ECOPHYSIOLOGY

Keith A. Christian · Jonathan K. Webb ·
Timothy J. Schultz

Energetics of bluetongue lizards (*Tiliqua scincoides*) in a seasonal tropical environment

Abstract We studied the physiological ecology of blue-tongue lizards (*Tiliqua scincoides*) on the Adelaide River floodplain in tropical Australia to determine the seasonal patterns of energy expenditure and to determine the mechanisms by which seasonal differences were achieved. Field metabolic rates (FMR) were significantly lower in the dry season (37.6 kJ kg^{-1} day^{-1}; $n=9$) than in the wet (127.3 kJ kg^{-1} day^{-1}; $n=7$). Water flux was also lower in the dry season (6.8 ml kg^{-1} day^{-1}; $n=9$) than in the wet (39.4 ml kg^{-1} day^{-1}; $n=7$). Measurements of body temperatures (T_b) and movements of free-ranging animals, and standard metabolic rate (SMR) of recently caught animals, allowed a detailed analysis of energy budgets for wet and dry seasons. In the dry, bluetongue lizards expended 90 kJ kg^{-1} day^{-1} less energy than in the wet season. Unlike some other lizards of the wet-dry tropics, SMR did not differ between seasons. About 5% of the seasonal difference in FMR was due to lower night time T_b during the dry season, and about 7% was due to lower diurnal T_b. The remaining 88% of the decrease in energy expended in the dry season was due to a substantial decrease in other costs that may include reproduction, growth, digestion and activity. If we assume the animals fed daily and the costs of digestion are taken into account, the estimates are: 14% of the savings result from lower T_b at night, 20% from lower T_b in the day, and 66% result from decreased activity. It is therefore apparent that, unlike some agamid and varanid lizards that use a combination of behavioural and physiological mechanisms to conserve energy when food and water are limited, bluetongue lizards primarily use behavioural mechanisms to achieve a dramatic reduction in energy expenditure in the dry season.

K. A. Christian (✉) · J. K. Webb · T. J. Schultz
School of Environmental Sciences,
Northern Territory University,
NT 0909 Darwin, Australia
e-mail: kchristi@ntu.edu.au
Fax: +61-8-89466706

Introduction

The wet-dry tropical region of northern Australia is characterised by high diurnal temperatures year-round but distinct wet and dry seasons (Ridpath 1985). Typically, over 75% of the annual precipitation falls during the wet season (Taylor and Tulloch 1985). The lack of moisture in the dry season limits plant growth, and insect numbers are greatly reduced compared to the wet season (Churchill 1994; Griffiths and Christian 1996). The dry season is thus a season of limiting resources for many animals (Christian et al. 1995, 1999a; Griffiths and Christian 1996). Most species of reptiles are much less conspicuous in the dry season, and some enter a period of aestivation (Christian et al. 1996a, 1996b, 1996c, 1996d; Kennett and Christian 1994). Others are active to some extent, but nevertheless expend less energy in the dry season compared to the wet. This reduction in field metabolic rate (FMR) can be accomplished by physiological mechanisms such as metabolic depression (Christian et al. 1996b, 1996c, 1999a, 1999b), and behavioural strategies such as thermoregulation at lower body temperatures (T_b) (Christian and Bedford 1995, Christian et al. 1996c, 1999b) and reduced activity (Christian et al. 1996b, 1996c, 1999b). Determining which strategies are employed by a species is critical to our understanding of the annual or life-time energy budgets of the animals. Furthermore, determining the range of strategies employed by different species is important to our broader understanding of how animals compensate during periods of scarce resources (Christian et al. 1999a).

Although we have some understanding of how many large, conspicuous reptiles (notably varanids and agamids) cope with seasonal fluctuations in resources, the consequences of this seasonality on other tropical taxa (particularly skinks and snakes) remains largely unexplored. Bluetongue lizards constitute a group of five

species of large viviparous skinks found throughout Australia (Cogger 2000). The common bluetongue, *Tiliqua scincoides*, is found in northern and eastern Australia and is locally abundant in places (Torr 1999). Despite its large size and ubiquity, there are relatively few detailed ecological studies on this widely distributed species (but see Koenig et al. 2001). Among squamates, skinks are regarded as having generally low standard metabolic rates, SMR (Andrews and Pough 1985) and poor aerobic abilities (Pough and Andrews 1984; Withers 1981). The closely related *Tiliqua* (*Trachydosaurus*) *rugosus* is described as slow moving with limited stamina and a high net cost of locomotion, which may be related to its body shape (John-Alder et al. 1986). Given its apparent similarity in morphology, phylogeny and ecology to *T. scincoides*, we hyphtesise a similar locomotory capacity in this species.

We studied a population of *T. scincoides* in the wet-dry tropics and measured FMR, water flux, T_b of free-ranging animals, and seasonal food availability in the field as well as resting and activity metabolism in the laboratory. We combined field and laboratory data to determine what mechanisms bluetongue lizards use to conserve energy in the dry season when food and water resources are scarce.

Materials and methods

Study sites

We studied bluetongue lizards on and near the Adelaide River floodplain, approximately 70 km east of Darwin, Northern Territory. The climate features a distinct wet (December through March) and dry (May through September) season separated by short transitional periods. The wet season is characterised by warm air temperatures (mean maximum of 31.7°C and mean minimum of 25.7°C in January in Darwin), high humidity and frequent rainfall. Dry season days are warm, with cool nights (mean maximum of 30.4°C and mean minimum of 19.3°C in July), low humidity and little or no rain (Taylor and Tulloch 1985).

Radio-telemetry

We located bluetongue lizards by slowly driving along a road that traversed the floodplain in the half hour prior to, and after, sunset. At the Northern Territory University, Darwin, we surgically implanted miniature temperature sensitive radio-transmitters (Holohil Systems, Canada, transmitter models BD-2T, PD-2T, SB-2T) into the abdominal cavity of the lizards. Prior to surgery, all transmitters were waterproofed and the whip antennas were enclosed in silicon tubes to prevent injury to internal organs and to facilitate removal of transmitters. Transmitters were then calibrated at 5°C increments between 5°C and 40°C in a water bath (Grant, USA) using a mercury thermometer traceable to a standard. Final mass of transmitters ranged between 2.8 and 5.2 g (mean =4.3 g) depending on the model. We matched transmitters to suit lizard size, such that all implanted transmitters weighed <1% of lizard body mass.

We implanted transmitters in 16 lizards (10 males, 6 females, mean SVL =32.8 cm, range 29.0–38.0 cm; mean mass =563 g, range 315–702 g) during 1998 (*n*=10) and 1999 (*n*=6). Lizards were anaesthetised at room temperature with a mixture of oxygen (0.6 l min⁻¹), Fluothane (2–5%) and nitrous oxide (1.0 l min⁻¹) administered with a Fluotech anaesthetic machine. Most lizards entered surgical-plane anaesthesia (loss of muscle reflex in limbs) after 20–40 min. Transmitters and surgical instruments were cold sterilised in 90% ethanol solution for 4 h prior to surgery. Prior to implantation we rinsed transmitters with sterile distilled water. Our surgical techniques were identical to those of Koenig et al. (2001) except that we closed scales with Histoacryl surgical glue. All lizards were held in captivity for 1 week following surgery to ensure that their wounds had healed prior to their release at the site of capture.

T_b and activity

We used an automated system with a large antenna, receiver and digital processor (Telonics, USA) connected to a data logger (Campbell CR10X, USA) to record T_b of free-ranging lizards. We recorded T_b of multiple lizards at the same time at 15-min intervals. Subsequently, hourly means were calculated for each individual and grand means were calculated for all the lizards sampled in a season for use in the energy budget calculations.

We obtained detailed information on the movements of bluetongue lizards in 1998 (59 days in the dry season and 24 days in the wet season) and in 1999 (26 days in the dry season and 26 days in the wet season). During the dry season we were able to locate lizard sleeping sites in the early morning and late afternoon. However, during the wet season many lizards moved long distances and we were usually only able to locate lizards once each day (early morning or evening). Locations of lizards were marked with flagging tape and were plotted onto an aerial photograph of the study site (using four compass bearings to fixed landmarks). For small movements we measured the straight-line distance between successive locations with a 50 m tape measure. For larger movements we measured the straight line distances between successive locations using a calibrated aerial photograph of the study site.

Food availability

We estimated seasonal prey availability by sweep netting and pit-fall trapping during the wet and dry seasons. For sweep netting we sampled the foliage (0–1 m above the ground) for invertebrates in four habitat types that were regularly used by foraging bluetongue lizards: the floodplain road edge habitat (predominantly introduced gamba grass *Andropogon gayanus*), ponded pasture floodplain habitat (predominantly introduced paragrass *Brachiaria mutica*), the leaf litter habitat on Beatrice Hill, and the introduced ground cover Calopo (*Calopogonium mucunoides*) on Beatrice Hill. Five samples (six sweeps per sample) were collected from each habitat type from five randomly chosen sites each spaced 50 m apart. A total of 20 samples were collected during each season (total of 120 sweeps). The sweep net contents were placed in 75% ethanol and were later sorted to the level of order. We used pit-fall traps to supplement our sweep-sampling, and these consisted of 20 l plastic buckets placed in three lines of ten traps (each trap 10 m apart) with each trap-line >50 m apart. Trap-lines sampled the road-edge habitat, paragrass habitat and bare ground on the floodplain. Traps were opened for two consecutive nights on each of 2 months (total of 4 nights) during each season (total of 120 trap nights per season). Traps were cleared by hand in the early morning and the number (and size) of each invertebrate order was recorded. We did not record ant numbers (Hymenoptera) in our pit-traps because ants are seldom eaten by bluetongue lizards (Greer 1989). Examination of the scats from bluetongue lizards indicated a mixed diet of invertebrates and plant material. Thus, the measurements of invertebrate abundance only represent a relative index of seasonal changes in this component of the diet. Although the abundance of plant material was not quantified, it is readily apparent that herbaceous material is very abundant in the wet season but is scarce or desiccated in the dry season (personal observation).

Field metabolism

We used the doubly labelled water (^{3}H-H_2^{18}O) technique (Lifson and McClintock 1966) to measure FMR and water flux of free ranging animals over a mean period of 19 days in the wet season and 54 days in the dry season. The FMR is a measure of the energy expended by an animal in its natural habitat over the period of measurement, and water flux is a measure of the amount of water an animal processes through its body each day (Nagy and Peterson 1988). Preliminary samples indicated that the longer period was required in the dry season to have sufficient turnover for analysis. Blood samples (0.3 ml) were taken from the caudal vein before injections of 200 μl of ^{18}O and 500 μl of tritiated water, 8–12 h after injection, and upon recapture. Isotopic samples were measured at the Division of Wildlife and Ecology, CSIRO, Canberra. The techniques for sample analysis to determine isotopic measurements of FMR and water flux are described in detail elsewhere (Christian and Green 1994; Christian et al. 1995, 1996b, 1996c, 1996d, 1998, 1999b). Because bluetongue lizards are omnivorous (Greer 1989; Christian, personal observation), the CO_2 values determined by the isotopic technique were converted to units of energy using the energy equivalent of 23.7 kJ l^{-1} CO_2, which is halfway between the conversion factors for a herbivorous diet and a diet of insects (Nagy 1982a). We have also calculated a predicted FMR based on an allometric equation from iguanid lizards (Nagy 1982a) for each season to compare with the measured values from bluetongue lizards.

The water economy index (WEI) is the ratio of water flux to FMR with the units of ml kJ^{-1} (Nagy and Peterson 1988). The ratio of water used per kJ of energy used is an indication of the extent to which an animal has adaptations to conserve water, and in conjunction with measurements of water flux, indicates how an animal maintains water balance under natural conditions (Nagy and Peterson 1988). Again, we used allometric equations for reptiles from arid and tropical regions (Nagy 1982b) to calculate predicted water flux rates for comparison with measured values from bluetongue lizards.

Laboratory measurements

We measured SMR at four temperatures in the laboratory at the Northern Territory University using respiratory gas analysis with an Ametek Applied Electrochemistry O_2 analyser (model S-3 A). Animals were kept at each temperature (18, 24, 30 and 36°C) in a controlled temperature chamber (Forma Scientific) for 12 h prior to, and during, measurements. Details of the gas analysis system have been provided elsewhere (Christian et al. 1995, 1996b, 1996c, 1998, 1999b). SMR was measured over 50 min intervals between 0000 and 0600 hours. Resting metabolic rate (RMR, measured in awake, resting lizards) was measured between 0900 and 1700 hours. Most lizards were fasted for at least 7 days prior to these measurements; however, in a separate experiment, three bluetongue lizards were fed a meal of mixed fruit and meat (mean meal size was 16.7±5.3% of lizard body mass) to determine the metabolic costs of digestion. The metabolic rate of these lizards was measured before feeding, then once each day and night for the following 6 days.

Activity metabolism was examined in four lizards during treadmill exercise using an open-flow respirometry circuit (Christian et al 1996b, 1996c). A clear acetate mask, fitted with a rubber diaphragm, ensured that all expired gases were collected. The exercise regime followed closely that of John-Alder et al. (1986). Briefly, maximal aerobic speed (0.80 km h^{-1}) was determined by steadily increasing treadmill speed until oxygen consumption (VO_2) no longer increased. VO_2 and carbon dioxide production (VCO_2) were calculated for every 2 min of exercise according to the equations of Withers (1977). The maximal oxygen consumption (VO_{2max}) was calculated from the 2 min periods of activity with the highest VO_2 recorded on 2 consecutive days, with the greater value reported here. We measured VO_{2max} at 30 and 35°C, with 1 week's rest between different temperatures. We also measured VO_2 in lizards exercising at a submaximal speed, 0.35 km h^{-1}. This speed represents a hypothetical foraging speed, based on field observations of this, and closely related, species (*Tiliqua rugosa*, John-Alder et al. 1986).

Energy budget calculations

The daily energy expenditure (FMR) was further investigated by dividing this total energy expended into components due to T_b and activity for each season by combining data from the laboratory and from the field. The 24 h day was divided into periods of day (0800–1800 hours) and night (the remaining 14 h). T_b were assumed to equal grand mean T_b measured during those periods during each season. These T_b were used in regression equations relating resting metabolism to T_b as determined by the laboratory measurements. The VO_2 values were converted to units of energy using the energy equivalent of 20.08 kJ l^{-1} O_2 (Benabib and Congdon 1992) and multiplied by the number of hours during night (resting metabolism during inactive period: RMI) and by the number of hours during the day (resting metabolism during active period: RMA). The sum of the calculated energy expenditures for these two periods represents the total resting metabolism (TRM) of a lizard under the thermal regime they experienced in the field during each season (Benabib and Congdon 1992).

The difference between the FMR and TRM is termed activity respiration (AR; Benabib and Congdon 1992) and represents the amount of energy expended in activities such as locomotion, digestion, and reproductive costs (Van Marken Lichtenbelt et al. 1993). The ratio of FMR/TRM is the field maintenance scope (Congdon and Tinkle 1982), and if the animal's body mass changes <1% per day, this value can be considered as the sustained metabolic scope (SusMS) (Peterson et al. 1990). The percentage of the total field metabolism allocated to activity (%AR) is calculated as AR/FMR ×100 (Anderson and Karasov 1981). The averaged intensity of activity is termed the field activity scope (AS) and is calculated by expressing the amount of energy spent during the activity period (due to both activity and RMA) as a multiple of RMA (Congdon and Tinkle 1982; Benabib and Congdon 1992). Thus, AS=(FMR−RMI)/RMA.

Results

Field work

We measured T_b of seven lizards in the wet season and six in the dry season. Grand means for day and night are shown in Table 1 and were used in conjunction with laboratory measurements of metabolism to estimate the energy expended by animals at rest in the field (Tables 1, 2).

FMR were significantly higher in the wet season than in the dry (ANCOVA: $F_{1,\ 12}$=25.2, P=0.0003, Table 2). Similarly, water influx (Table 3) was significantly higher in the wet season than in the dry (ANCOVA: $F_{1,\ 12}$=68.3, P<0.0001). Total body water as a percent of mass was significantly higher in the wet season (ANCOVA, after arcsine transformation: $F_{1,\ 12}$=8.6, P=0.013), but the small difference (mean=2.6%) may not be ecologically significant. The WEI (Table 3) was significantly greater in the wet season than in the dry ($F_{1,\ 13}$=21.5, P=0.0005). The 95% confidence interval around the measured FMR during the wet season (42.8–94.7 kJ day^{-1}) is higher than the predicted value of 34.3 kJ day^{-1}. The 95% confidence interval around the measured FMR during the dry season

Table 1 Mean body temperatures (T_b) of free-ranging *Tiliqua scincoides* recorded during the day (0800–1800 hours) and night (the remaining 14 h of the 24 h period) in the wet and dry seasons. The energy expended by animals at rest during both periods in the two seasons was calculated using the field T_b in the equations (for the respective seasons) expressing the relationship between T_b and standard metabolic rate, SMR (night) and resting metabolic rate, RMR (day) as measured in the laboratory. The energy values for the day represent metabolism during active periods (RMA) and energy values for the night represent metabolism during inactive periods (RMI)

Period	Wet season		Dry season	
	T_b (°C)	Energy expended (kJ kg^{-1})	T_b (°C)	Energy expended (kJ kg^{-1})
Day (RMA)	32.9	10.2	24.2	4.1
Night (RMI)	28.0	8.6	21.4	4.4

Table 2 Carbon dioxide production, field metabolic rates (*FMR*), and mean body mass of free-ranging *Tiliqua scincoides* during the wet and dry seasons. Standard deviations are shown in parentheses. The predicted FMR is based on the allometric equation for iguanid lizards of Nagy (1982a). The total resting metabolism (*TRM*) is the 24-h sum, and is the sum of the RMA and RMI values in Table 1. The amount of energy expended in activity (*AR*) is estimated as the difference between the FMR and TRM. The percentage of the total field costs allocated to activity (*%AR*) is calculated by AR/FMR ×100. Terms labelled (digesting) assume that the animals fed daily and their resting metabolic rates are therefore elevated. The field activity scope (*AS*) is calculated as the amount of energy spent during the activity period expressed as a multiple of RMA. The sustained field metabolic scope (*SusMS*) is calculated as FMR/TRM

	Wet season (n=7 lizards)	Dry season (n=8 lizards)
Mass	539 (43.2)	609 (83.1)
CO_2(ml g^{-1} h^{-1})	0.22 (0.08)	0.07 (0.03)
FMR (kJ kg^{-1}day^{-1})	127.3 (47.3)	37.6 (17.9)
FMR (kJ day^{-1})	68.7 (28.1)	22.8 (10.8)
Predicted FMR (kJ day^{-1})	34.3	37.8
TRM (kJ kg^{-1}day^{-1})	18.8	8.5
TRM (digesting) (kJ kg^{-1}day^{-1})	56.4	25.5
AR (kJ kg^{-1}day^{-1})	108.5	29.1
AR (digesting) (kJ kg^{-1}day^{-1})	70.9	12.1
%AR	85.2	77.4
%AR (digesting)	55.6	32.2
AS	12.7	8.8
AS (digesting)	3.7	1.2
SusMS	6.8	4.4
SusMS (digesting)	2.3	1.5

Table 3 Water flux rates and total body water (% body mass: *TBW*), as determined from isotopic analysis for field active *Tiliqua scincoides*during wet and dry seasons . The water economy index (*WEI*) is the ratio of water flux to FMR (Nagy and Peterson1988). Sample sizes and masses are as in Table 2. Standard deviations are in parentheses. The rates of water flux predicted by the allometric equations for arid and semi-arid zone reptiles and for tropical, subtropical zone reptiles (Nagy 1982b) are also shown

	Wet season	Dry season
Water influx (ml day^{-1})	23.7 (8.2)	4.1 (1.7)
Predicted: arid (ml day^{-1})	11.7	13.0
Predicted: tropical (ml day^{-1})	29.9	32.4
Water influx (ml kg^{-1}day^{-1})	44.0 (14.2)	6.8 (3.0)
TBW (%)	66.7 (1.6)	64.1 (1.7)
WEI (ml kJ^{-1})	0.35 (0.06)	0.20 (0.07)

discrete home ranges and often returned to the same sleeping sites. The mean distance between successive sleeping sites were not significantly different between the wet (115.6 m, SD =66.2) and dry (71.6 m, SD =36.8) seasons ($P=0.08$). However, the mean distance moved per day was significantly greater in the wet season (96.7 m, SD =62.2) than in the dry (15.8 m, SD =14.7) season ($P=0.001$). Lizards moved from their sleeping sites on 74% of days in the wet season, but only on 19% of days during the dry season ($P<0.0001$).

Table 4 shows the total number and relative abundance of invertebrate orders collected from sweep-netting and pit-fall trapping in wet and dry seasons. Invertebrates were more abundant during the wet season (for sweep samples: $F_{1, 38}=46.84$, $P<0.0001$; for pit-traps: $F_{1, 160}=18.30$, $P<0.0001$). In general, sweep samples contained fewer orders of invertebrates in the dry season compared to the wet season (Table 4). Aranea (spiders) and Orthoptera (grasshoppers and crickets) were the most abundant invertebrates found in sweep samples during both seasons. Beetles (Coleoptera) and spiders were the most abundant invertebrates recorded in pit-traps during both seasons.

Laboratory measurements

Measurements of SMR in the two seasons are shown in Fig. 1. There was no difference between the seasons at any of the four temperatures (ANCOVA, $P>0.05$). Thus, the data were combined to yield the following relation-

(13.7–31.8 kJ day^{-1}) is lower than the predicted value of 37.8 kJ day^{-1}. Thus, the measured values of FMR were greater than predicted (for an iguanid, Nagy 1982a) during the wet season but less than predicted in the dry season. The 95% confidence intervals around the measured water flux rates were compared with the predicted flux rates for reptiles from arid zones and from tropical habitats. The measured values were similar to the predicted value in the wet season but lower than predicted in the dry season assuming the model for tropical reptiles. The measured values were higher than predicted in the wet season but lower than predicted in the dry season assuming the model for arid zone reptiles. Thus, the dry season water flux rates were very low compared to other reptiles

The movements of ten lizards were monitored in each of the two seasons. Bluetongue lizards maintained

Table 4 The number (*n*) and relative abundance (%) of invertebrate orders from sweep-netting and pit-fall trapping during the dry and wet seasons. Note that we did not include ants (Hymenoptera) in the pit-fall trapping data

| Invertebrate orders	Sweep netting				Pit-fall trapping			
	Dry		Wet		Dry		Wet	
	N	%	n	%	n	%	n	%
Aranea	44	65.7	106	35.9	18	15.8	13	3.8
Blattodea	0	0.0	12	4.1	3	2.6	1	0.3
Chilopoda	0	0	0	0	1	0.9	1	0.3
Coleoptera	3	4.5	12	4.1	54	47.4	215	62.3
Diptera	2	3.0	13	4.4	0	0.0	0	0.0
Hemiptera	1	1.5	27	9.2	0	0.0	0	0.0
Hymenoptera	4	6.0	45	15.3	–	–	–	–
Lepidoptera	2	3.0	19	6.4	2	1.8	7	2.0
Mantodea	2	3.0	1	0.3	0	0.0	0	0.0
Odonata	0	0.0	2	0.7	0	0.0	0	0.0
Orthoptera	8	11.9	58	19.7	36	31.6	108	31.3
Phasmatodea	1	1.5	0	0.0	0	0.0	0	0.0
Total no. invertebrates	67		295		114		345	
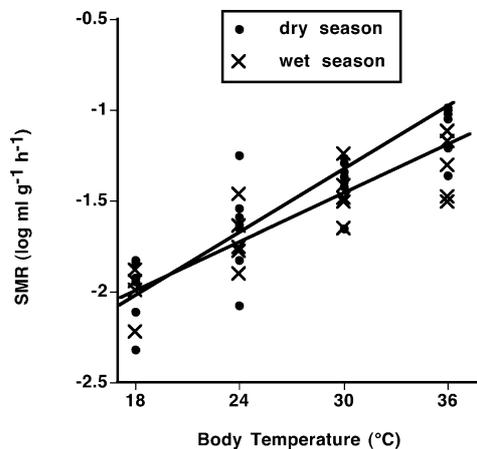
Fig. 1 Standard metabolic rate of bluetongue lizards as a function of T_b in the wet and dry seasons

ship between mass-specific VO_2 and T_b: ml O_2 g^{-1} h^{-1}= $0.001679 \times 10^{0.045T_b}$. There was no difference between RMR and SMR ($P > 0.05$ at each temperature). After feeding, the metabolic rate of bluetongue lizards increased to a peak 24–48 h after feeding, then metabolic rate gradually declined until it returned to the pre-feeding level about 4 days after feeding. The mean peak metabolism was 3.0 times resting (pre-feeding) metabolism (range 2.4–3.7 times resting metabolism). This factorial increase was used in energy budget calculations for a "digesting" animal, assuming that the lizards fed daily and therefore maintained the elevated metabolic rate associated with digestion.

At 35°C, VO_{2max} was 0.600 ± 0.144 ml O_2 $g^{-1}h^{-1}$, and at 30°C the mean maximal metabolic rate was 0.502 ± 0.138 ml O_2 $g^{-1}h^{-1}$, corresponding to a Q_{10} of 1.29. The respiratory exchange ratio remained below one throughout maximal exercise (0.93 and 0.77 at 35 and 30°C respectively). Sub-maximal metabolic rates were approximately two-thirds the maximal rates: 0.404 ± 0.045 ml O_2 $g^{-1}h^{-1}$ at 35°C and 0.336 ± 0.094 ml O_2 $g^{-1}h^{-1}$ at 30°C. Again, the respiratory exchange ratios

remained below one (0.84 and 0.93 at 35 and 30°C respectively).

Energy budget calculations

The measurements of FMR were combined with the laboratory measurements of metabolism to further explore the seasonal energetics of this species. Table 2 lists the calculated indices, most of which are substantially higher in the wet season (TMR, AR, AS, and SusMS), but %AR is only slightly higher. The FMR in the dry season was about 90 kJ kg^{-1} day^{-1} less energy than in the wet season. The field T_b data were combined with laboratory metabolism to estimate the parameters involved in this energy savings in the dry season. About 5% of the seasonal difference in FMR was attributable to lower T_b during the night in the dry season, and about 7% was attributable to lower T_b during the day. The remaining 88% of the decrease in energy expended in the dry season was due to decreased activity, broadly defined to include all factors other than the effects of temperature and resting metabolism, including digestion. If we assume that the lizards eat daily and maintain a metabolic rate three times resting metabolism, then the energy budget changes to reflect the higher daily energy expenditure at rest. Under this scenario, 14% of the energy conserved in the dry season was due to lower T_b at night, 20% was due to lower daytime T_b, and 66% was due to a reduction in activities other than digestion.

Discussion

Bartholomew et al. (1965) measured a mean daytime T_b of 32.6°C in captive bluetongue lizards housed outdoors in Brisbane, Queensland, remarkably similar to the daytime mean of 32.9°C we measured in free-ranging lizards in the wet season. The mean T_b of bluetongue lizards from suburban Sydney, New South Wales was 31.9°C while active in the field (Koenig et al. 2001).

Thus, active bluetongue lizards select relatively low activity T_bs, compared to many diurnal lizards (Table 2, Heatwole and Taylor 1987), in both temperate and tropical habitats. In the dry season, the bluetongue lizards remained in their burrows much of the time, resulting in daytime T_b being about 9°C cooler than in the wet season. At night, environmental temperatures are substantially lower in the dry season than in the wet season (Christian and Bedford 1995), resulting in lower dry season nighttime T_b. Thus, T_b are lower in the dry season because of a combination of behavioural and environmental factors.

Our SMR measurements are half those reported by Bartholomew et al. (1965) although the slopes with respect to temperature are similar for the two studies (0.045 in this study compared to 0.042). It is possible that this difference is due to differences in techniques, and it is unclear if the animals studied by Bartholomew et al. (1965) were postabsorptive. The three-fold difference in metabolic rate between fasted and fed lizards could easily account for the difference between the two studies. Studies on *Sceloporus* have emphasised the importance of controlling nutritional status and time of day in measuring SMR. There may be large increases in metabolic rate of fed lizards, and in measurements made during the normal waking hours (Niewiarowski and Waldschmidt 1992; Beaupre et al. 1993). Additionally, *Sceloporus* from different populations differ in their metabolic rates (Beaupre et al. 1993). These two groups of bluetongues (the present study and Bartholomew et al. 1965) were collected from sites over 3,500 km apart, therefore geographic variation could also explain the observed differences.

The seasonal pattern of low FMR during the dry season is correlated with measures of food availability, as is the case for the other lizard species that have been measured in wet-dry tropics (Christian and Green 1994; Christian et al. 1996b, 1996c, 1996d, 1998, 1999a, 1999b). The calculated indices (AR, %AR, AS, and SusMS) are generally high compared to other species, suggesting that a large proportion of the daily energy budget of this species is expended on activity (however, see an alternative analysis below). The percentages of total energy expended on activity, %AR (85.2 for wet season and 77.4 for dry season), are the highest reported values, although *Sceloporus variabilis* (70%; Benabib and Congdon 1992), *S. virgatus* (78%; Merker and Nagy 1984) and *Varanus mertensi* (73%; Christian et al. 1996d) have values approaching those of bluetongue lizards. The activity scope, AS, for bluetongue lizards is also the highest reported, with only *Eremias lugubris* (12.0; Nagy et al. 1984) and *S. variabilis* (10.8; Benabib and Congdon 1992) having similar values. The sustainable metabolic scope values, SusMS, for bluetongue lizards are higher than those of any other species reported to date (summarised in Christian et al. 1996c). These values are high for several reasons. First, the TRM of bluetongue lizards is unusually low because the SMR is at the low end of the range for a lizard of its size, and the daytime

RMR is no higher than that at night (this value is typically 1.4× SMR). The daytime T_b of bluetongue lizards are several degrees cooler than those of most diurnal lizards, which also reduces TRM. These relatively low T_b are due to thermoregulatory behaviour in the wet season, and due to the relatively cool temperatures inside the burrows in the dry season compared to above-ground refugia used by other species in the same region (Christian and Bedford 1995; Christian et al. 1996c, 1999b). The dry season burrows occupied by bluetongue lizards are more than 3°C cooler than the burrows used by *Varanus gouldii* at the same time of year (Christian and Weavers 1996). It is not known whether this difference is related to the characteristics of the black cracking soil of the Adelaide River floodplain or the insulating properties of thick matted grass on the floodplain.

The very high %AR values reported here for bluetongues are apparently related to high costs of digestion or activity, not reproduction. The %AR is high in both seasons, yet mating in this species does not occur until September–October. The additional metabolic cost of viviparity is not apparent until the latter stages of pregnancy in female reptiles (Beuchat and Vleck 1990; DeMarco and Guillette 1992). Thus, energetic costs related to reproduction are unlikely to be contributing to the high %AR values.

The effects of digestion can be examined separately from the effects of activity when activity is extremely low. For example, one female bluetongue lizard moved only 62 m in a straight line over 69 days. If we ignore this relatively small cost of activity, we can calculate its TRM as being equivalent to the FMR (27.1 kJ $kg^{-1}day^{-1}$). This equals a metabolic rate of 0.056 ml O_2 g^{-1} h^{-1}, which is 2.4 times the SMR at a mean T_b of 25.5. This indicates that the "resting" metabolism of this lizard was, in fact, over twice that predicted from laboratory measurements. We suggest this may be a result of the metabolic cost of digestion. Niewiarowski and Waldshmidt (1993) have previously noted that the cost of maintenance calculated from SMR underestimates the average cost of maintenance in recently fed lizards over a 24 h period by 2–4 times. If we assume these bluetongue lizards fed daily, and we incorporate the costs of digestion (as determined from our feeding experiments) into the daily resting metabolism, then the indices associated purely with activity are smaller (Table 2). Our observations of bluetongue lizards indicate that the assumption of regular (daily) feeding is realistic, at least during the wet season. The wet season indices labelled "digesting" in Table 2 are consistent with the indices of activity for other lizards in the wet-dry tropics (Christian et al. 1996b, 1996c, 1998, 1999b), and we suggest that they are more realistic than the indices that do not incorporate the metabolic costs of digestion.

Water flux follows the pattern of FMR, and is substantially lower in dry season (Table 3). Compared to the allometric equations for reptiles, the water flux of bluetongue lizards in the dry season was lower than expected, but it was within the expected range during the
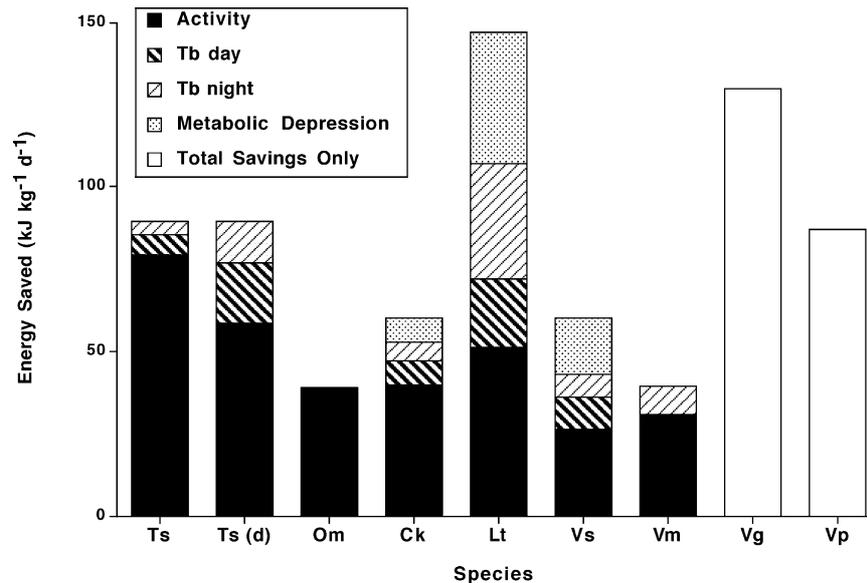
Fig. 2 Components of the energy saved, defined as the difference between the FMRs of the wet and dry seasons, by lizards in the wet-dry tropics of Australia. Species are identified as: *Ck Chlamydosaurus kingii* (Christian and Green 1994), *Lt Lophognathus temporalis* (Christian et al. 1999b), *Vs Varanus scalaris* (Christian et al. 1996c), *Vm V. mertensi* (Christian et al. 1996d), *Vg V. gouldii* (Christian et al. 1995), *Vp V. panoptes* (Christian et al. 1995), *Om Oedura marmorata* (Christian et al. 1998), *Ts Tiliqua scincoides* (this study); and *Ts*(d) *Tiliqua scincoides* (this study) assuming that the lizards are digesting. The components of energy include effects of daytime T_b, night T_b, seasonal metabolic depression, and activity (broadly defined). Note that data are not available to subdivide the energy savings for *Varanus gouldii* and *V. panoptes*, but the data are included for comparisons of total energy savings

wet season. Similarly, when compared to other reptiles in the wet-dry tropics of Australia, the water flux of bluetongue lizards was in the range of other species (but towards the low end) during the wet season, but the water flux of bluetongue lizards in the dry season was lower than all species measured except the frillneck lizard (Christian and Green 1994; Christian et al. 1995, 1996c, 1996d, 1998, 1999a). Thus, the reduced activity during the dry season effectively inhibits water flux compared to reptiles in the same environment and in arid environments generally. The WEI indicates that the water flux per unit energy was substantially higher in the wet season compared to the dry.

To date, all the studies of reptiles from the wet-dry tropics of Australia indicate that FMRs are lower in the dry season, but the mechanisms used to conserve energy in the dry season vary among species. Figure 2 compares energy savings in lizard species studied in the wet-dry tropics of Australia. The energy saved in the dry season (as compared to the wet season) is subdivided into components due to metabolic depression, decreased T_b at night, decreased T_b in the day, and activity. Lower T_b at night are largely passive effects of seasonal differences in environmental temperatures, although there is the potential for behavioural effects through sleeping site selection (Christian et al. 1984). Lower daytime T_b can result from seasonal differences in active thermoregulation in a thermally complex environment (Christian et al. 1983, 1996c, 1999b; Christian and Bedford 1995), but bluetongue lizards have lower T_b because they are inactive in cool burrows for much of the dry season. Although

available data (Fig. 2) do not allow a complete breakdown of energy saved for *Varanus gouldii* and *V. panoptes*, at least three species (*Chlamydosaurus kingii*, *Lophognathus temporalis*, and *Varanus scalaris*) use a combination of physiological and behavioural mechanisms to conserve energy in the dry season. Bluetongue lizards, however, do not use seasonal metabolic depression to conserve energy (Fig. 1). Nevertheless, they conserve considerable amounts of energy in the dry season using mostly (excluding the small component due to lower night time T_b) behavioural means (lower daytime T_b and reduced activity). Despite not employing metabolic depression, the mass-specific energy savings of bluetongue lizards in the dry season are comparable to all the species shown in Fig. 2 except *L. temporalis*, and *V. gouldii*.

The extent of seasonal FMR reduction during periods of relative inactivity can be calculated as active–inactive / active ×100. The extent of FMR and water flux reduction during inactive seasons is shown in Table 5 for lizards from the temperate zone and from the seasonal tropics. Although the animals in the seasonal tropics experience substantially higher temperatures than over-wintering animals in temperate regions (Christian et al. 1999a), tropical lizards can achieve substantial energy savings by using either behaviour or a combination of behaviour and metabolic depression.

What factors determine which mechanisms are employed to conserve energy in the dry season? The timing of the reproductive season of reptiles in the wet-dry tropics is, in part, determined by whether the species' origins (based on affinities with closely related species)

Table 5 Extent of FMR and water flux depression in the inactive season compared to the active season for lizards from temperate and seasonal tropical zones. Percent depression is calculated as: active season value − inactive season value/active season value ×100. Note that for *Aporosaura anchietae* active males were compared to inactive females during the summer

Species	% FMR depression	% Water flux depression	Climatic zone	Source
Agamidae				
Chlamydosaurus kingii	72.2	79.6	Tropical	Christian and Green 1994
Lophognathus temporalis	70.3	74.9	Tropical	Christian et al. 1999a
Lacertidae				
Aporosaura anchietae	27.7	88.9	Temperate	Robinson 1990
Gekkonidae				
Oedura marmorata	66.8	66.7	Temperate	Christian et al. 1998
O. marmorata	26.3	54.8	Tropical	Christian et al. 1998
Iguanidae				
Sauromalus obesus	78.3	96.2	Temperate	Nagy 1972; Nagy and Schoemaker 1975
Phrynosomatidae				
Sceloporus jarrovi	86.3	87.3	Temperate	Congdon et al. 1979
Scincidae				
Tiliqua scincoides	70.5	82.7	Tropical	Present study
Varanidae				
Varanus gouldii	66.3	61.5	Tropical	Christian et al. 1995
V. mertensi	32.8	0	Tropical	Christian et al. 1996a
V. panoptes	60.8	49.3	Tropical	Christian et al. 1995
V. rosenbergi	79.6	63.5	Temperate	Green et al. 1991
V. scalaris	47.2	72.5	Tropical	Christian et al. 1996a
V. varius	-	77.9	Temperate	Weavers 1983

are the tropical north or the temperate arid zone to the south (James and Shine 1985). Historical and phylogenetic factors may also determine whether or not metabolic depression has evolved, or, similarly, the reproductive season itself may restrict the feasibility of metabolic depression. Pythons from this region breed in the dry season and do not show metabolic depression (Bedford and Christian 1998). There may be other unknown factors that limit the physiological plasticity of some species. Habitat constraints may also be important. It is interesting that bluetongue lizards are able to maintain day-time T_b several degrees cooler than species that are inactive in less sheltered sites (Christian et al. 1996b, 1999b). Thus, species that, for whatever reasons, spend the dry season above ground may be forced to employ metabolic depression to conserve energy in the warmer microhabitats they inhabit. Determining which mechanisms are employed to conserve energy in the dry season is a challenge for our understanding of the ways animals interact with their environments in both evolutionary and physiological time.

References

Anderson RA, Karasov WH (1981) Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49:67–72

Andrews RM, Pough FH (1985) Metabolism of squamate reptiles: allometric and ecological relationships. Physiol Zool 58:214–231

Bartholomew GA, Tucker VA, Lee AK (1965) Oxygen consumption, thermal conductance, and heart rate in the Australian skink *Tiliqua scincoides*. Copeia 1965:169–173

Beaupre ST, Dunham AE, Overall KL (1993) Metabolism of a desert lizard: the effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption of *Sceloporus merriami*. Physiol Zool 66:128–147

Bedford GS, Christian KA (1998) Standard metabolic rate and preferred body temperatures in some Australian pythons. Aust J Zool 46:317–328

Benabib M, Congdon JD (1992) Metabolic and water-flux rates of free-ranging tropical lizards *Sceloporus variabilis*. Physiol Zool 65:788–802

Beuchat CA, Vleck D (1990) Metabolic consequences of viviparity in a lizard, *Sceloporus jarrovi*. Physiol Zool 63:555–570

Christian KA, Bedford GS (1995) Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. Ecology 76:124–132

Christian KA, Green B (1994) Seasonal energetics and water turnover of the frillneck lizard, *Chlamydosaurus kingii*, in the wet-dry tropics of Australia. Herpetologica 50:274–281

Christian KA, Weavers B (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol Monogr 66:139–157

Christian KA, Tracy CR, Porter WP (1983) Seasonal shifts in body temperature and use of microhabitats by the Galapagos land iguana. Ecology 64:463–212

Christian KA, Tracy CR, Porter WP (1984) The physiological and ecological consequences of sleeping site selection by the Galapagos land iguana *Conolophus pallidus*. Ecology 65:752–758

Christian KA, Corbett LK, Green B, Weavers BW (1995) Seasonal activity and energetics of two species of varanid lizards in tropical Australia. Oecologia 103:349–357

Christian KA, Green B, Kennett R (1996a) Some physiological consequences of aestivation by freshwater crocodiles, *Crocodylus johnstoni*. J Herpetol 30:1–9

Christian KA, Griffiths AD, Bedford GS (1996b) Physiological ecology of frillneck lizards in a seasonal tropical environment. Oecologia 106:49–56

Christian K, Green B, Bedford G, Newgrain K (1996c) Seasonal metabolism of a small, arboreal monitor lizard, *Varanus scalaris*, in tropical Australia. J Zool 240:383–396

Christian KA, Weavers B, Green B, Bedford G (1996d) Energetics and water flux in a semi-aquatic lizard *Varanus mertensi*. Copeia 1996:354–362

Christian KA, Bedford GS, Green B, Schultz T, Newgrain K (1998) Energetics and water flux of the marbled velvet gecko (*Oedura marmorata*) in tropical and temperate habitats. Oecologia 116:336–342

Christian KA, Bedford GS, Schultz TJ (1999a) Energetic consequences of metabolic depression in tropical and temperate-zone lizards. Aust J Zool 47:133–141

Christian KA, Bedford GS, Green B, Griffiths A, Newgrain K, Schultz T (1999b) Physiological ecology of a tropical dragon, *Lophognathus temporalis*. Aust J Ecol 24:171–181

Churchill SK (1994) Diet, prey selection and foraging behaviour of the orange horseshoe-bat, *Rhinonycteris aurantius*. Wildl Res 21:115—130

Cogger HG (2000) Reptiles and amphibians of Australia, 6th edn. Reed New Holland, Sydney

Congdon JD, Tinkle DW (1982) Energy expenditure in free-ranging sagebrush lizards (*Sceloporus graciosus*). Can J Zool 60:1412–1416

Congdon JD, Ballinger RE, Nagy KA (1979) Energetics, temperature, and water relations in winter aggregated *Sceloporus jarrovi* (Sauria: Iguanidae). Ecology 60:30–35

DeMarco V, Guillette LJ (1992) Physiological cost of pregnancy in a viviparous lizard (*Sceloporus jarrovi*). J Exp Zool 262:383–390

Green B, Dryden G, Dryden K (1991) Field energetics of a large carnivorous lizard, *Varanus rosenbergi*. Oecologia 88:547–551

Greer AE (1989) The biology and evolution of Australian lizards. Surrey Beatty, Chipping Norton, NSW

Griffiths AD, Christian KA (1996) Diet and habitat use of frillneck lizards in a seasonal tropical environment. Oecologia 106:39–48

Heatwole HF, Taylor J (1987) Ecology of reptiles. Surrey Beatty, Chipping Norton, NSW

James C, Shine R (1985) The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. Oecologia 67:464–474

John-Alder HB, Garland T, Bennett AF (1986) Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). Physiol Zool 59:523–531

Kennett R, Christian K (1994) Metabolic depression in aestivating long-neck turtles, *Chelodina rugosa*. Physiol Zool 67:1087–1102

Koenig J, Shine R, Shea G (2001). The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia. Wildl Res 28:215–227.

Lifson N, McClintock R (1966) Theory of the use of turnover rates of body water for measuring energy and material balance. J Theor Biol 12:46–74

Merker GP, Nagy KA (1984) Energy utilization by free-ranging *Sceloporus virgatus* lizards. Ecology 65:575–581

Nagy KA (1972) Water and electrolyte budgets of a free-living desert lizard, *Sauromalus obesus*. J Comp Physiol 79:39–62

Nagy KA (1982a) Energy requirements of free-living iguanid lizards. In: Burghardt GM, Rand AS (eds) Iguanas of the world: their behavior, ecology, and conservation. Noyes, Park Ridge, N.J., pp 47–59

Nagy KA (1982b) Field studies of water relations. In: Gans C, Pough FH (eds) Biology of the reptilia, vol 12. Academic Press, London, pp 483–501

Nagy KA, Peterson CC (1988) Scaling of water flux rate in animals. Univ Calif Publ Zool 120:1–172

Nagy KA, Shoemaker VH (1975) Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. Physiol Zool 48:252–262

Nagy KA, Huey RB, Bennett AF (1984) Field energetics and foraging mode of Kalahari Lacertid lizards. Ecology 65:588–596

Niewiarowski PH, Waldschmidt SR (1992) Variation in metabolic rates of a lizard: use of SMR in ecological contexts. Funct Ecol 6:15–22

Peterson CC, Nagy KA, Diamond J (1990) Sustained metabolic scope. Proc Natl Acad Sci USA 87:2324–2328

Pough FH, Andrews RM (1984) Individual and sibling-group variation in metabolism of lizards: the aerobic capacity model for the origin of endothermy. Comp Biochem Physiol 79A:415–419

Ridpath MG (1985) Ecology in the wet-dry tropics: how different? Proc Ecol Soc Aust 13:3–20

Robinson MD (1990) Summer field energetics of the Namib desert dune lizard *Aporosaura anchietae* (Lacertidae), and its relation to reproduction. J Arid Environ 18:207–215

Taylor JA, Tulloch D (1985) Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870–1983 inclusive. Aust J Ecol 10:281–295

Torr G (1999) True blue. Aust Geogr 55:52–67

Van Marken Lichtenbelt WD, Wesselingh RA, Vogel JT, Albers KBM (1993) Energy budgets in free-living green iguanas in a seasonal environment. Ecology 74:1157–1172

Weavers BW (1983) Thermal biology of *Varanus varius* (Shaw), the lace monitor. Ph. D. thesis, Australian National University, Canberra

Withers PC (1977) Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. J Appl Physiol 42:120–123

Withers PC (1981) Physiological correlates of limblessness and fossoriality in scincid lizards. Copeia 1981:197–204