Variation in Energy Metabolism and Water Flux of Free-Ranging Male Lace Monitors, *Varanus varius* (Squamata: Varanidae)

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ABSTRACT

The energy and water used by *Varanus varius* correlated with changes in weather, activity, and possibly the availability of prey. In summer, CO_2 production and water influx rates were high (0.147 mL CO_2 g^{-1} h^{-1} and 23.6 mL H_2O kg^{-1} d^{-1}) but substantially lower during autumn (0.053 mL CO_2 g^{-1} h^{-1} and 9.1 mL H_2O kg^{-1} d^{-1}) and winter (0.016 mL CO_2 g^{-1} h^{-1} and 2.4 mL H_2O kg^{-1} d^{-1}), increasing again in spring (0.052 mL CO_2 g^{-1} h^{-1} and 7.9 mL H_2O kg^{-1} d^{-1}). The summer-winter difference represented more than a ninefold reduction in energy expenditure and water flux. However, individual *V. varius* could manipulate their energy and water requirements by up to sixfold during the summer period by regulating activity. Although we found no adaptive benefits of increased or decreased level of activity, we did find that larger animals moved more frequently and over greater distances than smaller animals. We hypothesise that *V. varius* regulates its activity on the basis of the trade-off between energy expenditure through activity and energy acquisition through foraging.

Introduction

Animals need energy for metabolic requirements of maintenance and activity and for discretionary uses such as increasing biomass through growth, for storage, and for reproduction (Townsend and Calow 1981). The proximate factors and the pathways that influence energy balance in animals have been well documented. Studies in the laboratory have shown that body mass is a proximate determinant of metabolic expenditure in reptiles and have described a relationship between body size

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and standard metabolic rate (Bennett and Dawson 1976; Andrews and Pough 1985). Other laboratory studies have found that the rate of energy use by ectothermic vertebrates depends on body temperature (Bartholomew 1982; Andrews and Pough 1985). In these studies, resting (or standard) metabolic rates of reptiles increase two- or threefold in response to each 10.0°C increase in body temperature (Bennett and Dawson 1976; Christian and Conley 1994; Thompson and Withers 1997). Further laboratory studies have shown that lizards need up to eight times more energy during activity than while at rest (Bennett 1972; Bennett and Dawson 1976; Christian and Conley 1994). Collectively, these studies have led to large databases on momentary state and rates of energy flow in captive animals.

While much can be learned by a reductionist approach in the laboratory, applying this knowledge to animals in the field is complex. For example, poor physiological tolerance of water stress demonstrated in the laboratory may be offset by behaviours that are only expressed under field conditions. The development of the doubly labelled water (DLW) method has greatly advanced our understanding of the factors that influence animal energy expenditure and water balance in the natural environment because the animal is free to undertake its normal daily activities during measurement (Lifson and McClintock 1966; Nagy 1980).

Activity has often been implicated as a major source of variation in energy and water fluxes observed in doubly labelled water studies (Green et al. 1991a; Christian et al. 1995). Indeed, this comes as no surprise given that the energetic cost of staying warm and being active is predicted to be eight to 16 times more expensive than being inactive within refugia (Bennett and Nagy 1977). Merker and Nagy (1984) conducted a study on *Sceloporus virgatus* and found that energy expenditure was positively correlated with duration of activity over a breeding and nonbreeding period. In another study, no relationship between energy expenditure and activity was observed for *Sceloporus occidentalis* (Bennett and Nagy 1977). Hence, it seems that activity has an important influence on variation in energy and water intake as measured by DLW studies, though the evidence is equivocal.

We used the DLW method (Lifson and McClintock 1966; Nagy 1980) to measure the energy and water use of the lace monitor, *Varanus varius*. First, we quantified the effect of seasonal changes in weather parameters on energy and water use by monitors. Second, we examined whether activity explained variation in metabolic rates and water fluxes of wild monitors.

Finally, we evaluated the costs and adaptive benefits of activity on monitor energy expenditure and water flux.

Material and Methods

Study Area

This study was conducted at Lake Burrendong, in central-western New South Wales (NSW), Australia (32°40′S, 149°10′E), between November 1997 and October 1998. The topography is heterogeneous, ranging from grassland plains to steep rugged hills. Vegetation varies from forest to open woodland to open grassland, typical of much of the central tablelands of NSW.

The study area has a temperate climate. Meteorological data were obtained from the Bureau of Meteorology for the township of Wellington, 20 km from the study site. The warmest months are December to February with a mean monthly maximum air temperature of 22.6°C. The coldest months are June through August with a mean monthly minimum air temperature of 6.5°C. Mean annual rainfall was 618 mm, spread evenly throughout the year (1968–1997). The area typically receives 50 d of frost annually. Data on ambient air temperature, solar radiation, and hours of sunshine used in the analyses are also from the Wellington Meteorological Station.

Study Species

The lace monitor is a large arboreal monitor lizard ranging in length from 0.2 m to over 2 m and in mass from 200 g to over 14 kg (Weavers 1988). The monitors occupy sclerophyll forests and woodlands of the coast, ranges, slopes, and adjacent plains of eastern and southeastern Australia, from southeastern South Australia to Cape York Peninsula, Queensland (Cogger 1993). In southeastern Australia, lace monitors are active between September and May (spring, summer, and autumn) and generally inactive between June and August (winter; Guarino 2002).

Radiotracking and Activity Estimates

We used radiotracking techniques to relocate adult monitors for recapture and for activity analyses. Two models of two-stage transmitters were used: ICP-1 (Biotelemetry) and Sirtrack (Scientific and Industrial Research). Transmitters were stitched into denim harnesses (Green et al. 1991a). Each harness, complete with its radio transmitter, weighed between 10 and 45 g—always less than 1% of body mass. Harnesses were attached to monitors with contact cement (Selleys Gel Grip) at the base of the tail. The transmitter was placed longitudinally on the lateral side of the tail, directly behind the right leg.

The location of each animal was checked up to four times daily during the active period (i.e., from 0800 hours to 1800 hours) and once during the inactive phase (from 1900 hours to 0700 hours) of the spring, summer, and autumn months. During winter, lizard movements were uncommon, so sampling was less intensive—three field trips each of 5 d in total over the winter period. We estimated activity from data on activity area (estimated using minimum convex polygons for all locations collected over a turnover period), daily distances moved (estimated per animal as mean straight line distance between successive locations for each day), and movement frequency (calculated as number of days with movement divided by the number of days tracked).

Isotopic Measurements in the Field

Field metabolic rates (FMR) and water flux rates were measured continuously for adult monitors during the early summer (December), midsummer (January), late summer (February), autumn (March–May), winter (June–August), and spring (September–October) using DLW (Lifson and McClintock 1966; Nagy 1980). We captured monitors with a noose and pole apparatus or in wire-mesh cage traps (1.5 × 0.45 × 0.45 m) using rabbit meat as bait. Upon initial capture, each animal was transferred to a cloth bag and a blood sample of approximately 0.25 mL was taken from its ventral caudal vein with a sterile 23-gauge syringe. This sample was analyzed for background levels of ^{2}H and ^{18}O. The animals were then injected intraperitoneally with 1 mL of deuterated water (99.9% atoms excess; Ansto Industries) and with ^{18}O (95% atoms excess; Enritech), which was given at a rate of 0.2 mL kg^{-1} with an accuracy of ±0.4% or better (we determined accuracy by drawing water with the field syringe 100 times and then measuring the mass drawn on each occasion). Some animals were only injected with deuterated water to follow water flux. No fluid leakage was observed from any injection.

Animal mass was measured before and after isotope equilibration with a spring balance (±50 g) at an accuracy of ±0.5% or better. We calibrated the spring balance with standard lead weights to verify accuracy. There was no significant difference between initial and final masses for monitors being held over the 6-h equilibration period (paired $T_{70} = 0.81$, $P = 0.42$). Almost invariably, animals with food in the gut regurgitated it on capture. This occurred before mass measurement, bleeding, or injection of isotopes. The mass of the food items regurgitated varied from over 1 kg to less than 100 g. Occasionally, animals defecated on capture. Usually, this was before mass measurement, bleeding, or injection. About 6 h was allowed for equilibration of the isotopes (Weavers 1983), after which a second 0.25-mL blood sample was taken from the tail vein. Animals were then released at their respective point of capture. We recaptured monitors for a third blood sample and reweighing after 2–3 wk during the summer, after 4 wk during autumn, and after 10 wk during the winter seasons. Animals were reinjected with isotopes at the beginning of each seasonal period, and for some animals, this yielded a fourth blood sample. All blood samples were stored frozen (−20 °C) in plastic O-ring vials. Samples were returned to the laboratory where we vac-

uum distilled blood samples in Pasteur pipettes to extract the water fraction (Nagy 1983).

Isotopic Measurements in the Laboratory

Samples of extracted water were analysed for ^{18}O with a dual-inlet isotope-ratio mass spectrometer (V. G. Optima, Cheshire, England). Preparation for mass spectrometry involved incubating 20 μL of extracted water with a constant amount of CO_2 at 60°C overnight. Following this, the water sample was frozen using a dry ice–alcohol slurry and the equilibrated CO_2 (which then carried the signature of the ^{18}O enriched water) was sublimated to another tube using liquid nitrogen and then introduced into the mass spectrometer under vacuum. The ratios of the samples were then compared with a reference sample of CO_2 gas to provide a measurement of ^{18}O enrichment.

Our samples of extracted water were also analysed for deuterium using the same isotope-ratio mass spectrometer. Preparation for mass spectrometry involved reducing 5 μL of extracted water with 150 mg of Zn reagent at 500°C for 30 min in a Urey exchange tube (under vacuum; Coleman et al. 1982). Following reduction, the equilibrated $^{1}H_2$ and $^{2}H_2$ gas sample was introduced into the mass spectrometer under vacuum. Sample ratios were then compared against a reference water sample to provide a measurement of ^{2}H enrichment.

Energy and Water Content of Prey

We collected invertebrates and small vertebrates that are commonly found in the diet of V. varius. 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. Energy content was measured by bomb calorimetry using a Gallenkamp ballistic bomb calorimeter. Preparation involved grinding up the dried remains of each prey item in a coffee blender and compressing small portions into pellet form. The subsamples were then accurately weighed using a Sartorius MP2 digital scale and placed individually in a crucible and combusted. We determined calorific content by comparing the rise in temperature of each sample with that of benzoic acid standards (calorific content of 26.454 kJ g^{-1}; Grodzinski et al. 1975).

Calculations

Total body water (TBW) was determined by measuring the isotope dilution space of ^{18}O or ^{2}H (Nagy 1980). We corrected ^{2}H estimates of TBW using regression because ^{18}O values typically give more accurate TBW estimates than do ^{2}H isotope dilution spaces (Schoeller et al. 1980). The ^{2}H estimates of dilution space were greater than those measured by ^{18}O (mean 1.074 ± 0.005 SE).

CO_2 production rates were calculated using equation (2) of Nagy (1980), and water influx was calculated using equation (6) of Nagy and Costa (1980). Where TBW was not measured at both the beginning and end of a turnover period, we estimated it as percent body mass (we assumed that TBW changed linearly with body mass).

Varanus varius is carnivorous, feeding on a mixture of vertebrate and invertebrate prey (Guarino 2001). The diet is effectively protein with some fat; thus, we assumed a thermal equivalent of 25.7 kJ L^{-1} CO_2 (Nagy 1983). Percent lipid content of V. varius was estimated by assuming a lean body water space of 75% (Green et al. 1986). We estimated body condition as the ratio of mass divided by length cubed (Bolger and Connolly 1989).

We estimated prey consumption rates based on model 1, outlined in Christian and Green (1994). This model assumes that animals obtain some water from nonfood sources and is based on an estimate of metabolisable energy/water content of the animal's diet. This was determined by assuming that the diet of V. varius was composed of 94% vertebrate prey and 6% invertebrate prey (Guarino 2001) and weighting the energy and water content of prey, respectively. Thus, the diet yields 6.6 kJ g^{-1} fresh mass. Assuming that 82% of the energy from the diet is metabolisable (Avery 1971; Kitchell and Windell 1972), then 5.4 kJ g^{-1} is available for metabolism. This diet provides 0.85 mL of free and metabolic water for each gram fresh mass (Green et al. 1991a; Christian et al. 1995). Hence, 5.4 kJ g^{-1}/0.85 mL = 6.37 kJ mL^{-1} water from the diet. The water obtained from food is estimated as FMR/6.37, and the water from nonfood sources (i.e., drinking and or pulmocutaneous exchange) is estimated by subtracting this from the isotopically determined water influx. Prey consumption rates can be estimated as FMR/5.4 kJ g^{-1}. This estimation assumes that all energy expended by monitors is derived from food (i.e., they are in energy balance).

Statistics

We used Pearson product-moment statistic for correlations. Isotopic measures of FMR and water flux rates were compared using ANCOVA with body mass as the covariate. Differences among means were determined with Tukey-Kramer tests at $P < 0.05$ following a significant result in the ANOVA or ANCOVA. We corrected for body mass effects by regressing rate functions (water influx and CO_2 production) against body mass on a log-log scale and then used the regression slope as the exponent for body mass (we calculated a slope of 0.91 for water influx and 0.92 for CO_2 production). Thus, our mass-specific values for water influx and CO_2 were calculated accordingly: (water influx)/(body mass)$^{0.91}$; (CO_2 production)/(body mass)$^{0.92}$. Means are presented with standard deviations unless otherwise specified.

Results

Environment

Ambient air temperature, solar radiation, and hours of sunshine paralleled one another and were highest during summer, intermediate during the autumn and spring, and lowest during winter (Fig. 1). Indeed, solar radiation was highly correlated with temperature ($r_{287} = 0.53$, $P < 0.0001$) and hours of sunshine ($r_{287} = 0.59$, $P < 0.0001$); likewise, temperature and hours of sunshine were also correlated ($r_{287} = 0.42$, $P < 0.0001$). Rainfall over the study was even, ranging from 35.2 mm (early summer), 61.4 mm (midsummer), 22.2 mm (late summer), 163.9 mm (autumn), 305.6 mm (winter), and 168 mm (spring).

Body Composition

The body mass of monitors increased between captures by an average of 0.23% per day in spring, 0.05% per day in summer, and 0.05% per day in autumn and decreased by 0.07% per day in winter, but these values were not significantly different among seasons (ANOVA: $F_{5, 65} = 1.39$, $P = 0.238$; Table 1). Mean TBW content was 64.7 ± 5.0 SE (Table 1). Percent lipid content was significantly lower and TBW higher over the spring, compared with the rest of the seasons (repeated measures ANOVA: $F_{5, 23} = 3.08$, $P < 0.0284$), and body condition indexes during spring were lower compared to the other seasons (repeated measures: $F_{5, 23} = 9.08$, $P < 0.0001$).

Activity

Although monitors did not move every day, they usually emerged from their tree hollows on most clear days. Some animals, presumably after reaching an operating body temperature, moved from their hollows to forage along dry creek banks, among rocks, and within rabbit or rodent burrows; others remained perched on tree limbs or remained in their hollows.

The movement frequency of monitors was significantly higher during summer, intermediate during spring and autumn, and lowest during winter (ANOVA: $F_{5, 65} = 24.53$, $P < 0.0001$; Table 1). This variation among seasons was positively correlated with solar radiation ($r_{70} = 0.75$, $P < 0.0001$), hours of sunshine ($r_{70} = 0.71$, $P < 0.0001$), and ambient temperature ($r_{70} = 0.64$, $P < 0.0001$). There was no correlation between weather patterns and variation in movement frequency within each season.

The average distances moved per day by monitors was significant, being highest during the summer, intermediate during spring and autumn, and lowest during winter (ANOVA: $F_{5, 65} = 12.91$, $P < 0.0001$; Table 1). The variation in distances moved per day was positively correlated with solar radiation ($r_{70} = 0.57$, $P < 0.0001$), hours of sunshine ($r_{70} = 0.54$, $P < 0.0001$), and temperature ($r_{70} = 0.38$, $P < 0.004$). There was no
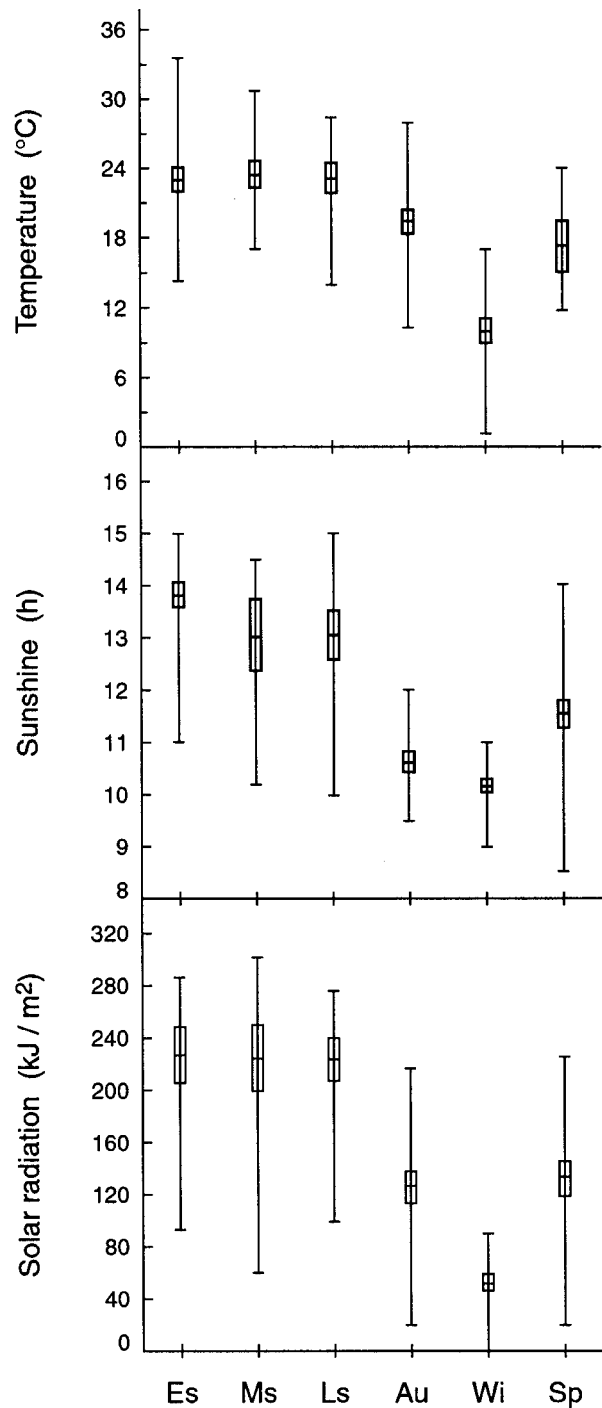

Figure 1. Seasonal means, daily ambient temperature, hours of sunshine, and solar radiation. Boxes represent 2 SD of mean while vertical bars represent the range. *Es* = early summer, *Ms* = midsummer, *Ls* = late summer, *Au* = autumn, *Wi* = winter, and *Sp* = spring.

Table 1: Physiological and ecological parameters for free-ranging male *Varanus varius* during different seasons over 1997–1998

	Early Summer	Midsummer	Late Summer	Autumn	Winter	Spring
Mass (g)	$5{,}584 \pm 412$ (13)	$4{,}986 \pm 874$ (22)	$5{,}314 \pm 763$ (11)	$5{,}031 \pm 809$ (10)	$4{,}932 \pm 681$ (7)	$4{,}641 \pm 722$ (8)
TBW (mL kg^{-1})	654 ± 24 (13)	643 ± 37 (22)	650 ± 24 (11)	643 ± 17 (10)	636 ± 49 (7)	657 ± 96 (8)
Lipid content (%)	9.6 ± 2.4	10.7 ± 3.7	10.0 ± 2.4	10.8 ± 1.7	11.4 ± 4.9	9.3 ± 2.6
Body condition index	21.0 ± 3.7	22.5 ± 2.3	21.1 ± 3.7	21.6 ± 2.4	20.9 ± 3.0	21.3 ± 3.1
Body mass change (% d^{-1})	$.05 \pm .23$ (13)	$.06 \pm .36$ (22)	$.05 \pm .26$ (11)	$.05 \pm .15$ (10)	$-.07 \pm .02$ (7)	$.23 \pm .24$ (8)
Movement frequency	$.81^A \pm .10$ (13)	$.58^B \pm .17$ (22)	$.45^B \pm .19$ (11)	$.45^{BD} \pm .18$ (10)	$.01^C \pm .01$ (7)	$.35^D \pm .13$ (8)
Straight line distance moved (m d^{-1})	$368^A \pm 94.2$ (13)	$266^B \pm 139$ (22)	$131^{BD} \pm 38$ (11)	$130^{BD} \pm 38$ (10)	$24^C \pm 12$ (7)	$142^D \pm 49$ (8)
Activity area (ha)	$87.9^A \pm 51.9$ (13)	$97.3^A \pm 43.7$ (22)	$58.6^A \pm 39.8$ (11)	$58.6^A \pm 39.7$ (10)	$7.4^B \pm 3.6$ (7)	$28.4^A \pm 18.8$ (8)
Water influx (mL kg^{-1} d^{-1})	$23.6^A \pm 4.4$ (13)	$14.4^B \pm 4.9$ (22)	$14.2^B \pm 4.9$ (11)	$9.1^C \pm 2.8$ (10)	$2.4^D \pm .5$ (7)	$7.9^C \pm 4.1$ (8)
CO_2 production (mL g^{-1} h^{-1})	$.147^A \pm .016$ (6)	$.097^B \pm .042$ (11)	$.077^{BC} \pm .025$ (6)	$.053^C \pm .029$ (7)	$.016^D \pm .009$ (7)	$.052^C \pm .019$ (7)
Daily energy expenditure (kJ kg^{-1} d^{-1})	91.6 ± 10.8 (6)	60.5 ± 26.6 (11)	48.2 ± 15.7 (6)	33.5 ± 18.6 (7)	10.3 ± 6.1 (7)	32.8 ± 12.2 (7)
Water influx from food (mL kg^{-1} d^{-1})	14.4 ± 1.7 (13)	9.5 ± 4.2 (11)	7.6 ± 2.5 (6)	5.3 ± 2.9 (7)	$1.6 \pm .9$ (7)	5.2 ± 1.9 (7)
Nonfood water influx (mL kg^{-1} d^{-1})	6.8 ± 2.8 (13)	5.2 ± 3.2 (11)	10.0 ± 3.7 (6)	3.9 ± 3.4 (7)	$.8 \pm .5$ (7)	2.8 ± 2.7 (7)
Food intake (g kg^{-1} d^{-1})	$17.0 \pm .18$ (13)	11.2 ± 4.9 (11)	8.9 ± 2.9 (6)	6.2 ± 3.4 (7)	1.9 ± 1.1 (7)	6.1 ± 2.3 (7)

Note. Values are means $\pm$ SD. Sample sizes are in parentheses. TBW = total body water. Seasonal means did not differ except those with superscripts. Superscript letters indicate values that differed at $P < 0.05$.

correlation between weather parameters and distances moved per day within each season.

Activity area varied among seasons, being higher during the summer, intermediate during the spring and autumn, and lowest during winter (ANOVA: $F_{5,65} = 6.48$, $P < 0.0001$; Table 1). Similarly, variation in activity area was positively correlated with solar radiation ($r_{70} = 0.50$, $P < 0.0001$), hours of sunshine ($r_{70} = 0.47$, $P < 0.0002$), and temperature ($r_{70} = 0.37$, $P < 0.004$).

Body mass of monitors was positively correlated with movement frequency ($r_{69} = 0.47$, $P < 0.0001$; Fig. 2), daily distance moved per day ($r_{69} = 0.36$, $P < 0.0044$), and activity area ($r_{69} = 0.40$, $P < 0.0015$). There was no correlation between our three measures of activity and TBW, percent lipid content, or body condition index.

Water Influx

Water influx represents all water taken in by monitors, from drinking, food (preformed and metabolic), and pulmocutaneous exchange with the environment. There were marked seasonal differences in mass-specific water influx rates (ANCOVA: $F_{6,65} = 36.54$, $P < 0.0001$; Table 1), which were high during the early, mid-, and late summer, intermediate in the autumn and spring, and low during the winter.

Seasonal changes in water influx correlated positively with hours of sunshine ($r_{70} = 0.71$, $P < 0.0001$), patterns of solar radiation ($r_{70} = 0.67$, $P < 0.0001$; Fig. 3), and to a lesser extent, ambient temperature ($r_{70} = 0.51$, $P < 0.0001$). Likewise, water influx was highly positively correlated with movement frequency ($r_{70} = 0.89$, $P < 0.0001$), average distance moved per
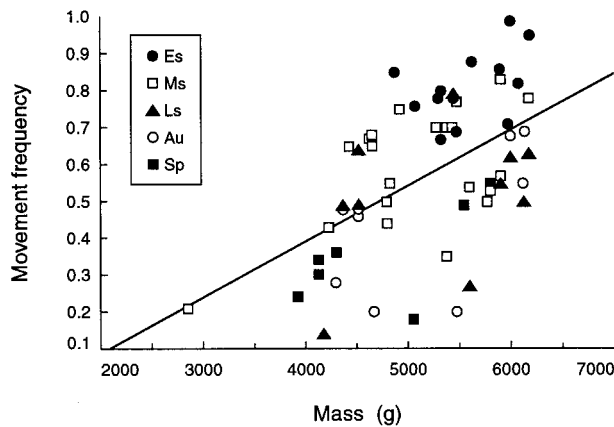
Figure 2. Movement frequency as a function of body mass for male lace monitors that were tracked continuously over 1997 and 1998 using radiotelemetry.

day ($r_{70} = 0.77$, $P < 0.0001$), and activity area ($r_{70} = 0.50$, $P < 0.0001$).

Weather parameters did not correlate with water influx within seasons. Conversely, variation in water influx within each season (excluding winter) was highly correlated to changes in movement frequency (Fig. 4; early summer $r_{10} = 0.81$, $P < 0.001$; midsummer $r_{20} = 0.75$, $P < 0.0002$; late summer $r_{10} = 0.79$, $P < 0.01$; autumn $r_{10} = 0.62$, $P < 0.01$; spring $r_6 = 0.90$, $P < 0.001$) and average distance moved per day (early summer $r_9 = 0.61$, $P < 0.01$; midsummer $r_{20} = 0.72$, $P < 0.0008$; late summer $r_{10} = 0.74$, $P < 0.01$; autumn $r_{10} = -0.05$, $P > 0.92$; spring $r_6 = -0.14$, $P > 0.80$). No correlation existed between water influx and activity area within each season. However, animals that moved more frequently and moved greater distances per day had higher water influx rates.

We conducted a stepwise multiple linear regression on log-transformed water influx data using predictor variables of weather parameters (temperature, sunshine, solar radiation), activity (movement frequency, distance moved, activity area), and body condition (body mass, body condition index, TBW, percent lipid content). Movement frequency, solar radiation, and body mass were retained in the final model at the $\alpha = 0.05$ level of significance ($F_{3, 53} = 169.76$, $P < 0.0001$, $r^2 = 0.90$). Of the variation explained by the model (90.5%), movement frequency accounted for 84.2%, which suggests that variation in water flux was mostly explained by activity (Table 2).

Energy Flux

The CO_2 production rates differed significantly between seasons, being highest in early summer and lowest in winter (ANCOVA: $F_{6, 38} = 13.86$, $P < 0.0001$; Table 1). Similarly, seasonal changes in CO_2 production paralleled weather conditions,

correlating positively with hours of sunshine ($r_{44} = 0.63$, $P < 0.0001$), patterns of solar radiation ($r_{44} = 0.74$, $P < 0.0001$; Fig. 5) and temperature ($r_{44} = 0.51$, $P < 0.002$). Likewise, CO_2 production was highly correlated to movement frequency ($r_{44} = 0.86$, $P < 0.0001$), average distance moved per day ($r_{44} = 0.82$, $P < 0.0001$), and activity area ($r_{44} = 0.45$, $P < 0.005$).

Within season comparisons revealed no correlation between weather parameters and CO_2 production. However, variation within each season was highly correlated to changes in movement frequency (early summer $r_4 = 0.81$, $P < 0.001$; midsummer $r_{11} = 0.91$, $P < 0.0006$; late summer $r_4 = 0.48$, $P < 0.05$; autumn $r_5 = 0.88$, $P < 0.008$; spring $r_6 = 0.76$, $P < 0.01$; combined summer $r_{25} = 0.79$, $P < 0.0001$; Fig. 6). To a lesser extent, average distance moved per day correlated with CO_2 production but only for midsummer ($r_{11} = 0.68$, $P < 0.05$) and the combined summer periods ($r_{25} = 0.66$, $P < 0.004$). No correlation existed between CO_2 production and activity area within each season. Nevertheless, animals that moved more frequently and moved greater distances per day expended more energy per day.

We conducted a stepwise multiple linear regression with log-transformed CO_2 production as our response variable against predictor variables of weather parameters (temperature, sunshine, solar radiation), activity (movement frequency, distance moved, activity area) and body condition (body mass, body condition index, TBW). Movement frequency, solar radiation and body mass were again retained in the final model at the $\alpha = 0.05$ level of significance ($F_{3, 31} = 35.84$, $P < 0.0001$, $r^2 = 0.78$; Table 2). Of the variation explained by the model (77.7%), movement frequency accounted for 71.8%, which suggests that variation in CO_2 production, like water flux, was mostly explained by activity (Table 2).
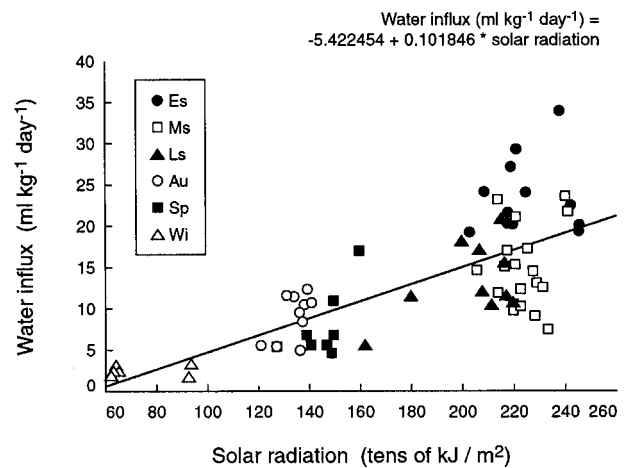

Figure 3. Water influx by male lace monitors in relation to changes in solar radiation over spring, summer, autumn, and winter.
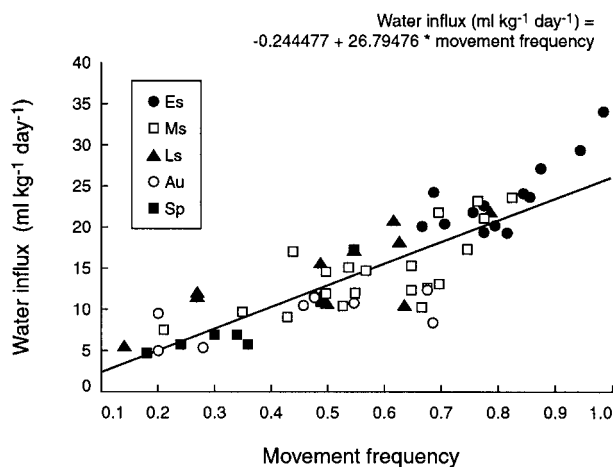
Figure 4. Water influx as a function of movement frequency for adult male monitors during summer, autumn, and spring.

Prey Consumption Rates

The energy and water content of prey items are shown in Table 3. Prey consumption changed seasonally, paralleling changes in CO_2 production (Table 1). These estimates of prey consumption represent minimum requirements (i.e., food energy required = energy expended) because the model used assumes energy balance. Based on our model, a 1-kg monitor would require 2.2 kg of assimilated prey per year to remain in energy balance.

The percent of water influx from nonfood sources was quite high, ranging from 55% to 35% across all seasons (Table 1). Thus, it seems that a significant fraction of water influx by *V. varius* is derived from sources other than food, through either drinking or pulmocutaneous exchanges. This was supported by the lower than expected R^2 for the relationship between CO_2 production and rate of water influx ($F_{1,43} = 174.91$, $P < 0.0001$, $r^2 = 0.80$; log-log transformation). Further, there was a significant negative relationship between nonfood water intake and movement frequency ($F_{1,38} = 40.8$, $P < 0.0001$, $r^2 = 0.53$), indicating that animals that moved more frequently had higher nonfood water influx rates than those that moved less frequently. However, there was no relationship between TBW, percentage lipid content, or body condition index and nonfood water influx rate.

Discussion

Seasonal Differences

The rates of energy and water turnover for *Varanus varius* are strongly seasonal and reflect variations in activity and thermal weather conditions. Despite these differences, there were no major or consistent changes in body mass (Table 1) in any of the study animals, supporting the notion that they were generally maintaining water and energy balance during the active release periods (excluding winter).

The variation in TBW, percent lipid content, and body condition estimates (Table 1) between spring and all the other seasons (for the 10 animals) indicated clear seasonal differences in the size of body fat reserves and reflects that animals are unable to feed over winter and, hence, rely on body fat reserves for sustenance. However, we view these results with caution because using body water space to estimate lipid content can result in large errors, especially when they have not been calibrated with realised values of lipid and nonbody lipid tissue (Speakman 2001).

As expected for an ectothermic vertebrate occupying temperate latitudes, this study clearly shows that water influx rates and field metabolism of *V. varius* were highest during summer and lowest during winter (Table 1), roughly paralleling the between-season declines in weather conditions (Fig. 1).

For many reptiles, body temperature has a positive influence on the rates of resting metabolism (Christian and Conely 1994; Thompson and Withers 1997) and active metabolic rate (Christian and Weavers 1994; Christian et al. 1995). In our study, ambient temperature declined from 23°C in the summer to 10°C in the winter (Fig. 1). This temperature decline presumably caused a drop in resting metabolic rate that would in part explain seasonal depression in field metabolic rate (Table 2; Fig. 5). The other influence on FMR is activity. Indeed, movement frequency and distances moved also declined as the season progressed from summer to winter; hence, the proportion of energy expended through activity would also have reduced, further depressing field metabolic rate (Table 2). Thus, the direct effects of temperature and activity can explain the seasonal trend in metabolic rate. Similarly, energy expenditure in *Varanus rosenbergi* appears driven by solar radiation and activity (Christian and Weavers 1994) and rate of water loss by *Varanus gouldii* appears driven by activity and weather (Green 1972). Similar patterns have been reported for the tropical varanids, but their cue for inactivity is the onset of dry conditions as opposed to unfavourable thermal conditions (Christian and Green 1994; Christian et al. 1995).

Temperature and activity do not act entirely independently to influence energy and water balance because activity is dependent on solar radiation (itself correlated with temperature; Figs. 3–6). There is also a behavioural component driving activity, with decisions on whether or not to forage driven by food availability and the costs and benefits of food acquisition. This latter influence will be most evident within single seasons, where seasonal parameters do not vary substantially.

Intrasummer Differences

During the early, mid-, and late summer, solar radiation, ambient temperatures, and hours of sunshine changed little (Fig.

1) and were well above the minimum required by *V. varius* for thermoregulation (Weavers 1983). In contrast, monitor activity declined as the summer season progressed. Animals were active an average of 80% of days in early summer, 60% in midsummer, and 45% in late summer (Table 1; Figs. 4, 6). Corresponding estimates of energy expenditure and water turnover declined from 90 kJ kg^{-1} d^{-1} and 21 mL kg^{-1} d^{-1} during early summer, to 51 kJ kg^{-1} d^{-1} and 16 mL kg^{-1} d^{-1} during midsummer, and to 32 kJ kg^{-1} d^{-1} and 12 mL kg^{-1} d^{-1} during the late summer—a threefold decline for energy expenditure and a twofold decline in water influx (based on Figs. 4, 6). As a consequence of the curvilinear relationship between energy expenditure and movement frequency, the energy required by monitors is far less than the water required per increment drop in activity (Fig. 6). This suggests that the costs of being active are far greater in terms of energy expenditure than for the corresponding requirements of water.

We believe that these trends in activity, in the absence of changes in thermal conditions, are tied to seasonal changes in food availability. In our study, the number of freshly caught monitors that had food in their stomachs declined from 90% in early summer, to 44% in midsummer, and finally, to 14% in late summer (Guarino 2001). The type of prey taken also changed. Nestling birds and mammals (particularly rabbits) were only plentiful during early summer (A. Newsome, unpublished data). Seasonal trends in energy expenditure similar to ours, except for the tropical monitors *V. gouldii* and *Varanus panoptes*, have been interpreted as a response to a shortage of prey (Christian et al. 1995). And supplemental feeding significantly increased the homerange size of *V. albigularis*, suggesting that activity is constrained by prey availability (Phillips 1995). In our study, monitors reduced their energy requirements by threefold through reductions in activity as the summer progressed, which we interpret as a behavioural response to reduced prey availability. We suggest that monitors became less active as the summer progressed because the energetic costs of activity were outweighed by the foraging costs of finding, capturing, ingesting, and metabolising food items.

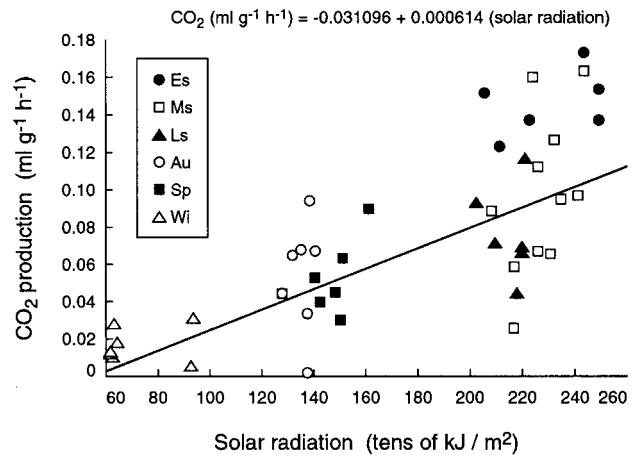An additional influence that may have contributed to the

Figure 5. CO_2 production of male lace monitors as a function of solar radiation over spring, summer, autumn, and winter.

elevated rates of energy expenditure and water flux observed during the early summer was reproductive activity. Female monitors come into oestrous during the early summer (Carter 1991) and male monitors actively searched and courted females during this period. We observed some males moving over 1 km in 1 d in search of females. Merker and Nagy (1984) reported a similar pattern (although at a much smaller scale) for a small 5-g diurnal lizard, *Sceloporus virgatus*, and suggested that the differences in activity were in response to changes in reproductive status. This pattern of behaviour (e.g., adjusting outputs) is consistent with the hypothesis that lizards can change their activity in a manner that ultimately enhances their survival (Merker and Nagy 1984).

Interindividual Differences

Interindividual variability in field metabolism and water influx has been noted in other studies on varanids (Green 1972; Vernet et al. 1988; Green et al. 1991*a*,1991*b*) and squamates (Congdon

Table 2: Summary of stepwise multiple regression relating water influx and CO_2 production to weather conditions, activity, and body condition

Model	Standard Error	Type II SS	*F* Value	Partial r^2	*P*
Log water influx:					
Movement frequency	.226	2.023	35.05	.842	.0001
Solar radiation	.001	2.062	35.74	.054	.0001
Mass	.000	.292	5.07	.009	.0286
Log CO_2 production:					
Movement frequency	.496	17.796	66.62	.718	.0001
Solar radiation	.032	1.137	4.26	.031	.0470
Mass	.000	1.239	4.64	.028	.0391

and Tinkle 1982; Bradshaw et al. 1987; Nagy et al. 1991; Peterson et al. 1998).

In our study, the most striking interindividual difference was observed during the midsummer period, where we found a sixfold difference in the amount of energy expended for two individual monitors (Fig. 6). This, it appears, was related to body mass—a difference of 1.2 kg was noted between the two monitors. Although, we found small differences in energy expenditure for most of the monitors of the same size, for two individuals (of the same size) there was greater than a twofold difference in energy expenditure. Thus, it seems that both body size and balancing selection have an important influence on the rates of energy expenditure in lace monitors.

The benefits of being less active as opposed to more active for animals of the same size remain equivocal—less active animals have lesser energy demands and therefore need to eat less than more active animals. Hence, we might not expect a relationship between activity (movement frequency, distances moved, activity area) and body condition (TBW, percent lipid content, or body condition index) for animals of the same size, and we found no such relationship. We did find a relationship between movement frequency and body mass—larger animals moved more often than smaller animals, perhaps reflecting the greater demands of larger animals for food. Body size appears to be the only strong influence on variation in activity levels among individuals and, hence, on variation in their absolute energy expenditure and water influx.

Water Economy Index

A water economy index (WEI) has been proposed (Nagy and Peterson 1988) to assess the water fluxes of animals relative to
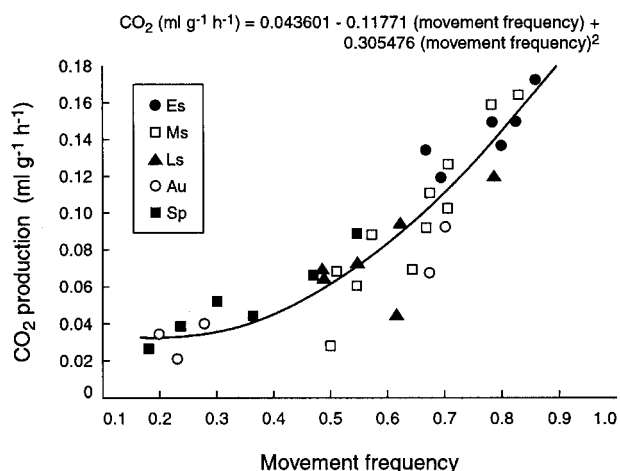

CO_2 (ml g^{-1} h^{-1}) = 0.043601 - 0.11771 (movement frequency) + 0.305476 (movement frequency)^2

Figure 6. CO_2 production in relation to the movement frequency of male lace monitors over spring, summer, and autumn.

their rates of energy expenditure. The lower this ratio, the less water animals use for the same energy output. Desert vertebrates (0.081 mL kJ^{-1}) tend to have lower WEIs than their nondesert relatives (0.2 mL kJ^{-1}; Nagy and Peterson 1988). In our study, *Varanus varius* exhibited WEI values of 0.25 ± 0.07 mL kJ^{-1} for the early summer, midsummer, and autumn, and 0.40 ± 0.28 mL kJ^{-1} for the late summer. Excluding late summer, these results suggest that *V. varius* process a similar amount of water relative to energy output as the desert reptiles and are also at the upper end of the theoretical range for her-

Table 3: Water and energy content of some vertebrate and invertebrate prey items

Species	Mass (g)	Water (% Body Mass)	Energy (kJ g^{-1}) Fresh	Dry
Vertebrate:				
Mus domesticus	17	68.5 ± 5.3	8.0 ± 1.3	24.4 ± 1.4
Oryctolagus cuniculus (juvenile)	90	74.8 ± 1.2	5.5 ± .5	21.7 ± 1.8
O. cuniculus (adult)	1,200	67.3 ± 2.8	7.6 ± 1.1	23.3 ± 1.7
Small lizards	4	74.0 ± 1.1	5.3 ± .4	20.4 ± 1.2
Rattus sp.	120	69.5 ± 1.4	6.7 ± .6	21.9 ± 1.2
Total vertebrate		70.2 ± 4.5	7.2 ± 2.5	22.7 ± 3.0
Invertebrate:				
Arachnida	P	69.8	7.0 ± .5	23.3 ± 1.5
Chilopoda	P	74.1	4.4 ± .5	21.7 ± 1.7
Coleoptera	P	64.3	8.5 ± .1	23.7 ± 1.5
Oligochaeta	P	76.2	3.5 ± .4	14.8 ± 1.0
Orthoptera	P	66.8	8.1 ± 1.3	22.3 ± 1.3
Scorpionida	P	64.5	7.9 ± .1	22.3 ± 1.0
Total invertebrate		69.8 ± 4.8	6.8 ± 2.0	22.2 ± 4.0
Grand mean		70.0 ± 4.6	7.1 ± 2.3	22.5 ± 3.5

Note. Values are means ± SD. P = pooled sample.

bivorous vertebrates that do not drink water (Nagy and Peterson 1988). The WEI values reported here for *V. varius* resemble other published values for temperate varanids (Vernet et al. 1988; Dryden et al. 1990; Green et al. 1991*a*, 1991*b*).

The WEIs for the late summer period were high and almost double those in the other seasonal phases, probably because of environmental and behavioural influences. Although we observed some of our telemetered monitors emerging from their hollows on rainy days, this would not account for the high nonfood water intake rates because only 22.2 mm of rain fell. In contrast, we did see a large number of telemetered and nontelemetered monitors either swimming in or drinking from farm reservoirs during the late summer period, which would account for the higher nonfood water intake rates found. It has been suggested that during periods of low food acquisition, increased water influx through nonfood sources may be advantageous because it presumably reduces metabolic expenditure associated with water conservation via solute linked reabsorption by the kidneys and cloaca (Green et al. 1997). In this regard, it seems behavioural adjustments are just as important as physiological tolerances for manipulating energy expenditure relative to energy acquisitions. Thus, monitors that moved more may have used nonfood water influx as a compensatory mechanism to reduce energy expenditure.

Acknowledgments

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