried remains were ground in a Wiley mill and weighed subsamples (about 0.5 g) were combusted in a ballistic bomb calorimeter (Gallenkamp) to measure energy content. Weighed samples of benzoic acid were used as standards.

Air and mound temperatures were measured by means of a Fluke rapid response digital thermometer.

All mean values are given with ± 1 S. D., and statistical comparisons were made by ANOVA followed by t-tests.

Results

The mean monthly maximum and minimum air temperatures for September on Kangaroo Island are around 15 and 9 °C respectively (Australian Bureau of Meteorology). These temperatures are substantially lower than those recorded in active termitaria at the same time of year; individual mound temperatures ranging between 22 and 32 °C (WATSON & ABBEY, 1986).

The first sign of activity by hatchling *V. rosenbergi* is the appearance of a small hole, about 1 cm in diameter (Fig. 2), on the termitarium surface in spring. The position of the hole corresponds to the point of entry made by the ovipositing female the previous summer, and the associated narrow tunnel runs down to the nesting chamber. It is clear from the small size of the tunnel and the entrance hole, that the hatchlings dig their own way out of the termitarium, without any adult assistance. No adult *V. rosenbergi* were ever observed to dig into termite mounds during spring.

The hatchlings do not emerge from the termitarium until outside air temperatures are sufficiently warm; hatchlings come to the tunnel entrance and flick their tongue across the outside surface of the entrance. Surface temperatures taken adjacent to the tunnel entrance showed that the frequency with which hatchlings came to the entrance increased as the surface temperature approached that of the nest chamber. When the mound surface temperature reached the same level as the interior of the termite nest, the young would emerge onto the surface and bask, before moving away from the mound to forage. The young may make frequent returns to the nest during the day, when they may bask or re-enter the mound. In the late afternoon the young enter the mound and remain there overnight. The mean body mass of 59 hatchlings from six broods was 19.1 ± 1.9 g at the time of first emergence. The four hatchlings that were dried for carcass analysis had a mean body mass of 19.9 ± 0.8 g, a mean energy content of 24.8 ± 1.0 kJ g⁻¹ dry matter, and a mean total energy content of 113 ± 22 kJ.

The young may continue to use the termitaria for overnight refuge for several months after hatching. Four young were recaptured at two termite mounds in late January (i.e. about 4 months after hatching); they weighed between 70 and 84 g and had lost the bright orange colouring around the throat that is present at hatching (Fig. 3). However, the hatchlings are subject to intense predation, mainly by corvid birds, and very few young survive their first year. At one mound, eight of the resident ten hatchlings were preyed on within the first two weeks of emergence. Of the remaining two, another was killed at the age of 23 months by an adult *V. rosenbergi*, although no attempt was made to eat the young (Fig. 4).

During spring some termitaria are severely damaged by the monotreme short-beaked echidna (*Tachyglossus aculeatus multiaculeatus*). This insectivore gains entry to the termitarium by enlarging the hatchling access tunnel and feeds on the termites thus exposed. On four occasions hatchlings have been found dead from puncture wounds inflicted by the powerful claws and spines of the echidna as it digs into the mound.

The young all gained in body mass during the course of the isotope turnover periods, indicating that they were successfully foraging away from the mound. Scats collected from active young contained mainly invertebrate parts (insects and spiders)

	Mass (g)	TBW (ml kg ⁻¹)	H ₂ O In (ml kg ⁻¹ d ⁻¹)	CO ₂ (ml g ⁻¹ h ⁻¹)	ME (kJ kg ⁻¹ d ⁻¹)
Hatchlings					
	19.9±1.6 (7)	770±18	61.2±7.9	0.485±0.068	282
(Spring)	24.1±3.3 (5)	794±13	76.8±15.2	0.484±0.103	299
Pen	27.3±3.3 (4)	791±9	10.4±5.6	0.069±0.022	43
Adults					
(Spring)	1219±299(8)	727±34	14.4±6.6 (6)	0.100±0.025	62
(Summer)	1140±369(24)	743±40	17.9±5.4 (21)	0.179±0.085 (21)	112
(Winter)	1193±190(12)	711±40	6.5±2.5 (10)	0.036±0.025	23

Tab. 1. FMR and water influx of hatchling and adult *V. rosenbergi*.

with some vertebrate long bones probably from small lizards. Scats collected from hatchlings prior to their emergence from termitaria contained termite exoskeletal parts, indicating that hatchlings utilise termites as food at least for the early post-hatching period.

The water influx rates and field metabolic rates of hatchlings during spring are shown in Table 1. The values for hatchlings from two separate termitaria are similar, there being no significant differences in any of the parameters measured. However, a group of four young that were maintained in a large enclosure away from their nest showed significantly lower water influx rates ($p < 0.001$) than young utilising termitaria. In addition, only two of the penned young provided reliable FMRS, the other two showing insufficient isotope turnover to yield positive FMR estimates. Even so, the two reliable FMR estimates for penned hatchlings (Tab. 1) were outside the 99.9 % confidence limits of FMRs for mound hatchlings, and therefore significantly lower ($p < 0.001$).

Discussion

It appears that *V. rosenbergi* eggs hatch in early September, but the hatchlings do not complete digging an escape tunnel and exit to the mound surface until two or three weeks later. It is not known if it takes that long a period for the young to actually dig out; they may be active in the nest chamber for most of that period and only spend a few days digging out. Even after reaching the surface, it may take several days before the young actually emerge; warm sunny conditions being needed to allow the young to bask. The hatching and emergence procedure in *V. rosenbergi* is similar to that described for *V. nitoticus* (COWLES, 1930) and inferred for *V. prasinus* (GREENE, 1986); adults play no part in the escape of hatchlings from the nest. This is in sharp contrast to the situation in *V. varius* where adults, of unknown familial identity, assist the release of hatchlings (CARTER, 1998).

The total body water pools (TBVV) of the emergent young are quite high (around 78 % of body mass) indicating the absence of significant body fat reserves at hatching. The mean energy content of hatchlings (113 kJ) is about half that of *V. rosenbergi* eggs (209 kJ) at laying (GREEN et al., 1991); i.e. half the energy content of eggs is metabolised during the seven months of incubation. Once active outside the mound, the young forage actively and gain weight quite rapidly, with a mean daily rate of increase of 2.15 to 0.91 % ($n = 12$). During this early period of activity the FMRs of the young are about five times those registered by adults in the same season (Tab. 1), and water flux rates are similarly higher. Assuming the metabolisable energy content of insect prey is 4.31 kJ g⁻¹ fresh mass for a uricotelic insectivore (BELL, 1990), it can be calculated that young with a mean FMR of 290 kJ kg⁻¹ day⁻¹ would require 67 g prey kg⁻¹ day⁻¹. Thus a 20 g hatchling requires about 1.3 g food each day to satisfy metabolic expenditures.

Assuming that 85 % of the mass of prey is available as free and metabolic water (DRYDEN et al., 1990), this level of prey consumption would generate 57 ml H₂O kg⁻¹ day⁻¹. Therefore approximately 83 % of the total water influx (69 ml kg⁻¹ day⁻¹) is derived from food, the remainder presumably derived from pulmocutaneous exchange of water, mainly within the humid termitarium.

The mass specific FMRs and water influx rates of young denied access to a termitarium, and being subject to the same environmental conditions as adults, were significantly lower than young using termitaria as refuges, and were not significantly

different to adult rates during spring. This indicates that the high FMRs of young using termitaria is predominantly due to the high overnight and diurnal temperatures in the mound relative to ambient conditions that generally exist during spring. Most days in spring are relatively cool and often overcast, so that adults and young without access to mounds may not be able to bask for sufficient time to achieve high enough body temperatures to become active.

Thus a termitarium represents a valuable resource for young *V. rosenbergi*.

- a) it allows the young to maintain a relatively high body temperature throughout the day and night which is conducive to the anabolic processes of growth,
- b) it allows the young to minimise the time required for basking after emerging from the mound, thereby reducing the time of exposure to predation,
- c) on cool days it provides the young with a source of external heat which can maximise the time available for daytime foraging, and
- d) it provides an abundant source of termites (food) in the immediate posthatching period.

There are no comparative data available for FMRs, food intake and water influx for hatchlings or young of any other varanid species. It would be particularly interesting to compare these parameters in species that use termitaria and those that do not while occupying the same or similar environments.

V. rosenbergi and *V. varius* are the two most southerly distributed varanids in the world (KING & GREEN, 1993), and both species employ termitaria for ovipositing. It seems likely that the use of termitaria for the incubation of eggs and the early growth of young is the most important selective feature that has allowed these two species to occupy and persist in such cool, southerly habitats.

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