Field energetics of a large carnivorous lizard, *Varanus rosenbergi*

Brian Green,[1] Gil Dryden,[2] and Kaye Dryden[3]

[1] C.S.I.R.O., Division of Wildlife and Ecology, P.O.Box 84 Lyneham, A.C.T. 2602, Australia
[2] Dept. of Biology, Slippery Rock University, Slippery Rock, PA 16057, USA
[3] RD3, Slippery Rock, PA 16057, USA

Summary. Field metabolic rates (FMRs; CO_2 production) and water influx rates of *Varanus rosenbergi* were measured seasonally by means of doubly-labelled water ($^3H_2^{18}O$). Metabolic rates and water influxes were highest in summer (0.18 ml CO_2 g^{-1} h^{-1} and 17.9 ml H_2O kg^{-1} day^{-1}) and lowest in winter (0.04 ml CO_2 g^{-1} h^{-1} and 6.5 ml H_2O kg^{-1} day^{-1}). FMRs and water fluxes were intermediate in spring. It is estimated that a 1-kg *V. rosenbergi* would need to consume 4.7 kg of prey each year to remain in energy balance and that the energy commitment to egg production requires a 40% increase in the food acquisition of a gravid female in late spring and early summer. It is calculated that water influxes in summer are totally provided from food but in other seasons, particularly winter, pulmocutaneous water exchange and/or drinking are significant avenues of water intake.

Key words: *Varanus rosenbergi* – Doubly labelled water – Field metabolic rate – Water influx – Energy budget

Isotopic water has been used to study the water and energy requirements of a broad range of free-living reptiles, particularly lizards (Nagy 1982 a, b; Nagy and Peterson 1989). However, most of these field studies have been confined to a single season, usually spring or summer when reptiles are generally more active.

One of the earliest isotopic water turnover studies of a reptile was conducted on *Varanus gouldii rosenbergi* (Green 1972), a sub-species that has since become elevated to the status of a species, *V. rosenbergi* (Storr 1980). This large carnivorous lizard, known as a "goanna", occupies temperate habitats along the southern coast of Australia and exhibits major seasonal variations in its activity patterns (Green and King 1978), body temperature profiles (King 1980) and water flux rates (Green 1972).

The present study was carried out to measure field metabolic rates (CO_2 production), in addition to water influx rates, on a seasonal basis. This allows accurate estimates to be made of prey consumption rates in the different seasons and allows an assessment of the annual energy budget and partitioning of water influxes in *V. rosenbergi*. The study also provides an assessment of the energy cost associated with breeding.

Materials and methods

The study was carried out between 1986 and 1988 at Flinders Chase National Park, at the western end of Kangaroo Island, South Australia. The goannas were captured by digging them from their burrows, usually in the early morning when they were less active. They were placed in hessian sacks and taken to the laboratory where they were weighed and fitted with transmitters (Biotrack) that were stitched into denim harnesses and glued to the lateral region of the tail base with contact cement.

Following the collection of a blank blood sample (about 1 ml) from the caudal vein, the animals were given intra-peritoneal injections of tritiated water (1 ml containing 185 MBq) and $H_2^{18}O$ (0.35 ml of 95% atoms excess). The animals were retained for 6 h to permit equilibration of the isotopes, after which a further blood sample was collected. The animals were then released at their respective points of capture. The goannas were recaptured between 12 and 120 days after release, depending on the season, when they were re-weighed, bled again and then released.

All blood samples were stored frozen in plastic vials and thawed just prior to analysis. The blood samples were subjected to vacuum sublimation (Vaughan and Boling 1961) and the extracted water was analysed for isotope content. Tritiated water activities were determined by adding 100 μl of extract to 3 ml of cocktail (P.C.S., Amersham) and counting to 1% error in a Beckman 2800 L.S.C. The ^{16}O:^{18}O ratios in water extracts were determined by incubating 100-μl aliquots with standard charges of CO_2 gas at 80° C overnight. The equilibrated CO_2 gas samples were drawn off and analysed with a VG Isogas 903 isotope ratio mass spectrometer.

The total body water pools of animals were calculated by comparing the isotope concentrations of equilibrated blood samples with standard dilutions of the injected isotopes. Water flux rates and CO_2 production rates were calculated from the decline in both isotopes during the release periods (Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980), assuming that mass-specific water pool sizes did not change and that any changes in body mass

and absolute pool size were linear. Estimates of metabolised energy were derived from CO_2 production rates by assuming a thermal equivalent of 26 kJ l^{-1} CO_2.

A collection was made of invertebrates and small vertebrates that were commonly available as prey or carrion on Kangaroo Island. The specimens were obtained in fresh condition and frozen until analysed. The free water content of prey was determined by mass change after drying to constant mass in a forced air oven at 50° C. The dried remains were ground and sub-samples of about 0.5 g were accurately weighed (Sartorius MP2) and combusted in a ballistic bomb calorimeter (Gallenkamp).

Freshly laid eggs of *V. rosenbergi* were weighed and placed in boiling water for 15 min to set the protein contents. This facilitated the separation of the "yolk" and "white" fractions and subsequent analysis. The separated egg fractions were dried to constant mass at 50° C and the dry masses recorded. The dry fractions were then steeped and rinsed in diethyl ether three times to remove the lipids and then re-dried to provide fat-free dry masses. Protein was determined by Kjeldahl digestion of fat-free residues and subsequent micro-diffusion analysis (Conway 1962), using a conversion of 6.25 g protein g^{-1} N. The ash content of fat-free residues was determined by ashing at 550° C and total hexose by the method of Messer and Green (1979). The dry mass of the shell was also determined for each egg.

Statistical comparisons of data were made by ANOVA and subsequent Fisher's LPSD tests. Mean values are given with SD. Statistical significance was accepted for P values <0.05.

Results

The composition of potential dietary items on Kangaroo Island is shown in Table 1. In general, the crude composition of terrestrial vertebrates and invertebrates is similar; they have relatively high and uniform free water and available energy contents. Since the identifiable composition of the diet of *V. rosenbergi* is 33% invertebrate

and 66% vertebrate in terms of biomass (King and Green 1979), it can be assumed that each gram fresh mass of the general diet of this species provides 6.08 kJ of energy. Assuming that about 82% of total energy intake is metabolisable (Avery 1971; Kitchell and Windell 1972) 5.00 kJ of energy are available for metabolism from each gram of ingested food. Prey would provide 0.71 ml of free water and 0.85 ml of free and metabolic water combined per gram fresh mass (Dryden et al. 1990; Green et al. 1991).

There were no significant differences between the seasons with respect to the mean initial body masses of the animals that were studied; all of them can be regarded as adults. During each season there were no consistent or major changes in the body masses of individuals during the release periods; there were mass gains in 16 turnover periods, mass losses in 17 and no detectable change in 4 periods. In 70% of cases the mass variations during the experimental period were within 6% of initial body mass, the largest mass loss being 11% in summer and the greatest mass gain being 19.6% in spring.

There were no significant differences between the seasons with respect to the mass specific total body water pools of goannas, and a combined mean value of $73.0 \pm 4.1\%$ of body mass was calculated.

There were major differences between the seasons with respect to both water influx and metabolic rates (Table 2). The lowest turnover rates were recorded during winter (6.5 ml H_2O kg^{-1} day^{-1}, 0.036 ml CO_2 g^{-1} h^{-1}) and the highest during summer (17.9 ml H_2O kg^{-1} day^{-1}, 0.179 ml CO_2 g^{-1} h^{-1}). During spring the water influx rates were significantly higher than in winter ($P<0.01$) but not significantly different to those of summer. The

Table 1. a, b. Water and energy content of some vertebrates p is pooled sample. Water and energy content of some invertebrates

a

Species	Mass (g)	(*n*)	Water (% of Mass)	Energy (kJ g^{-1}) Fresh	Energy (kJ g^{-1}) Dry
Leiolopisma sp.	p		73.6	5.16	19.53
Gehyra variegata	4	8	74.0 ± 1.4	5.31 ± 0.47	20.43 ± 1.16
Mus domesticus	15	9	65.9 ± 1.5	7.57 ± 0.48	22.20
Rattus fuscipes	120	8	69.5 ± 1.4	6.65 ± 0.59	21.88 ± 1.19
Macropus eugenii	4500	5	69.6 ± 1.0	6.45 ± 0.47	21.19 ± 1.47
$\bar{x} \pm SD$			70.5 ± 3.3	6.23 ± 1.00	21.05 ± 1.09

b

	Water (%)	Energy (kJ g^{-1}) Fresh	Energy (kJ g^{-1}) Dry
Hymenoptera larvae			
Pterolocera amplicornis	82.0	4.48	23.70
Perga affinis	76.2	5.55	23.26
Isopods	64.9	5.05	14.40
Palassid beetles	65.4	8.61	24.92
Earthworms	76.2	3.53	14.79
	74.0	5.52	21.25
Centipedes	71.9	6.11	21.74
Scorpions	68.9	7.54	24.06
Cockroaches	70.4	5.67	18.93

Table 2. Seasonal changes in the water influx and field metabolic rates of *Varanus rosenbergi*. Mean $\pm$ SD. Number of samples in parentheses

	Mass (g)	TBW (ml kg^{-1})	H$_2$O Influx (ml kg^{-1} d^{-1})	CO$_2$ Production (ml g^{-1} h^{-1})	Metabolized Energy (kJ kg^{-1} d^{-1})
Winter (May–Sept)	1193 $\pm$ 190 (12)	711 $\pm$ 40 (12)	6.5 $\pm$ 2.5 (10)	0.036 $\pm$ 0.025 (10)	22.5
Spring (Oct–Nov)	1219 $\pm$ 299 (8)	727 $\pm$ 34 (8)	14.3 $\pm$ 6.6 (6)	0.100 $\pm$ 0.025 (6)	62.4
Summer (Dec–Mar)	1140 $\pm$ 369 (24)	743 $\pm$ 40 (24)	17.9 $\pm$ 5.4 (21)	0.179 $\pm$ 0.085 (21)	111.7

field metabolic rates in spring were significantly lower than in summer ($P < 0.05$) but significantly higher than in winter ($P < 0.001$).

The goannas metabolised 22.5 kJ kg^{-1} day^{-1} during the winter months, and 62.4 and 111.7 kJ kg^{-1} day^{-1} in spring and summer respectively. These metabolic rates would require the ingestion of 4.5, 12.5 and 22.3 g prey kg^{-1} day^{-1} respectively in order to maintain energy balance.

The contents of the hard-boiled goanna eggs were pale cream in colour and there was no clear division of the egg contents into "yolk" and "white" fractions. However, it was possible to peel a paler surface layer away from the rest of the egg contents and this was considered to represent egg "white". This fraction represented only 12.5 $\pm$ 2.4% of the total dry egg contents and contained a higher mass-specific lipid content than the "yolk"; 61.4 $\pm$ 6.3% of the dry egg "white" was lipid compared to 45.8 $\pm$ 0.9% of the dry "yolk". The total lipid content of the eggs was 13.8 $\pm$ 0.5% of fresh mass, while the protein content was 10.75 $\pm$ 1.53% of fresh mass. The ash content of the eggs was 9.0% of dry matter (3% of fresh mass) and total hexose represented less than 1% of the fresh egg mass. The calculated energy content of the eggs was 8.1 $\pm$ 0.4 kJ g^{-1} fresh mass.

Discussion

Since there were no consistent or major changes in the body masses of the study animals it can be assumed that they were generally maintaining water and energy balance during the release periods. The similarity of the total body water estimates in the different seasons suggests that there were no clear seasonal variations in the size of body fat reserves within the population.

The seasonal rates of water influx determined for *V. rosenbergi* in this study are similar to those reported for animals at the same locality by Green (1972). The rates of water influx for *V. rosenbergi* in summer are similar to those that have been reported for other active varanids inhabiting semi-arid and arid environments (Green 1972; Vernet et al. 1988; Weavers 1983; Green et al. 1986; Dryden et al. 1990). They are also close to the value predicted for semi-arid/arid reptiles (Nagy 1982a); 20.3 ml H$_2$O kg^{-1} day^{-1} for a reptile with a body mass of 1140 g.

The pronounced seasonal pattern in water influx is also seen in the metabolic rates of the animals, their food

consumption rates and their general activity. During winter, *V. rosenbergi* do not emerge from their burrows very often and even then only for comparatively brief periods (Green and King 1978). However, there are enough sunny days to enable them to undertake limited foraging and feeding in winter. The species is most active during summer when the days are much longer and warmer and prey is more abundant.

Field metabolic rates have only been determined for a few other varanid species but these appear similar to those of *V. rosenbergi*; 101 kJ kg^{-1} day^{-1} in *V. giganteus* (Green et al. 1986) 79 kJ kg^{-1} day^{-1} in *V. komodoensis* (Green et al. 1991). However, the FMRs in all of these varanids are about double those for similar-sized iguanid lizards, the reptilian group whose field energetics have been most extensively studied (Nagy 1982b). This reflects the active foraging behaviour characteristic of varanids (Pianka 1982) and the wide aerobic metabolic scope that they exhibit (Bartholomew and Tucker 1964; Bennett 1973).

The estimates of water influx and metabolic rates in free-living *V. rosenbergi* were associated with a high level of variability; coefficients of variation for water influxes ranging between 30% in summer and 46% in spring, while for CO$_2$ production the range was between 25% in spring and 69% in winter. The main source of this variability appears to be behavioural, and has been noted in other varanids; *V. gouldii gouldii* (Green 1972), *V. griseus* (Vernet et al. 1988) and *V. giganteus* (Green et al. 1986). It is clear that detailed studies of the activity patterns of individuals are needed, in conjunction with isotope turnover studies, in order to account for the variability in the rates of water and energy use of varanid lizards.

The contribution of food water (i.e. free and metabolic water combined) to total water influx varied between the seasons. In winter, the mean daily food consumption of 4.5 g kg^{-1} day^{-1} would provide 3.8 ml of water to the total influx of 6.5 ml kg^{-1} day^{-1}, i.e. 58% of total influx. In spring, food would provide 10.6 ml H$_2$O kg^{-1} day^{-1}, equivalent to 74% of the total water intake, while in summer the water derived from food (19.0 ml kg^{-1} day^{-1}) would provide all of the water intake. The alternative sources of water intake available to animals are drinking and the pulmo-cutaneous exchange of water vapour with that in the atmosphere. Winter is the wettest season on Kangaroo Island and so soil moisture levels are greatest at this time. In addition, the goannas are inside their burrows most of the time, so it is likely that

Table 3. Composition of 3 *V. rosenbergi* eggs

	Mass (g)	Dry Matter (%)	Water (%)	Shell (%)	Fat (%)	Protein (%)	Energy (kJ g⁻¹)
	25.69	32.0	68.0	2.64	13.41	11.55	8.17
	24.88	33.3	66.7	2.88	14.30	11.72	8.56
	26.39	28.9	71.1	2.87	13.75	8.99	7.69
$\bar{x}$	25.65	31.4	68.6	2.80	13.82	10.75	8.14
SD	0.76	2.3	2.3	0.14	0.45	1.53	0.44

pulmo-cutaneous exchange of water, rather than drinking, accounts for the difference between total water influx and that derived from food. In spring the goannas are quite active and would be in a position to exploit drinking water to some extent. However, the relative contributions to water influx by this avenue and vapour exchange cannot be assessed. In summer, the driest season on Kangaroo Island, there is a negligible contribution by drinking and vapour exchange to the total water influx and in this season water influxes provide an accurate alternative estimate of food consumption rates to those provided by metabolic rate estimates.

It is possible to construct a total annual energy budget for *V. rosenbergi* from the measured field metabolic rates, assuming that summer and winter each have a duration of 120 days and that FMRs are similar in autumn and spring, each of which extends for 60 days. An average adult goanna of 1 kg body mass would expend 13 400 kJ of energy during summer and need to consume 2 680 g of prey, while during a similar period in winter the same goanna would expend only 2 700 kJ and consume 540 g of prey. During spring and autumn combined, such an animal would metabolise 7 490 kJ and consume 1 498 g of prey. Thus an average adult goanna expends 23 600 kJ and requires about 4 720 g of prey a year to maintain itself in energy balance.

This energy budget only applies to *V. rosenbergi* individuals in energy balance; energy expenditure and/or food consumption will be higher for animals that are growing or laying down fat reserves, and for females that are producing eggs. The total energy stored in an average clutch of *V. rosenbergi* can be calculated as follows. The mean clutch size in this species is 14 (King and Green 1979), and eggs have a mean mass of 25.7 g and an average energy content of 8.1 kJ g⁻¹ fresh mass (Table 3). Thus the total energy stored in a clutch is 2 914 kJ. This represents an increase in the total annual energy expenditure of about 12% for a breeding female. However, a lean female entering the breeding season would need to acquire this extra energy, as well as the additional energy for biochemical elaboration, during 4 months or so covering spring and early summer.

There are no estimates available for the energy costs involved in the biochemical elaboration of goanna eggs; however, in *Cnemidophorus tigris,* a small insectivorous lizard, the increase in metabolic rate associated with egg production is about 11% (Anderson and Karasov 1988). If a similar increase in energy expenditure applies to *V. rosenbergi* then gravid females would expend an extra 1 220 kJ in the biochemical elaboration of eggs. Thus the total energy cost of egg production is about 4 134 kJ

(2 914 + 1 220 kJ). This represents an increase of about 40% in the energy acquisition requirements of a gravid female during the breeding season (i.e. 3 744 kJ in spring plus 6 700 kJ in the first half of summer: 10 444 kJ in all). The energy expended in egg production represents the need for an extra 830 g of prey above that for maintenance in the field.

Unless prey or carrion are abundant during the breeding season it seems likely that female *V. rosenbergi* would find it difficult to obtain the energy required to produce a clutch of eggs every year. If a female fails to breed in one year she may enter the winter season with enhanced body fat reserves that may improve her chances of breeding successfully the following year. It has been shown that a number of varanid species can produce two clutches of eggs a year in captivity when provided with abundant food (Horn and Visser 1989)

It is therefore likely that reproductive success in *V. rosenbergi* varies substantially between years and localities, depending on the abundance of food, and that longevity counterbalances the variations in recruitment of young into goanna populations.

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