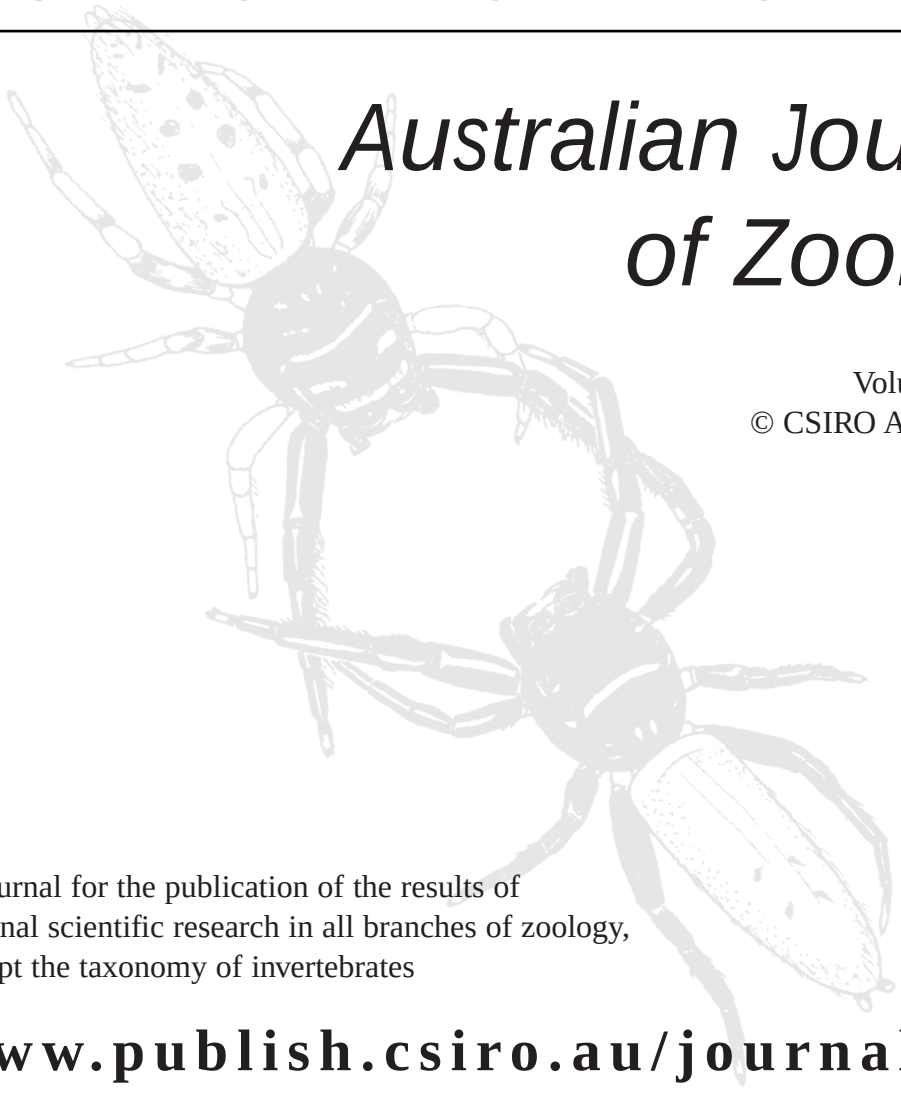
CSIRO PUBLISHING

Australian Journal of Zoology

Volume 46, 1998



A journal for the publication of the results of original scientific research in all branches of zoology, except the taxonomy of invertebrates

www.publish.csiro.au/journals/ajz

All enquiries and manuscripts should be directed to
Australian Journal of Zoology
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7622
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: david.morton@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

 Australian Journal of Zoology, 1998, **46**, 317–328

Standard metabolic rate and preferred body temperatures in some Australian pythons

Gavin S. Bedford and Keith A. Christian

Faculty of Science, Northern Territory University, Darwin, NT 0909, Australia.

Abstract

Pythons have standard metabolic rates and preferred body temperatures that are lower than those of most other reptiles. This study investigated metabolic rates and preferred body temperatures of seven taxa of Australian pythons. We found that Australian pythons have particularly low metabolic rates when compared with other boid snakes, and that the metabolic rates of the pythons did not change either seasonally or on a daily cycle. Preferred body temperatures do vary seasonally in some species but not in others. Across all species and seasons, the preferred body temperature range was only 4.9°C. The thermal sensitivity (Q_{10}) of oxygen consumption by pythons conformed to the established range of between 2 and 3. Allometric equations for the pooled python data at each of the experimental temperatures gave an equation exponent of 0.72–0.76, which is similar to previously reported values. By having low preferred body temperatures and low metabolic rates, pythons appear to be able to conserve energy while still maintaining a vigilant 'sit and wait' predatory existence. These physiological attributes would allow pythons to maximise the time they can spend 'sitting and waiting' in the pursuit of prey.

Introduction

Oxygen consumption during the inactive period of a day (standard metabolic rate) has been used extensively as a tool to examine energy use of reptiles (Benedict 1932; Bennett and Dawson 1976; Chappell and Ellis 1987; Waldschmidt *et al.* 1987). Standard metabolic rate (SMR) in reptiles is directly affected by body mass (M) and body temperature (Tb) (Benedict 1932; Dmi'el 1972; Bennett and Dawson 1976; Andrews and Pough 1985; Waldschmidt *et al.* 1987; Chappell and Ellis 1987). The metabolic rate in reptiles may vary according to the season (Tsuji 1988; Christian *et al.* 1996*a*), species (Bennett and Dawson 1976; Secor and Nagy 1994), reproductive condition (Bennett and Dawson 1976), ecdysis state (Taylor and Davies 1981), thermal acclimation, circadian rhythms, time since feeding, age, sex and social state (references in Bennett and Dawson 1976; Waldschmidt *et al.* 1987; Secor and Diamond 1995). SMR may also vary with geographic location and foraging mode (Dunham *et al.* 1988; Secor and Nagy 1994; Beaupre 1995*a*, 1995*b*).

Because metabolic rate is positively related to Tb in reptiles, Tb directly affects energy requirements. Preferred body temperature ($T_{b_{pref}}$) has been defined as the temperature a reptile would choose if given the opportunity (Huey 1982). Preferred body temperatures of reptiles may vary among species (Dill 1972; Rosen 1991; Shine 1991), and $T_{b_{pref}}$ varies seasonally (Hirth and King 1969; Scott *et al.* 1982; Slip and Shine 1988*a*; Rosen 1991) in many, but not all reptiles (Christian and Bedford 1995). By changing their seasonal body temperatures through active thermoregulation, reptiles can influence their seasonal energy balance (Christian *et al.* 1996*a*, 1996*b*).

The foraging mode of lizards strongly influences SMR, such that 'actively foraging' species use significantly more energy at rest than 'sit and wait' lizards (Bennett and Gleeson 1979; Huey and Pianka 1981). A similar pattern also exists among some snake species, with 'active' foraging species having higher SMR than 'sit and wait' foragers (Secor and Nagy 1994). The

0004-959X/98/040317

present study examines the relationship between foraging mode and metabolism of some Australian snakes. Pythons, excluding *Aspidites melanocephalus*, appear to rely primarily on 'sit and wait' predation, as does the death adder (*Acanthophis praelongus*) (Mirtschin and Davis 1992). The black-headed python (*Aspidites melanocephalus*) appears to be an active foraging species (authors' observation), as is the western brown snake (*Pseudonaja nuchalis*) (Mirtschin and Davis 1992). Some python species use both foraging modes when conditions allow, although species of *Morelia* appear to exclusively use the 'sit and wait' technique (Slip and Shine 1988*b*, 1988*c*; authors' observations).

The principal aims of this paper are to report metabolic rates of several Australian python taxa and to examine these with respect to foraging mode, seasons, time of day, allometric scaling, thermal sensitivity and the metabolic rates of some non-python snakes. We also investigate whether the $T_{b_{pref}}$ varies between seasons and, if so, the degree to which this variation affects the animals overall rate of energy use.

Methods

Study animals

We measured the metabolic rates of seven taxa of Australian pythons, two species of Australian elapid snakes and one acrochordid snake. The python taxa were: children's python (*Antaresia childreni*), Stimson python (*Antaresia stimsoni*), carpet python (*Morelia spilota variegata*), diamond python (*Morelia spilota spilota*), black-headed python (*Aspidites melanocephalus*), water python (*Liasis fuscus*) and olive python (*Liasis olivaceus*). The two elapid species were the northern death adder (*Acanthophis praelongus*) and the western brown snake (*Pseudonaja nuchalis*). Standard metabolic rates were also determined for the file snake (*Acrochordus arafurae*) during the late wet season (March/April).

Five of the python species (*Antaresia childreni*, *Liasis fuscus, L. olivaceus*, *Aspidites melanocephalus*, *Morelia spilota variegata*) were caught by hand in the wet/dry tropics and were housed in an outside animal house in individual cages that were subject to the environmental conditions and photoperiod of Darwin, Northern Territory, Australia. The Stimson pythons (*Antaresia stimsoni*) were caught near Alice Springs in central Australia but were housed in Darwin as long-term captives. Long-term captive-bred diamond pythons (*Morelia s. spilota*) were obtained from the region of Sydney, New South Wales, where the climate is characterised as sub-tropical (Slip and Shine 1988*a*, 1988*b*, 1988*c*). Death adders were caught from the Hayes Creek area 130 km south of Darwin. The western brown snakes (*P. nuchalis*) were caught in the Darwin region. File snakes (*A. arafurae*) were captured during the late wet season while they were migrating upstream at Scott Creek Crossing, Marrakai Station, 70 km east of Darwin.

In order to reduce the effects of some of the variables that can influence metabolism (listed above), we chose animals that were not in the process of ecdysis, had fed regularly (within14 days post-digestive), and were non-reproductive. Animals that appeared not to have adjusted to captivity, as evidenced by continuous striking or continually moving around the cage, were not used in experiments.

Measurement of O_2 consumption

Standard metabolic rates were measured during the normal period of inactivity (day), and resting metabolic rates (RMR) were measured during the normal period of activity (night). Metabolic rates were determined by measurement of oxygen consumption in an open flow system. Animals were weighed to the nearest gram and individually placed in clear perspex chambers with tight-fitting lids (32.5 × 32.5 × 15 cm). An air inlet hose entered near the base of the box and the exit hose through which the air sample was drawn was placed in the opposite corner on the lid of the chamber. The flow of air through each of the animal chambers was maintained by Reciprotor 506R (Denmark) pumps. The volume of air was measured by Top-Trak (Sierra Instruments, USA) flow meters. Three animals were monitored concurrently in a temperature-controlled cabinet (Forma Scientific or Thermoline). Metabolic rates were measured at four experimental temperatures (24, 27, 30 and 33°C). The variation of temperature within the cabinet was ± 0.5°C (Christian *et al.* 1996*a*).

Air was drawn from the room into a 10-mm PVC tube, through the chamber containing the animal, through a drying column (silica gel), and through the air pump, and a sub-sample of air was taken for measurement. Flow meters were calibrated periodically using a soap bubble burette, but the factory calibration was accurate in all cases. Flow was adjusted according to the size of the animal and temperature, ranging from 80 mL min^{-1} for animals less than 100 g at 24°C up to 1.5 L min^{-1} for animals over 4 kg at 33°C.

Air samples from the animal chamber and the room air (at 1.8 m above the floor) were drawn through an R-2 pump (Ametek, Pittsburgh, PA) and into an Applied Electrochemistry S-3A/II oxygen analyser (Ametek, Pittsburgh, PA). Before passing into the oxygen sensor, both samples (animal and control room air) were further dried with a column of desiccant (Drierite, USA), then passed through a column of CO_2 absorbent (Dragersorb 800, Germany), following the methods of Christian *et al.* (1996*a*). Oxygen consumption was converted to units of energy using a factor of 19.35 J mL^{-1} O_2 (Nagy 1983).

Each of the chambers was sampled for 2 h of each 6-h cycle of the system as regulated by a controller-activated solenoid switch (ECC50; SMC Corporation, Japan). Animals were monitored over a 24-h period at each temperature. Initially all oxygen measurements were recorded on a 3-channel ABB SE120 paper chart recorder, but for the last 20 months of the study we recorded all data with a MacLab (8e, ADInstruments: Australia) system connected to a Macintosh LC475 computer. Data were collected at the rate of one record every 25 s. The MacLab system recorded flow rates and oxygen consumption. SMR was measured for each species during both the wet and dry seasons, and RMR was measured in the wet season.

Measurements of $T_{b_{pref}}$

Animals were placed individually in a temperature gradient during the wet and the dry seasons to determine the $T_{b_{pref}}$. The thermal gradient consisted of a large aquarium (1.8 m long × 0.5 m high × 0.4 m wide). At one end of the gradient was either a 150-W clear globe or a 120-W infrared globe (Phillips SE120). The temperature in the gradient ranged from 22.5°C to 65°C. Crumpled paper was placed in the bottom of the thermal gradient so that pythons could hide under cover, but still obtain heat from the substrate. Body temperatures were taken mid-body from each animal over 3–5 d at random intervals during the day using a Raynger 2EM infrared thermometer (Raytek Inc. USA). Spot checks of core body temperatures taken with a Fluke 51 type K thermocouple thermometer (Fluke USA, Inc.) revealed negligible (<0.2°C) differences between cloacal and surface temperatures (as measured with the infrared thermometer).

Thermal sensitivity and allometry

Thermal sensitivity (Q10) is the rate at which oxygen consumption increases as temperature increases by 10°C (Bennett and Dawson 1976). This was determined over a range of 24–33°C using pooled data of all python taxa, because sample sizes were too small for comparisons between individual taxa.

Q_{10} levels were determined using the equation:

$$\text{Log Q10} = (\log \dot{V}_{O_2}(2) - \log \dot{V}_{O_2}(1) \times 10 / (t_2 - t_1))^{-1} \quad (1)$$

(Schmidt-Nielsen 1990) where t_1 and t_2 are the low and high temperatures at which the $\dot{V}_{O_2}(1)$ and $\dot{V}_{O_2}(2)$ were measured.

Allometric relationships were determined at each of the four temperatures using pooled data so that a large range of body masses could be analysed using the equation:

$$\text{SMR (as } \dot{V}_{O_2} \text{ mL h}^{-1}) = aM^b$$

where M = mass (g), a is an empirically determined constant for the metabolic rate of a 1-g animal, and b is the slope of the regression line for oxygen consumption on a double logarithmic scale (Bennett and Dawson 1976).

Energy saving due to a change in $T_{b_{pref}}$

Two species of snakes exhibited a shift in $T_{b_{pref}}$ between seasons, and we calculated the energy saving resulting from the shift. The mean metabolic rates of the snakes were determined at each temperature, then converted to an energy value (kJ d^{-1}).

Statistical analyses

Oxygen consumption data were analysed in 30-min blocks corresponding with the period when oxygen consumption was lowest. Data were tested for normality using a Kolomogorov–Smirnov test for each species at each temperature, and all data were normally distributed and the variances were homogeneous (Bartlett's test). Because oxygen consumption rate varies with body mass, mass was used as a covariate. All analyses of variance and covariance were calculated using log-transformed data (Zar 1984).

The assumption of independence of samples for analysis of variance (Zar 1984) was violated in some parts of this study. Our data on SMR between seasons are based primarily on independent samples (different individuals tested in each season), but for a few species we were unable to obtain a sufficient number of animals. In these cases, we measured oxygen consumption rates on the same snakes in each season. This non-independence does not necessarily introduce any significant problems in statistical analysis as long as either (a) animals are used only once at any temperature, or (b) variances across repeated measures of the same individual are similar in magnitude to the variances between individuals (Leger and Didrichson 1994). Data for SMR among species and between seasons were treated as independent samples because both of the above-mentioned conditions were met, and the data were analysed using analysis of covariance (ANCOVA). Standard and resting metabolic rates were analysed using paired t-tests for all species at all temperatures.

For ease of comparison with previously published results, the data from pythons at 30°C was mass-corrected as an alternative to ANCOVA. The data were corrected for mass using the equation 'mass specific metabolic rate' = log10 (SMR/Body Mass^x), where x is the slope of the allometric equation for metabolism (Garland *et al.* 1987; Potvin *et al.* 1990). A 1-sample t-test was used for this comparison, with the metabolic rate from the literature as an expected value.

Preferred body temperatures among species and between seasons were analysed using a 2-factor analysis of variance (ANOVA). Q_{10} and allometric equations were determined by regression analysis.

Results

SMR comparisons

To determine whether there was a species difference in SMR, the data were compared at each of the four experimental temperatures. There were no differences among species with respect to SMR at any temperature ($P > 0.4$ in all cases). Similarly, SMR values were not different between seasons (ANCOVA, $P > 0.05$).

Daily cycles in metabolic rate at each temperature

The SMR and RMR were compared using paired t-tests, and the results are presented in Table 1. Resting metabolic rate was significantly higher than SMR in *A. arafurae* at 30°C ($P = 0.025$) but not at 27°C ($P > 0.05$). Resting metabolic rate was higher than SMR for *L. fuscus* ($P = 0.026$) at 33°C. The RMR for *M. s. variegata* was higher than SMR at 27°C ($P = 0.046$).

Comparisons of $T_{b_{pref}}$

Table 2 shows seasonal $T_{b_{pref}}$s for each species. Of the nine taxa examined, only three had a significant seasonal difference in $T_{b_{pref}}$. *Aspidites melanocephalus* had a higher $T_{b_{pref}}$ in the wet season than in the dry ($P < 0.0001$), as did *L. fuscus* ($P < 0.0001$) and the elapid *P. nuchalis* ($P < 0.0001$).

Comparisons of $T_{b_{pref}}$ among the taxa revealed that *Acanthophis praelongus* and *L. fuscus* (33.7 and 33.0°C respectively) had significantly higher $T_{b_{pref}}$ in the wet season than the other taxa examined (ANOVA, $P < 0.01$). Among species of snake in the dry season, *A. melanocephalus* had a significantly lower $T_{b_{pref}}$ than six of the eight taxa (ANOVA, $P < 0.01$).

Thermal sensitivity (Q_{10}) of SMR

The mean Q_{10} for pooled data from all species was 2.60 (Table 3). When the data were divided into two separate thermal categories, the Q_{10} changed slightly. At the lower range of 24–30°C, the Q_{10} was 2.39, but at 30–33°C the Q_{10} was 2.94. All three results are within the usual range of thermal sensitivities for reptiles of between 2 and 3 (Bennett and Dawson 1976; Chappell and Ellis 1987).

Table 1. Comparison of standard (SMR) and resting (RMR) metabolic rates of ten taxa of Australian pythons

Mass and oxygen consumption (mL h^{-1}) are presented as means. In general, probability values support the null hypothesis that there is no difference between SMR and RMR. Probability values were not corrected for multiple comparisons

Species	T_b	*n*	mass	SMR $\dot{V}_{O_2}$ mL h^{-1}	s.d.	RMR $\dot{V}_{O_2}$ mL h^{-1}	s.d.	*P*
Acrochordus	27	4	1047.7	28.38	15.54	30.24	5.76	0.87
arafurae	30	4	1047.7	24.66	18.24	44.52	23.76	0.03[A]
Aspidites	24	3	1027.5	37.80	25.80	31.08	19.14	0.22
melanocephalus	27	3	1027.5	55.20	47.40	46.38	36.00	0.32
	30	3	1027.5	74.88	64.44	69.84	55.92	0.43
	33	3	1027.5	103.56	96.36	89.52	84.48	0.24
Acanthophis	24	3	105.5	3.84	1.20	4.32	1.14	0.71
praelongus	27	3	105.5	5.40	3.24	5.22	1.56	0.87
	30	3	105.5	5.04	1.98	4.74	2.16	0.29
	33	3	105.5	7.32	3.30	5.94	2.34	0.21
Antaresia childreni	24	8	331.7	11.52	7.56	16.98	13.08	0.17
	27	6	372.6	18.18	9.36	17.88	8.16	0.78
	30	8	331.7	24.24	12.96	21.90	14.10	0.08
	33	6	372.5	34.02	21.42	32.94	23.28	0.54
Liasis fuscus	24	4	1306.9	18.90	7.20	19.32	7.20	0.79
	27	4	1306.9	23.28	10.14	27.30	10.02	0.40
	30	4	1306.9	29.34	11.16	35.88	14.22	0.11
	33	4	1306.9	52.50	19.86	66.30	19.68	0.03[A]
Liasis olivaceus	24	6	3000.7	44.94	24.36	61.50	30.66	0.05
	27	6	3000.7	77.04	49.02	76.98	42.24	0.99
	30	5	3323.2	111.42	48.42	119.40	61.98	0.39
	33	6	3000.7	103.5	67.74	112.92	76.32	0.14
Antaresia stimsoni	24	3	360.7	21.60	12.90	14.10	6.96	0.58
	27	3	360.7	18.72	4.80	18.36	4.92	0.92
	30	5	349.9	20.22	9.96	17.64	5.58	0.43
	33	4	371.8	29.52	6.84	21.00	3.60	0.11
M. s. spilota	24	4	1516.5	43.08	7.92	36.72	14.46	0.47
	27	4	1516.5	63.24	3.72	52.50	14.10	0.23
	30	4	1516.5	81.30	48.60	55.38	24.18	0.12
	33	4	1516.5	78.18	9.84	83.64	5.58	0.51
Morelia s. variegata	24	8	1938.4	50.52	49.92	53.58	55.14	0.45
	27	7	2170.0	64.08	64.32	67.08	65.64	0.05[A]
	30	7	2173.5	57.84	58.14	57.12	58.14	0.60
	33	5	2828.7	125.52	112.44	148.38	132.12	0.13
Pseudonaja	24	3	214.1	7.92	2.28	13.08	10.02	0.37
nuchalis	27	3	214.1	11.16	4.32	12.42	7.74	0.59
	30	3	214.1	14.4	4.20	20.58	12.24	0.32
	33	3	214.1	15.90	5.04	17.34	7.08	0.37
All data at	24	51	1252.1	27.00	27.06	28.44	29.76	0.53
each	27	52	1146.0	36.42	38.04	35.58	36.66	0.50
temperature	30	52	1090.3	41.76	42.90	41.40	44.04	0.87
	33	44	1186.0	59.16	63.42	62.82	71.16	0.11

[A]indicates a significant result.

Table 2. Preferred body temperatures ($T_{b_{pref}}$, °C) during the dry and wet seasons
The climate of the geographic distribution of the snake species is broadly characterised. Means are presented with sample size of the number of individuals used, and standard deviations in parentheses Probability values are not corrected for multiple comparisons

Species	Climate	Dry $T_{b_{pref}}$ (°C)	Wet $T_{b_{pref}}$ (°C)	Wet *v.* Dry
Aspidites melanocephalus	Tropical	28.1 (4, 3.4)	31.7 (3, 2.5)	$P < 0.01$
Antaresia childreni	Tropical	29.5 (3, 3.2)	29.3 (3, 3.3)	$P = 0.85$
Liasis fuscus	Tropical	30.0 (6, 3.9)	33.0 (4, 2.2)	$P < 0.01$
L. olivaceus	Tropical	30.6 (4, 2.8)	31.2 (3, 1.7)	$P = 0.30$
Antaresia stimsoni	Arid–Temperate	31.5 (3, 2.9)	31.5 (3, 3.0)	$P = 0.96$
Morelia s. spilota	Sub-tropical	31.3 (3, 2.8)	31.0 (4, 1.6)	$P = 0.48$
M. s. variegata	Temperate–Tropical	29.1 (3, 2.2)	29.5 (4, 2.4)	$P = 0.54$
Pseudonaja nuchalis	Tropical	29.6 (3, 2.1)	32.5 (3, 1.9)	$P < 0.01$
Acanthophis praelongus	Tropical	30.3 (3, 4.5)	33.7 (3, 3.1)	$P = 0.25$

Table 3. Thermal sensitivity of metabolism with increasing temperature
The table shows Q_{10} values calculated over the entire temperature range (24–33°C) and also Q_{10} values calculated over two subsets of the thermal range: temperatures below 30°C (24–30°C) and above 30°C (30–33°C)

Species	*n*	Q_{10} 24–33°C	Q_{10} 24–30°C	Q_{10} 30–33°C
Aspidites melanocephalus	5	2.58	2.57	2.51
Antaresia childreni	6	2.75	2.21	2.53
Liasis fuscus	4	2.03	1.48	2.52
Liasis olivaceus	6	3.00	4.10	1.87
Antaresia stimsoni	9	2.38	2.16	2.67
Morelia s. spilota	13	2.92	2.69	3.31
Morelia s. variegata	7	2.50	2.09	3.44
Combined species	50	2.60	2.39	2.94

Allometric relationships of SMR

There was a significant relationship between the mass of pythons and their metabolic rates at the experimental temperatures (ANCOVA, $F_{3,494} = 61.52$; $P < 0.0001$). For each of the different experimental temperatures the pooled allometric equations were as follows:

$$24°C\ \dot{V}_{O_2}\ mL\ h^{-1} = 0.441M^{0.76}$$

$$27°C\ \dot{V}_{O_2}\ mL\ h^{-1} = 0.399M^{0.72}$$

$$30°C\ \dot{V}_{O_2}\ mL\ h^{-1} = 0.394M^{0.76}$$

$$33°C\ \dot{V}_{O_2}\ mL\ h^{-1} = 0.362M^{0.74}$$

Comparison of SMR among species using mass-corrected data

SMR data on several boid species (obtained from the literature) was compared with the results obtained in this study. Table 4 shows the metabolic data in original and mass-corrected form. Appendix 1 presents the results of t-tests, but only trends are mentioned here because there were too many non-independent tests without Bonferroni correction.

Australian pythons have metabolic rates lower than those of at least seven of the nine species of boas examined (*Corallus caninus, C. enhydris, Candoia carinatus, Epicrates angulifer, E. cenchria, E. colubrina* and *Lichanura trivirgata*), and the larger Australian python species (*L. fuscus, L. olivaceus, A. melanocephalus, M. s. spilota* and *M. s. variegata*) all had lower metabolic rates than that of another species of boa, *A. dumerili* (Appendix 1). Only the boa, *Boa constrictor,* had a metabolic rate similar to those of the Australian pythons. *A. arafurae* had a metabolic rate lower than that of *E. angulifer,* but similar to those of the other boa species. Six of the seven Australian python taxa in this study had lower metabolic rates than that of *P. regius*, but most had metabolic rates similar to those of the other non-Australian pythons examined (Benedict 1932; Hutchinson *et al*. 1966; Chappell and Ellis 1987).

Table 4. Metabolic rates from the literature and this study in mass-corrected terms
Mass and metabolic rates are presented as means

Species	Mass (g)	Metabolic rate $\dot{V}_{O_2}$ mL h^{-1}	Mass-corrected $\dot{V}_{O_2}$ mL min^{-1} g^{exp}	Reference
Python curtis	3000	56.01	3.350	Chappell and Ellis 1987
Python regius	800	19.01	3.114	Chappell and Ellis 1987
Python reticulatus	18000	397.16	5.516	Chappell and Ellis 1987
Python sebae	22000	362.42	3.631	Chappell and Ellis 1987
Python molurus	14000	241.73	3.562	Chappell and Ellis 1987
Morelia spilota	2000	64.91	3.128	Chappell and Ellis 1987
Epicrates cenchria	700	16.35	3.103	Chappell and Ellis 1987
Boa constrictor	13000	183.93	3.615	Chappell and Ellis 1987
Corallus caninus	700	11.50	3.213	Chappell and Ellis 1987
Corallus enhydris	1000	22.28	3.161	Chappell and Ellis 1987
Lichanura trivirgata	300	8.44	2.942	Chappell and Ellis 1987
Acrantophis dumerili	3000	53.32	3.365	Chappell and Ellis 1987
Candoia carinatus	800	14.10	3.207	Chappell and Ellis 1987
Eryx colubrinus	150	5.12	2.797	Chappell and Ellis 1987
Boa constrictor	9900	207.9	3.458	Benedict 1932
Epicrates angulifer	12400	384.4	3.364	Benedict 1932
Python molurus	14800	266.4	3.555	Vinegar *et al.* 1970
Python reticulatus	30200	875.8	3.493	Benedict 1932
Python molurus	12370	222.66	3.534	Hutchison *et al.* 1966
Aspidites melanocephalus	974	48.16	2.920	this study
Antaresia childreni	320	18.25	2.756	this study
Liasis fuscus	1479	41.90	3.123	this study
Liasis olivaceus	2761	91.14	3.142	this study
Antaresis stimsoni	347	17.62	2.806	this study
Morelia s. spilota	1250	55.39	3.011	this study
M. s. variegata	1467	47.67	2.943	this study
Acrochordus arafurae	1050	28.6	3.138	this study
Acanthophis antarcticus	102	6.14	2.594	this study
Pseudonaja nuchalis	214	14.39	2.565	this study

Discussion

As a group, boids have lower metabolic rates than other reptiles (Bennett and Dawson 1976; Andrews and Pough 1985), and the Australian pythons we studied have particularly low metabolic rates. The allometric relationships and thermal sensitivity of the animals reported here were similar to those of other reptiles. Standard metabolic rate was not different among species or seasons, and there was no difference between SMR and RMR for 30 of 33 comparisons. These patterns of metabolic rate are less variable than those of many other reptiles (Beaupre 1993; Secor and Nagy 1994).

Several species of diurnally active squamates show seasonal variation in SMR (Scott *et al.* 1982; Christian and Conley 1994; Beaupre 1995*b*; Christian *et al.* 1996*a*, 1996*b*). The lack of seasonal change in metabolic rate of the pythons examined in this study may be related to the fact that their SMRs are low compared with those of most other reptiles. Hence, pythons may already be operating at a minimal level of energy expenditure. Low food availability and other resource uncertainties characterise most Australian habitats (Flannery 1994) and may make low SMR and the conservation of energy necessary in these snakes.

Metabolic rates of many reptiles vary with a circadian rhythm such that the RMR of reptiles is generally 1.2–1.5 times higher than SMR (Bennett and Dawson 1976; Andrews and Pough 1985). However, SMR and RMR are not different in the few python and boa species previously examined (Benedict 1932; Chappell and Ellis 1987). Only three species in this study (*M. s. variegata*, *L. fuscus, A. arafurae*) had a significantly higher RMR, and in each case this difference was only at a single temperature that corresponded fairly closely to the wet season $T_{b_{pref}}$ of the species in question (29.5°C for *M. s. variegata*, 33.0°C for *L. fuscus* and 27°C for *A. arafurae*). Thus, these temperatures may stimulate these species to maintain a higher resting metabolic rate.

Acrochordus arafurae has been characterised as having a low metabolic rate from both ecological (Shine and Lambeck 1985; Shine 1986) and physiological data (Seymour *et al.* 1981). The SMR of this species was not different from that of any of the snakes analysed; however, their SMR was low compared with the general allometric equation for snakes (Bennett and Dawson 1976).

Chappell and Ellis (1987) found that metabolic differences among species, genera and even families of snakes, were largely due to mass and temperature. However, in our comparisons with published results, most differences were between Australian pythons and the subfamily Boinae, with seven Australian python taxa having lower metabolic rates than eight of the nine boid species presented by Chappell and Ellis (1987). These results could indicate a metabolic divergence between the subfamilies Pythoninae and Boinae.

Most snake species examined in this study were predominantly 'sit and wait' foragers, except *P. nuchalis* and possibly *A. melanocephalus* (authors' observations). The SMRs of all these species were similar, in striking contrast to those of some other snakes that differ in foraging mode. The diurnal, 'active' foraging colubrid snake (*Masticophis*) has a SMR twice that of the 'sit and wait'-foraging sidewinder rattlesnake (*Crotalis*) (Secor and Nagy 1994).

Most boids have a low active body temperature (Cogger and Holmes 1960; Regal 1966; Slip and Shine 1988*a*). Low $T_{b_{pref}}$s have ecological consequences such as a lower metabolic rate (therefore lower energy expenditure), and longer nocturnal periods suitable for activity. In some tropical areas boids would be able to remain active over a 24-hour period.

The $T_{b_{pref}}$s of three of the species studied were higher in the wet than in the dry season, and two of those were active foragers. However, the $T_{b_{pref}}$s of five python taxa did not change with season. These included small snakes in the children's python complex (*A. childreni* and *A. stimsoni*), the carpet/diamond python complex (*Morelia s. spilota* and *M. s. variegata*), and the large *L. olivaceus* (Table 3). It is likely that three tropical species (*A. childreni, M. s. variegata, L. olivaceus*) would be able to achieve a $T_{b_{pref}}$ at some time during the day throughout the year in northern Australia (Christian and Bedford 1995, 1996). However, during winter in central Australia it would be difficult for *A. stimsoni* to attain a high and stable body

temperature. Hence, although the $T_{b_{pref}}$s of *A. stimsoni* and *M. s. spilota* are comparable to other pythons, it is unlikely that these species would be able to attain high body temperatures during the cold months.

In previous studies, Shine and Madsen (1996) found no appreciable seasonal difference in the T_b of *L. fuscus* during a telemetry study, and Slip and Shine (1988*a*) found that the $T_{b_{pref}}$ of the temperate-zone *Morelia s. spilota* is lower than that of tropical python species. Some *M. s. spilota* used in this study had been in the tropics for several years, and their thermoregulatory behaviour and physiology may have changed.

Although we did not find seasonal shifts in SMR, a change in thermoregulatory strategy between seasons would enhance the conservation of energy in seasons with lower food and water resources (Christian *et al.* 1995, 1996*a*, 1996*b*). The energy saving during the dry season resulting from the seasonal shift in $T_{b_{pref}}$ was calculated for *A. melanocephalus* and *P. nuchalis*. It was assumed that each snake could maintain the $T_{b_{pref}}$ for 12 hours per day. The calculated energy saved by reducing $T_{b_{pref}}$ by 3.6°C was 4.02 kJ d^{-1} for *A. melanocephalus*. A 2.9°C fall in $T_{b_{pref}}$ corresponds with a decline of 0.36 kJ d^{-1} in the amount of energy used by *P. nuchalis*.

Although Australian pythons appear to use a low-energy strategy during all seasons, additional energy savings can be achieved by decreasing body temperatures a few degrees. Thus, pythons could decrease body temperatures when food and water resources are very limited. The results presented here are limited to laboratory studies. Field studies are required to fully understand the relationships between the availability of prey and the activity and metabolism of pythons.

Acknowledgments

We thank Tim Schultz, Tony O'Grady, Greg Fyfe, Trevor Sullivan, Rick Shine and Peter Harlow. Funding was provided by the Northern Territory University. This work was completed under the permits of the Parks and Wildlife Commission of the Northern Territory and the Northern Territory University Animal Experimentation Ethics Committee.

References

Andrews, R. M., and Pough, F. H. (1985). Metabolism of squamate reptiles: allometric and ecological relationships. *Physiological Zoology* **58**, 214–231.

Beaupre, S. J. (1993). An ecological study of oxygen consumption in the mottled rock rattlesnake, *Crotalus lepidus lepidus*, and the black-tailed rattlesnake, *Crotalus molossus molossus*, from two populations. *Physiological Zoology*. **66**, 437–454.

Beaupre, S. J. (1995*a*). Comparative ecology of the mottled rock rattlesnake, *Crotalus lepidus*, in Big Bend National Park. *Herpetologica*. **51**, 45–56.

Beaupre, S. J. (1995*b*). Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology*. **76**, 1655–1665.

Benedict, F. G. (1932). The physiology of large reptiles with special reference to the heat production of snakes, tortoises, lizards, and alligators. Carnegie Institute of Washington, Publication No. 425, Washington, DC.

Bennett, A. F., and Dawson, W. R. (1976). Metabolism. In 'Biology of the Reptilia. Vol. 5'. (Eds C. Gans and W. R. Dawson.) pp. 127–223. (Academic Press: London.)

Bennett, A. F., and Gleeson, T. T. (1979). Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus*. *Copeia* **1979**, 573–577.

Chappell, M. A., and Ellis, T. M. (1987). Resting metabolic rates in boid snakes: allometric relationships and temperature effects. *Journal of Comparative Physiology* **157**, 227–235.

Christian, K. A., and Bedford, G. S. (1995). Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii,* in tropical Australia. *Ecology* **76**, 124–132.

Christian, K. A., and Bedford, G. S. (1996). Thermoregulation by the spotted tree monitor, *Varanus scalaris*, in the seasonal tropics of Australia. *Journal of Thermal Biology* **21**, 67–73.

Christian, K. A., and Conley, K. E. (1994). Activity and resting metabolism of varanid lizards compared with 'typical' lizards. *Australian Journal of Zoology* **42**, 185–93.

Christian, K. A., Corbett, L. K., Green, B., and Weavers, B. W. (1995). Seasonal activity and energetics of two species of varanid lizards in tropical Australia. *Oecologia* **103**, 349–357.

Christian, K. A., Green, B., Bedford, G. S., and Newgrain, K. (1996*a*). Seasonal metabolism of a small, arboreal monitor lizard, *Varanus scalaris*, in tropical Australia. *Journal of Zoology* **240**, 383–396.

Christian, K. A., Griffiths, A. D., and Bedford, G. S. (1996*b*). Physiological ecology of frillneck lizards in a seasonal tropical environment. *Oecologia* **106**, 49–56.

Cogger, H. G., and Holmes, A. (1960). Thermoregulatory behaviour in a specimen of *Morelia spilota variegata* Gray (Serpentes : Boidae). *Proceedings of the Linnean Society of New South Wales* **85**, 328–333.

Dill, C. D. (1972). Reptilian core temperatures: variation within individuals. *Copeia* **1972**, 577–579.

Dmi'el, R. (1972). Relation of metabolism to body weight in snakes. *Copeia* **1972**, 179–181.

Dunham, A. E., Miles, D. B., and Reznick, D. N. (1988). Life history patterns in squamate reptiles. In 'Biology of the Reptilia. Vol. 16'. (Eds C. Gans and R. B. Huey.) pp. 441–522. (Alan R. Liss: New York.)

Flannery, T. (1994). 'The Future Eaters.' (Reed Books: Sydney.)

Garland, T. Jr, Else, P. L., Hulbert, A. J., and Tap, P. (1987). The effects of endurance training and captivity on activity metabolism of lizards. *American Journal of Physiology* **252**, R450–R456.

Hirth, H. F., and King, A. C. (1969). Body temperatures of snakes in different seasons. *Journal of Herpetology* **3**, 101–102.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In 'Biology of the Reptilia. Vol. 12'. (Eds C. Gans and F. H. Pough.) pp. 25–90. (Academic Press: London.)

Huey, R. B., and Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology* **62**, 991–999.

Hutchison, V. H., Dowling, H. G., and Vinegar, A. (1966). Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*. *Science* **151**, 694–696.

Leger, D. W., and Didrichson, I. A. (1994). An assessment of data pooling and some alternatives. *Animal Behaviour* **48**, 823–832.

Mirtschin, P., and Davis, R. (1992). 'Snakes of Australia, Dangerous and Harmless'. (Hill of Content: Melbourne.)

Nagy, K. A. (1983). Ecological energetics. In 'Lizard Ecology: Studies of a Model Organism'. (Eds R. B. Huey, E. R. Pianka, and T. W. Schoener.) pp. 24–54. (Harvard University Press: Cambridge.)

Potvin, C., Lechowicz, M. J., and Tardif, S. (1990). The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* **71**, 1389–1400.

Regal, P. J. (1966). Thermophilic response following feeding in certain reptiles. *Copeia* **1966**, 588–590.

Rosen, P. C. (1991). Comparative field study of thermal preferenda in garter snakes *(Thamnophis)*. *Journal of Herpetology* **25**, 301–312.

Schmidt-Neilsen, K. (1990). 'Animal Physiology: Adaptation and Environment'. (Cambridge University Press: Cambridge.)

Scott, J. R., Tracy, C. R., and Pettus, D. (1982). A biophysical analysis of daily and seasonal utilisation of climate space by a montane snake. *Ecology* **63**, 482–493.

Secor, S. M., and Diamond, J. (1995). Adaptive responses to feeding in Burmese pythons: pay before pumping. *Journal of Experimental Biology* **198**, 1313–1325.

Secor, S. M., and Nagy, K. A. (1994). Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* **75**, 1600–1614.

Seymour, R. S., Dobson, G. P., and Baldwin, J. (1981). Respiratory and cardio-vascular physiology of the aquatic snake, *Acrochordus arafurae*. *Journal of Comparative Physiology* **144**, 215–227.

Shine, R. (1986). Ecology of a low energy specialist: food habits and reproductive biology of the Arafura filesnake (*Acrochordidae*). *Copeia* **1986**, 424–437.

Shine, R. (1991). 'Australian Snakes: A Natural History.' (Reed Books: Sydney).

Shine, R., and Lambeck, R. (1985). A radiotelemetric study of movements, thermoregulation and habitat utilisation of Arafura filesnakes (Serpentes : Acrochordidae). *Herpetologica* **41**, 351–361.

Shine, R., and Madsen, T. (1996). Is thermoregulation unimportant for most reptiles? An example using water pythons *(Liasis fuscus)* in tropical Australia. *Physiological Zoology* **69**, 252–269.

Slip, D. J., and Shine, R. (1988*a*). Thermoregulation of free-ranging diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Copeia* **1988**, 984–995.

Slip, D. J., and Shine, R. (1988*b*). Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology* **22**, 323–330.

Slip, D. J., and Shine, R. (1988*c*). Habitat use, movements and activity patterns of free-ranging diamond pythons, *Morelia spilota spilota* (Serpentes : Boidae): a radiotelemetric study. *Australian Wildlife Research* **15**, 515–531.

Taylor, B. M., and Davies, S. (1981). Changes in the weight dependence of metabolism during the sloughing cycle of the snake *Thamnophis sirtalis parietalis*. *Comparative Biochemical Physiology* **69A**, 113–120.

Tsuji, J. S. (1988). Seasonal profiles of standard metabolic rate of lizards (*Sceloporus occidentalis*) in relation to latitude. *Physiological Zoology* **61**, 230–240.

Vinegar, A., Hutchison, V. H., and Dowling, H. G. (1970). Metabolism, energetics, and thermoregulation during brooding of snakes of the genus *Python* (Reptilia, Boidae). *Zoologica: New York Zoological Society* **55**, 19–50.

Waldschmidt, S. R., Jones, S. M., and Porter, W. P. (1987). Reptilia. In 'Animal Energetics. Vol. 2, Bivalvia through Reptilia'. (Eds T. J. Pandian and F. J. Vernberg.) pp. 553–620. (Academic Press: New York.)

Zar, J. H. (1984). 'Biostatistical Analysis.' 2nd Edn. (Prentice-Hall: Englewood Cliffs, NJ.)

Appendix 1. Mass-corrected metabolic rates of Boidae

Values from this study were compared with those in the literature using t-tests. The *t* and *P* values are presented with the number of specimens used in parentheses.

Species	*Acrochordus arafurae* ($n = 3$)	*Aspidites melanocephalus* ($n = 11$)	*Antaresia childreni* ($n = 13$)	*Liasis fuscus* ($n = 11$)	*Liasis olivaceus* ($n = 9$)	*Antaresia stimsoni* ($n = 6$)	*Morelia s. spilota* ($n = 8$)	*Morelia s. variegata* ($n = 6$)
Acrantophis dumerili	$t = 0.085$	$t = 5.05$	$t = 2.11$	$t = 2.30$	$t = 7.21$	$t = 1.69$	$t = 3.35$	$t = 3.88$
	$P = 0.94$	$P = 0.001$	$P = 0.05$	$P = 0.04$	$P < 0.001$	$P = 0.14$	$P = 0.01$	$P = 0.008$
Boa constrictor	$t = -1.95$	$t = 0.85$	$t = -0.68$	$t = -2.25$	$t = 0.74$	$t = -0.43$	$t = 0.11$	$t = -0.69$
	$P = 0.15$	$P = 0.42$	$P = 0.51$	$P = 0.05$	$P = 0.48$	$P = 0.68$	$P = 0.92$	$P = 0.52$
Corallus caninus	$t = 1.719$	$t = 9.11$	$t = 4.82$	$t = 6.70$	$t = 13.47$	$t = 3.75$	$t = 6.48$	$t = 8.31$
	$P = 0.18$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.009$	$P < 0.001$	$P < 0.001$
C. enhydris	$t = 0.214$	$t = 5.72$	$t = 2.56$	$t = 3.03$	$t = 8.25$	$t = 2.03$	$t = 3.87$	$t = 4.62$
	$P = 0.84$	$P < 0.001$	$P = 0.02$	$P = 0.01$	$P < 0.001$	$P = 0.09$	$P = 0.005$	$P = 0.004$
Candoia carinatus	$t = 1.317$	$t = 8.21$	$t = 4.21$	$t = 5.72$	$t = 12.08$	$t = 3.29$	$t = 5.78$	$t = 7.32$
	$P = 0.23$	$P < 0.001$	$P = 0.001$	$P = 0.001$	$P < 0.001$	$P = 0.02$	$P < 0.001$	$P < 0.001$
Epicrates angulifer	$t = -3.63$	$t = -2.93$	$t = -3.20$	$t = -6.34$	$t = -5.07$	$t = -2.34$	$t = -2.81$	$t = -4.80$
	$P = 0.04$	$P = 0.01$	$P = 0.007$	$P < 0.001$	$P = 0.001$	$P = 0.06$	$P < 0.02$	$P = 0.003$
E. cenchria	$t = 0.411$	$t = 6.17$	$t = 2.86$	$t = 3.51$	$t = 8.93$	$t = 2.26$	$t = 4.21$	$t = 5.10$
	$P = 0.71$	$P < 0.001$	$P = 0.01$	$P = 0.005$	$P < 0.001$	$P = 0.06$	$P = 0.003$	$P = 0.002$
Eryx colubrinus	$t = 0.607$	$t = 6.61$	$t = 3.15$	$t = 3.19$	$t = 9.62$	$t = 2.48$	$t = 4.55$	$t = 5.58$
	$P = 0.59$	$P < 0.001$	$P = 0.008$	$P = 0.002$	$P < 0.001$	$P = 0.05$	$P = 0.002$	$P = 0.001$
Lichanura trivirgata	$t = 0.599$	$t = 6.59$	$t = 3.14$	$t = 3.97$	$t = 9.59$	$t = 2.47$	$t = 4.54$	$t = 5.56$
	$P = 0.59$	$P < 0.001$	$P = 0.008$	$P = 0.002$	$P < 0.001$	$P = 0.05$	$P = 0.002$	$P = 0.001$
M. spilota	$t = -1.82$	$t = 0.96$	$t = -0.61$	$t = -2.12$	$t = 0.92$	$t = -0.37$	$t = 0.20$	$t = -0.56$
	$P = 0.15$	$P = 0.36$	$P = 0.55$	$P = 0.06$	$P = 0.38$	$P = 0.73$	$P = 0.85$	$P = 0.59$
Python curtis	$t = -0.27$	$t = 4.62$	$t = 1.83$	$t = 1.84$	$t = 6.56$	$t = 1.48$	$t = 3.02$	$t = 3.42$
	$P = 0.80$	$P = 0.001$	$P = 0.09$	$P = 0.09$	$P = 0.001$	$P = 0.19$	$P = 0.02$	$P = 0.01$
Python molurus	$t = -1.61$	$t = 1.62$	$t = -0.17$	$t = -1.41$	$t = 1.93$	$t = -0.04$	$t = 0.70$	$t = 0.15$
	$P = 0.21$	$P = 0.13$	$P = 0.87$	$P = 0.19$	$P = 0.09$	$P = 0.97$	$P = 0.50$	$P = 0.89$
Python regius	$t = 0.21$	$t = 5.70$	$t = 2.55$	$t = 3.01$	$t = 8.22$	$t = 2.02$	$t = 3.85$	$t = 4.60$
	$P = 0.85$	$P = 0.001$	$P = 0.02$	$P = 0.01$	$P < 0.001$	$P = 0.09$	$P = 0.005$	$P = 0.004$
Python reticulatus	$t = -2.75$	$t = -0.97$	$t = -1.89$	$t = -4.21$	$t = -2.05$	$t = -1.35$	$t = -1.29$	$t = -2.66$
	$P = 0.07$	$P = 0.35$	$P = 0.08$	$P = 0.002$	$P = 0.07$	$P = 0.23$	$P = 0.23$	$P = 0.04$
Python sebae	$t = -1.88$	$t = 1.00$	$t = -0.58$	$t = -2.08$	$t = 0.98$	$t = -0.35$	$t = 0.23$	$t = -0.52$
	$P = 0.16$	$P = 0.34$	$P = 0.57$	$P = 0.06$	$P = 0.35$	$P = 0.74$	$P = 0.83$	$P = 0.62$

Manuscript received 23 April 1998; accepted 22 September 1998