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Goanna Metabolism: Different to Other Lizards, and if so, What are the Ecological Consequences?

GRAHAM THOMPSON

Abstract

Standard, maximal and field metabolic rates of different species of *Varanus* have been determined and are discussed in terms of different parameters such as ecology, behaviour, diet, home ranges, etc. In general, actively foraging goannas exceed all three different metabolic rates of similar-sized lizards with exception of two small species which are rather ambush predators. The higher field metabolic rate of large goannas seems to be correlated with larger home ranges.

Key words: Varanids, goannas, metabolism, ecology

Introduction

The metabolism of the goannas has often been compared with other lizards (BARTHOLOMEW & TUCKER 1964; BENNETT 1972, 1982; BENNETT & DAWSON 1976; ANDREWS & POUGH 1985; BECK & LOWE 1994; CHRISTIAN & CONLEY 1994). BARTHOLOMEW and TUCKER (1964), in one of the earliest comparative reports, suggest that goannas bridge the gap in metabolic rate that has generally been assumed to exist between reptiles and mammals. Subsequently, BENNETT (1972) reports the standard metabolic rate of *V. gouldii* to be similar to that of a comparably sized lizard, however, its capacity to transport oxygen during activity was higher than for other lizards.

Although ANDREWS and POUGH (1985) reported a statistical variation among families of squamate reptiles, a posteriori Tukey test showed that the family with the highest mean standard metabolic rate (Varanidae) and the family with the lowest mean standard metabolic rate (Boidae) were not statistically different ($P > 0.05$). There were, however, differences in the standard metabolic rate among ecological groups, with day-active predators having a significantly higher metabolic rate than do reclusive predators, and the latter having a significantly higher metabolic rate than do fossorial predators.

More recently CHRISTIAN and CONLEY (1994) report the standard metabolic rate of *Tiliqua rugosa*, a large-bodied, slow moving, omnivorous skink, not to be different to that of *V. rosenbergi*, *V. gouldii*, *V. panoptes* and *V. mertensi* at 35 °C. However, *T. rugosa* had a lower maximal metabolic rate than the four goannas at 35 °C. BECK and LOWE (1994) report the resting metabolism of the relatively large, sedentary, carnivorous *Heloderma horridum* and *H. suspectum* to be significantly lower than that for similar-sized goannas.

Metabolic rate per unit body mass generally declines with increasing body mass (BENNETT & DAWSON 1976). Very often the relationship between metabolism and body mass is not linear, making it difficult to analyse or deal with the relationship quantitatively. To normalise the variance and to obtain a linear relationship, it is often appropriate to logarithmically-transform the data for both variables (i.e., $\log Y = \log a + b \log X$, where a and b are regression coefficients). The value of b therefore provides the ratio of the exponential rate of change in the dependent variable for a given change in the independent variable (most often mass). If we wish to compare the metabolism of two different organisms of different mass, it is most often

accomplished by the general form of a power curve, or the allometric formula (HUXLEY 1932; MCMAHON & BONNER 1983): $y = ax^b$, where a and b are constants. a is the power coefficient and b is the power exponent or the slope of the regression line representing the relationship between the logarithmically-transformed dependent variable and the logarithmically-transformed independent variable. The allometric relationship is descriptive and does not explain the underlying reason(s) for the relationship.

The theoretical and empirical relationship between body mass and metabolic rate have been controversial issues for many years (KLEIBER 1932, 1961; BRODY 1945; von BERTALANFFY 1957; GUNTHER 1975; HEUSNER 1982, 1984; WITHERS 1992). For vertebrates, 0.75 is still the best approximation for scaling inter-specific metabolism to body mass. Reptiles, however, seem to be different with standard metabolic rate scaling with body mass$^{0.80}$ (ANDREWS & POUGH 1985).

There are three basic metabolic measures used to compare the metabolism of reptiles. Standard metabolic rate, which is measured at a constant temperature, during their post-absorptive and quiescent phases (normally at night for goannas), untethered, in a dark 'indifferent' environment and after the lizard has been held in captivity for several days. These data are generally highly repeatable. Maximal metabolic rate is measured by collecting gas samples from lizards' expired air while running on a motorised treadmill at a given body temperature. Problems associated with having lizards run at their aerobic maximum without recruiting anaerobic resources and at a constant rate for a sustained period invariably results in a higher level of experimental error than for measuring standard metabolic rate. Field metabolic rate is measured by the injection of doubly labelled water and measuring the loss of isotopic hydrogen and oxygen molecules (NAGY 1983). The accuracy of this technique has been addressed (see BRADSHAW et al. 1987; NAGY 1989), however, as the researchers have no control over the behaviour, movement, body temperature, feeding and other variables that influence lizard metabolism, there is often considerable intra-specific variability. In addition, there is appreciable variability between seasons in reported field metabolic rates for goannas (CHRISTIAN et al. 1995; CHRISTIAN et al. 1996a,b) requiring considerable caution to be used in the comparisons.

This paper endeavours to succinctly compare the metabolism of goannas with other lizards and to describe the ecological consequences of these differences.

Results

Standard metabolic rate

The standard metabolic rate of *Varanus* scales inter-specifically with body mass$^{0.92}$ (THOMPSON & WITHERS 1992, 1994, 1997a; THOMPSON et al. 1995). This differs significantly from the inter-specific scaling for squamates that have a mass exponent of approximately 0.80 (ANDREWS & POUGH 1985). An inspection of Figure 1 indicates that the standard metabolic rate for small goannas is about the same as that for other lizards of a similar size and body temperature (T_b). However, as the goannas get larger, their mass-specific standard metabolic rate increases compared with other squamates.

ANDREWS and POUGH (1985) report the mean intra-specific mass exponent for squamates to be 0.67. Goannas have a significantly higher intra-specific common pooled mass exponent for standard metabolic rate, at about 0.97 (THOMPSON & WITHERS 1997a).
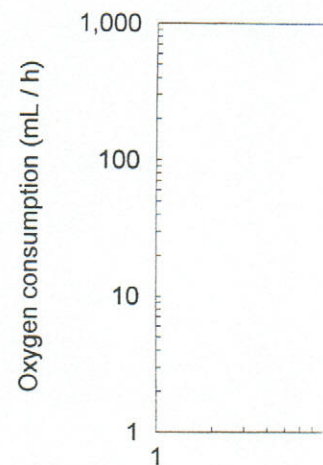

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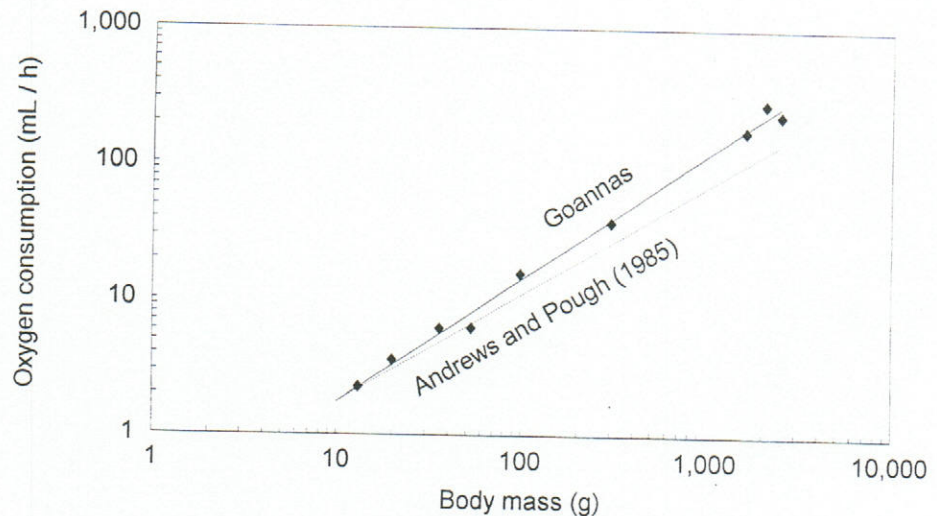r intra-specific common
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Fig. 1. Inter-specific comparison of standard metabolic rate for goannas (Thompson & Withers 1997a) and the dotted regression line for other squamates (Andrews and Pough, 1995). Diamonds represent means for nine species of goannas.

When Thompson and Withers (1997a) grouped nine species of *Varanus* into widely-foraging (*V. caudolineatus*, *V. gilleni*, *V. tristis*, *V. eremius*, *V. gouldii*, *V. rosenbergi*, *V. panoptes* and *V. giganteus*) and relatively sedentary (*V. acanthurus* and *V. brevicauda*), the relatively sedentary group had a significantly lower standard metabolic rate.

Maximal metabolic rate

The maximal metabolic rate for *Varanus* scales inter-specifically with body mass$^{0.72}$ (Thompson & Withers 1997a). Data for maximal metabolic rate for other squamates are insufficient to provide an overall estimation of the inter-specific mass exponent, however, for the five (6 data sets) species included in Figure 2 the inter-specific mass exponent is 1.19. The maximal metabolic rate for goannas is significantly higher than that for these lizards (Fig. 2, Thompson & Withers 1997a).

Thompson and Withers (1997a) report three arboreal species (*V. caudolineatus*, *V. gilleni* and *V. tristis*, 17.4mass$^{0.61}$ at 35 °C) to have a significantly higher maximal metabolic rate than terrestrial varanid species (4.8mass$^{0.81}$ at 35 °C, Fig. 3).

Field metabolic rate

Field metabolic rate is influenced by a range of factors including behaviour, movement, body temperature and feeding, therefore the variability is likely to be appreciable among species. Data from Green et al. (1986, 1991a, b), Dryden et al. (1990, 1992), Christian et al. (1995, 1996a, b) and Thompson et al. (1997) have been used to estimate the field metabolic rate of *Varanus* (Tab. 1). These data have been compared with that reported by Nagy (1982) for a variety of lizard species (Fig. 4). There is a significant difference between the field metabolic rate of *Varanus* and the
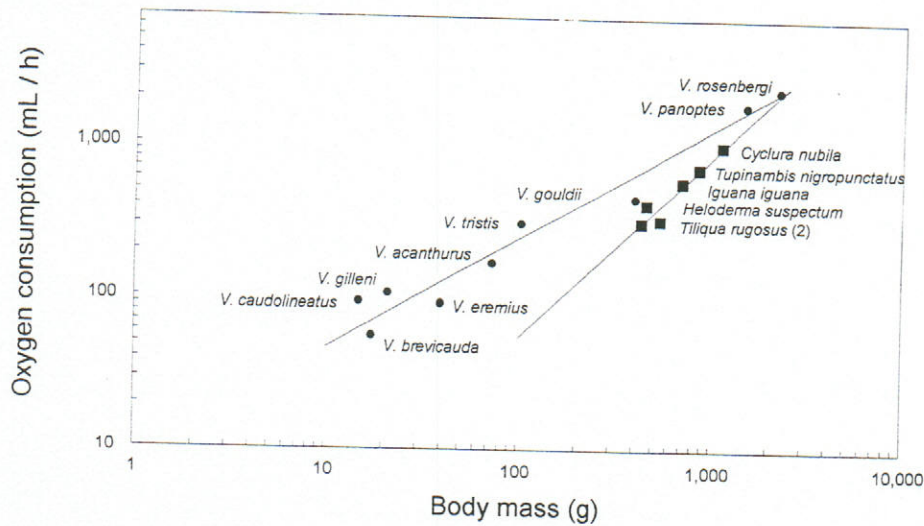
Fig. 2. Inter-specific comparison of maximal metabolic rate for goannas and selected other lizards. Data for goannas from THOMPSON and WITHERS (1997a) and other lizards from GLEESON et al. (1980), BENNETT and JOHN-ALDER (1984), JOHN-ALDER et al. (1983, 1986), CHRISTIAN and CONLEY (1994) for other species.
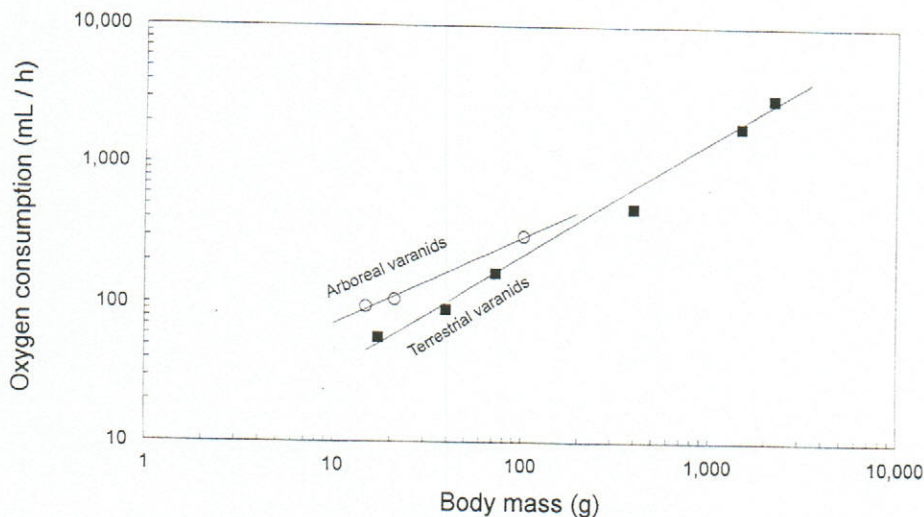

Fig. 3. Inter-specific comparison of maximal metabolic rates for arboreal and terrestrial goannas. Open circles arboreal, filled squares terrestrial goannas (THOMPSON & WITHERS 1997a).

saurians (ANCOVA, $F_{1,35} = 9.52$, $P < 0.01$, body mass as the covariate) with goannas being generally higher. The regression equation to predict field metabolic rate for the 11 species of goannas is $\log_{10}$ mL CO_2 h^{-1} = $-$ 0.51 ($\pm$ se 0.182) + 0.94 ($\pm$ se 0.058) $\log_{10}$ mass, with mass in grams.

Species

V. caudolineatus
V. acanthurus
V. scalaris
V. gouldii
V. rosenbergi
V. mertensi
V. bengalensis
V. panoptes
V. giganteus
V. salvator
V. komodoensis

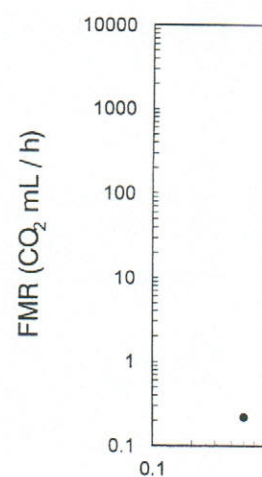Tab. 1. Field metabolic r

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| Species	season	Mass (g)	CO_2 mL g^{-1} h^{-1}	Source
V. caudolineatus	Summer	10.4	0.46	THOMPSON et al. 1997
V. acanthurus	Sp/Su	60	0.10	DRYDEN et al. 1990
V. scalaris	Wet	66.4	0.21	CHRISTIAN et al. 1996a
V. gouldii	Early wet	1106	0.36	CHRISTIAN et al. 1995
V. rosenbergi	Summer	1193	0.18	GREEN et al. 1991a
V. mertensi	Wet	1208	0.20	CHRISTIAN et al. 1996b
V. bengalensis	Dry	2560	0.25	DRYDEN et al. 1992
V. panoptes	Early wet	3404	0.24	CHRISTIAN et al. 1995
V. giganteus	Summer	5570	0.17	GREEN et al. 1986
V. salvator	Dry	7600	0.19	DRYDEN et al. 1992
V. komodoensis	Spring	16620	0.13	GREEN et al. 1991b

Tab. 1. Field metabolic rates for goannas
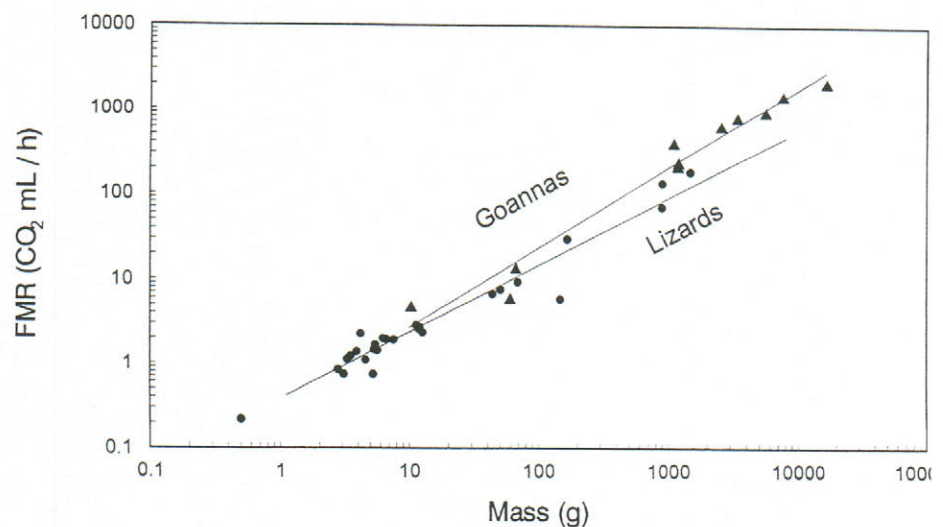
Fig. 4. Inter-specific comparison of field metabolic rates for goannas (filled triangles, data from Tab. 1) and a selection of other lizards (filled circles, NAGY 1982).

Home range

Is the higher field metabolic rate of goannas associated with larger home ranges or activity areas? Activity area data from GREEN and KING (1978), WEAVERS (1993), KING et al. (1989), PHILLIPS (1995, pers. comm.) THOMPSON (1994) and THOMPSON, DE BOER, and PIANKA (1999) are compared with the regression line reported by CHRISTIAN and WALDSCHMIDT (1984) for a variety of widely-foraging lizard species (Fig. 5). It is evident from an inspection of Figure 5 that the activity areas of goannas are approximately an order of magnitude larger than those for similar sized lizards.
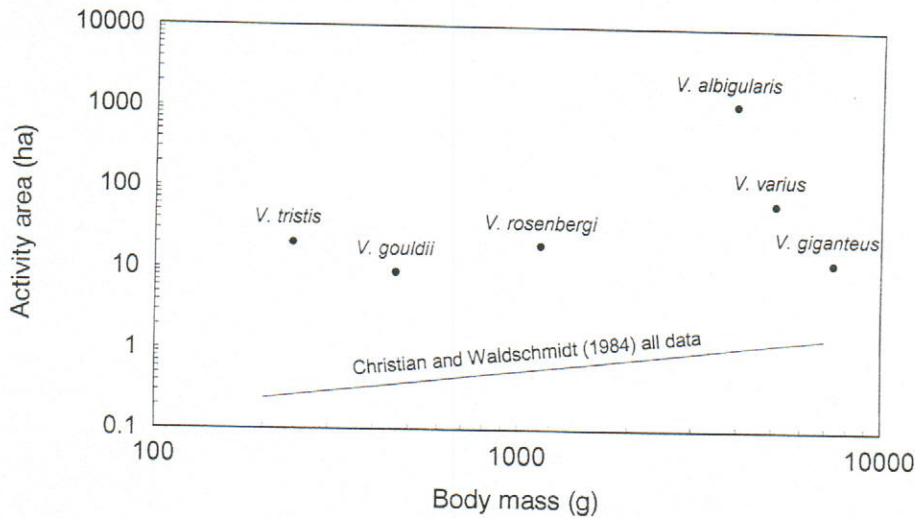
Fig. 5. Comparison of the activity areas of goannas (GREEN & KING 1978; WEAVERS 1993; KING et al. 1989; PHILLIPS 1995, pers. comm; THOMPSON, DE BOER & PIANKA, unpub.) with the regression line for other widely-foraging lizards (CHRISTIAN & WALDSCHMIDT 1984). Fig. adapted from THOMPSON et al. (1999).

Discussion

Evidence suggests that the ecology of a lizard is linked with its metabolism (ANDREWS & POUGH 1985; BECK & LOWE 1994; GARLAND and LOSOS 1994). An intra-specific mass exponent for standard metabolic rate for goannas near unity means that there is no energetic size advantage as an individual grows. The calorific intake to sustain basal levels of body functioning is directly proportional to body mass. This is in contrast to many other squamates where the intra-specific metabolic scaling (b) = 0.67, and the mass-specific calorific needs for larger individuals are comparatively lower than those of the smaller individuals. As a consequence it is possible foraging areas and the quantity of prey digested are likely to be larger for adult goannas than for similar-sized species where the intra-specific mass-exponent is approximately 0.67. This increased energy requirement could then influence the diet, foraging strategy, foraging time and preferred body temperature of goannas. Most large lizards, other than *Varanus*, are herbivorous (POUGH 1973; ZIMMERMAN & TRACY 1989), which may suggest a relationship between diet and metabolic scaling. Most goannas are carnivorous (SHINE 1986; LOSOS & GREENE 1988; WEAVERS 1989; JAMES et al. 1992; PIANKA 1994), with the main exception being *V. olivaceus*, which is omnivorous, feeding primarily on molluscs, crustaceans, and fruits but not leaves, buds or flowers (AUFFENBERG 1988). Although a number of herbivorous lizards are insectivorous as juveniles and sub-adults they change to a herbivorous diet as they increase their body mass (POUGH 1973). Large goannas might be required to have a high energy carnivorous diet in preference to a herbivorous diet to obtain sufficient energy (GOLLEY 1961) to sustain the higher standard metabolic rate.

Reptiles that are primarily carnivorous use a range of foraging strategies along a continuum from sit-and-wait to widely-foraging (PIANKA 1986). Goannas have been

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generally described as widely-foraging (Losos & Greene 1988; James et al. 1992). Huey and Pianka (1981) suggest that daily energy requirements of widely-foraging lizards are about 1.3-1.5 times greater than those of sit-and-wait predators; food gains are about 1.3-2.1 times higher for the widely-foraging lizards. However, Anderson and Karasov (1981) report the field metabolic rate to be approximately 1.5 times the resting levels for *Callisaurus draconoides*, which spends less than 2 % of its 10 h activity period in movement compared with 3.3 times for *Cnemidophorus tigris*, which spends 91 % of its 5 h activity period moving. Though the widely-foraging *C. tigris* had the higher rate of energy expenditure, its foraging efficiency (metabolisable energy intake/energy expended) was higher than that of the sit-and-wait *C. draconoides*. There are no data on the foraging efficiencies of widely-foraging vs sit-and-wait large lizards. Larger goannas with comparatively higher metabolic requirements may be forced to adopt the widely-foraging mode (Losos & Greene 1988; James et al. 1992) to sustain their resting level of metabolism because either the sit-and-wait strategy or a herbivorous diet is inadequate to provide their energy requirements. Alternatively, the relatively high metabolism of large goannas may have developed in response to their widely-foraging strategy and carnivorous diet (Pough 1973). When the phylogeny of goannas is better understood, it may be possible to speculate on the diet and foraging behaviour of the ancestral form, a precursor to answering the possible causal evolutionary relationship between diet and metabolism for this family of lizards.

The comparatively low standard metabolic rate of the two relatively sedentary goannas (*V. brevicauda* and *V. acanthurus*) compared with the more widely-foraging *Varanus* species is consistent with the findings of Beck and Lowe (1994) who report the relatively large, sedentary carnivorous *Heloderma horridum* and *H. suspectum* to have a low standard metabolic rate. Dryden et al. (1990) suggests the relatively inactive and secretive *V. acanthurus* is possibly a sit-and-wait predator, a foraging mode associated with reduced energy expenditure (Anderson & Karasov 1981). The short-limbed morphology (Thompson & Withers 1997b), diet (Pianka 1994) and small activity area (James 1996) of *V. brevicauda* when taken together suggest this varanid is possibly also a sit-and-wait predator which would correspond with its low metabolism.

The generally higher maximal metabolic rate for goannas compared with other lizards provides this family of saurians with the aerobic capacity to forage over a wide area. This higher maximal aerobic capacity maybe due to the relative size, structure and gas perfusion efficiency in goanna lungs compared with other lizards (Perry 1983, 1989). This is possibly reflected in the significantly larger activity areas or home ranges of most goannas compared with similar-sized lizards (Fig. 5).

Maximal metabolic rate for three arboreal goannas (*V. caudolineatus*, *V. gilleni* and *V. tristis*) is higher than for the other terrestrial species, although the maximal metabolic rate for the arboreal *V. scalaris* is lower than that for terrestrial species (Christian et al. 1996a). This suggests that the maximal metabolic rate for arboreal goannas might be generally higher than for terrestrial species with the difference for *V. scalaris* being a reflection of research protocol differences. This hypothesis would be relatively easy to test as *V. mitchelli*, *V. varius*, *V. glauerti*, *V. keithhornei* and *V. prasinus* are all Australian arboreal goannas and accordingly should have higher maximal metabolic rates than similar-sized, widely-foraging, terrestrial goannas. *V. pilbarensis* and *V. glebopalma* are rock-dwelling goannas that scamper over large boulders, an activity that requires considerable vertical movement. Given the habitat

of these goannas, they may also have maximal metabolic rates similar to those of the arboreal species; again this hypothesis is easy to examine.

The mass exponent difference between standard ($\approx$0.92) and maximal ($\approx$0.72) metabolic rate results in high aerobic factorial scopes (maximal metabolic rate / standard metabolic rate) for the smaller species. The factorial scope for *V. caudolineatus* of 35 reported by THOMPSON and WITHERS (1997a) supports the earlier finding of BICKLER and ANDERSON (1986) for the high factorial scope ($\approx$28) for the morphologically and ecologically similar *V. gilleni*. Even *V. brevicauda* has an aerobic factorial scope ($\approx$21, THOMPSON & WITHERS 1997a) that is higher than that for most other squamates ($\approx$10, BENNETT 1982). It is, however, not as high as the two small arboreal species *V. caudolineatus* and *V. gilleni*. This suggests that both body mass and ecology / performance traits are linked to aerobic factorial scope with small goannas generally having a higher factorial scope, and the small arboreal species having a higher factorial scope than the terrestrial species.

Maximal metabolic rates for goannas seem to be reflected in the habitat choice and foraging mode. If goanna ecology is the primary determinant of their mass-specific maximal metabolic rate then it could be hypothesised that the mass-specific maximal metabolic rate for *V. baritji* would be similar to *V. acanthurus* as they are ecologically and morphologically similar (KING & HORNER 1987). There is little or no information on the natural history or ecology of a number of small goannas such as *V. storri*, *V. kingorum*, *V. prasinus* and *V. primordius*. However, the relatively short hind-limbs and the thick, short-tail of *V. brevicauda*, *V. primordius* and *V. storri* suggest that they are neither arboreal, nor perhaps widely-foraging predators and are possibly sit-and-wait predators or forage over a relatively small activity area. If there is a close association between activity area size, foraging mode and perhaps morphology with metabolism, these goannas would have comparatively low maximal metabolic rates and perhaps a low standard metabolic rate.

It is difficult to speculate on the maximal metabolic rate for *V. mitchelli* as so little is known about its ecology, other than it is both semi-aquatic (around streams) and arboreal. CHRISTIAN and CONLEY (1994) report the maximal metabolic rate for *V. mertensi* to be lower than that for other similar-sized goannas; however, without more detailed data on its ecology it is difficult to draw a link between its metabolism and activity patterns but its low standard and maximal metabolic rates (CHRISTIAN & CONLEY 1994; THOMPSON & WITHERS 1998) would suggest it is relatively sedentary.

The mass exponents for standard and field metabolic rates for saurians are about 0.80 (ANDREWS & POUGH 1985; NAGY 1982). The mass exponents for standard and field metabolic rates for *Varanus* are about 0.92-0.94 (THOMPSON & WITHERS 1997a). The mass exponents for maximal metabolic rates for goannas and other saurians differ significantly from the mass exponents for standard and field metabolic rates for goannas. Standard or maintenance levels of metabolism are an obvious component of both maximal and the field metabolic rate. The 'activity' component of field metabolic rate is affected by factors such as behaviour, movement, body temperature, feeding and reproductive status. The link between standard and maximal metabolic rates is not clear. A positive correlation has been reported between standard and maximal metabolic rates for some squamates and anurans (BENNETT & RUBEN 1979; BENNETT 1982; TAIGEN 1983, LOUMBOURDIS & HAILEY 1985). However, other studies of lizards (POUGH & ANDREWS 1984) and salamanders (FEDER 1987) suggest no necessary relationship between the metabolic rate of rest and activity. Data presented here suggests that the and field metabolic r

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rimordius and *V. storri*
raging predators and are
iall activity area. If there
ing mode and perhaps
nparatively low maximal

or *V. mitchelli* as so little
tic (around streams) and
al metabolic rate for *V.*
: however, without more
veen its metabolism and
olic rates (Christian &
t is relatively sedentary.
es for saurians are about
oonents for standard and
pson & Withers 1997a).
and other saurians differ
ield metabolic rates for
in obvious component of
y* component of field
ment, body temperature,
and maximal metabolic
d between standard and
Bennett & Ruben 1979;
However, other studies
Eder 1987) suggest no
activity. Data presented

here suggests that there may be a stronger link between mass exponents for standard and field metabolic rates than standard and maximal metabolic rates.

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An in situ Con
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Abstract

Philippine rainforests with
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Key words: Gray's M

Introduction

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