Resting metabolic rates in boid snakes: allometric relationships and temperature effects*

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Summary. Resting metabolic rates (RMR) of 34 species from 18 genera of boas and pythons (Serpentes: Boidae), with body masses ranging from 2 to 67,800 g, were determined as oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) at three ambient temperatures (T_a).

The temperature coefficient of metabolism (Q_{10}) averaged 2.61 between T_a of 20–30 °C and 2.65 between 30 and 34 °C. The respiratory exchange ratio RE ($= \dot{V}_{CO_2}/\dot{V}_{O_2}$) increased slightly with increasing T_a (0.795 at 20 °C, 0.819 at 30 °C, and 0.834 at 34 °C). Interspecific differences in Q_{10} and RE were slight or insignificant.

A multiple regression relating metabolism ($\dot{V}_{O_2}$) to mass and T_a explained 97% of the variance in the pooled interspecific data. The mass exponent was 0.806, which is approximately the same as reported for squamates and for all reptilian taxa combined. The mean within-species slope (0.732) was significantly less than the slope for pooled data, but did not differ significantly from 0.75. In 40 of 42 cases (14 species at 3 T_a), within-species slopes did not differ from each other. Values of the adjusted mean Y, from covariance analysis, were significantly and positively correlated with mass, indicating that the mass coefficient increases with increasing mass.

Considerable variation in metabolic rate is apparent both within and between ecological and taxonomic categories.

Introduction

The theoretical and empirical relationships between body mass (M) and metabolic rate (MR)

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remain controversial despite years of study. Much of the debate has concerned the mass exponent 'b' in the familiar power function $MR = aM^b$. On theoretical grounds, two values have been proposed for the mass exponent: 0.67 from surface-volume considerations (Hemmingsen 1960; Kleiber 1961) and from dimensional analysis (Heusner 1982, 1984), and 0.75 based upon principles of mechanical support and muscle biophysics (McMahon 1973). The discrepancy was partially resolved by Feldman and McMahon (1983), whose analysis of empirical data suggests that 0.75 is statistically appropriate for interspecific comparison while 0.67 is valid for intraspecific comparison. Tests of these models have generally used the extensive data set available for mammals. However, even in this well-studied group the precise value of 'b' is uncertain. Hinds and MacMillen (1984) and Hayssen and Lacy (1984) report interspecific 'b' values quite different from 0.75 among various mammalian lineages. Moreover, mammals are characterized by relatively low within-species variation of adult body mass (which reduces the resolution of estimates of slope), and consequently are poor subjects for intraspecific comparisons.

Recognizing these problems, Andrews and Pough (1985) examined the intra- and interspecific allometry of resting metabolism in squamate reptiles, which show considerably greater variation in adult body mass than is present in mammals. Using published data on 107 species they computed an overall mass exponent of 0.80 for interspecific comparisons. These results confirmed the earlier calculations of Bennett and Dawson (1976). Values of 'b' for intraspecific comparisons averaged 0.67 for 17 species (as predicted by Heusner and by Feldman and McMahon), but showed high variance. Andrews and Pough (1985) also reported that ecological considerations, such as food type and foraging strategy, influenced metabolic rate

to a greater extent than did phylogenetic relationships.

In this paper we describe results from an investigation of metabolism in a variety of boas and pythons (Serpentes: Boidae). Except for a few studies on temperature and metabolism during incubation behavior in pythons (Vinegar et al. 1970; Van Mierop and Barnard 1978; Harlow and Grigg 1984), the Boidae have received little attention from comparative physiologists. However, for several reasons they are particularly attractive for examining allometric relationships. Boids form a cohesive taxon which is not closely related to other ophidian groups. Nevertheless, the family contains considerable ecological diversity, ranging from fossorial and semiaquatic forms to heavy-bodied ground-dwellers to slender, highly arboreal species. There is wide variation in mass both within and between species: the adults of large boas and pythons may be more than 1,000 times larger than their young, and interspecific variation in maximum adult mass is equally great.

We obtained metabolic measurements (oxygen consumption and carbon dioxide production) at three ambient temperatures on an extensive sample of boids. We used these data to investigate several important questions of metabolic scaling, including: (1) within and between-species values of the mass exponent; (2) size-related changes in the mass coefficient; (3) effects of temperature and of phylogenetic and ecological factors on metabolic rate.

Materials and methods

Animals. We performed metabolic measurements on 251 individuals of 34 species from 18 genera. Our primary intention was to obtain large intraspecific sample sizes containing considerable mass variation, but for interspecific comparisons we also accepted small sample sizes (even single individuals) of rare species. Most of the snakes were borrowed from private collectors, educational institutions, or zoos. A few were collected from the wild. We housed the animals in a walk-in environmental room maintained at 30 ± 0.2 °C and 70–80% relative humidity, with a 12L:12D photoperiod. Animals were fasted before metabolic measurements. We considered a 7-day fast adequate to insure that small to moderate-sized snakes (<5 kg) were postabsorptive; longer fasts (up to 14 days) were used for 5–10 kg individuals, and snakes larger than 10 kg were fasted at least 30 days. All animals were healthy and non-reproductive during the measurement period.

Measurements. Rates of oxygen consumption ($\dot{V}_{O_2}$; ml/h and ml/[kg·h]), and in most cases carbon dioxide production ($\dot{V}_{CO_2}$; ml/h and ml/[kg·h]), were determined in open-circuit respirometry systems. To accommodate snakes of different sizes, we used seven respirometry chambers with volumes ranging from 300 ml to 250 l. These were placed in environmental cabinets which controlled ambient temperature (T_a) to within 0.2 °C. The T_a was determined with 36-gauge thermocouples placed inside of the respirometry chambers. For snakes <5 kg, we assumed body temperature (T_b) = T_a. For larger snakes, which might maintain a significant gradient between T_b and T_a (e.g., Vinegar et al. 1970), we taped additional thermocouples to the floor of the chamber. The animals rested upon one or more of the couples, thereby providing an estimate of T_b (in no case did steady-state T_b exceed T_a by more than 0.3 °C). We made $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ measurements at three T_a (= T_b): 20, 30, and 34 °C. The two lower temperatures were chosen because they are probably experienced in nature by most of the species we used, and for comparison to a considerable body of published data. We selected 34 °C because higher T_a were not tolerated by some boids. Snakes were subjected to different T_a in random order. For small snakes (<500 g), at least 4 h (usually 6–8 h) was allowed for thermal equilibration after T_a was changed. We lengthened the equilibration period to 12–24 h for larger animals (500 g–5 kg) and to 24–48 h for snakes heavier than 5 kg.

We made measurements only when snakes were resting, as judged from 1–2 h of stable and minimal $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data and by visual inspection. Most of the animals remained coiled and inactive for the duration of experiments, except for initial exploratory movements when first placed in the metabolism chambers. However, we were unable to obtain useful data from a few individuals that were continuously active at a particular T_a or T_a's. Andrews and Pough (1985) suggest that metabolic measurements on reptiles be performed at known phases of the circadian cycle. Unfortunately, little or no information on daily activity patterns is available for the majority of the species we studied. We made most of our measurements during the day; spot-checks on a number of individuals indicated that day- and night-time measurements from resting animals were usually quite similar.

Air flow rates through the respirometry chambers from 30 ml/min to 10 l/min (STPD) were maintained ($\pm 2\%$) with Applied Materials AFC-550 mass flow controllers; Gilson rotometers equipped with needle valves were used to control flow rates from 10 to 30 ml/min ($\pm 5\%$). In most cases (except for species from xeric habitats), the air stream was humidified to 40–70% R.H. after flow rate measurement but prior to entering the respirometry chamber. At flow rates greater than 50 ml/min, a fraction of the excurrent air from the chamber was dried, passed through the CO_2 sensor (Applied Electrochemistry CD-3A, Anarad AR-50, or Beckman LB-2), scrubbed of CO_2 and redried, and passed through the O_2 sensor (Applied Electrochemistry S-3A). At lower flow rates the entire excurrent stream was routed through the sensors. The O_2 and CO_2 analyzers were periodically referenced against dry air diverted from upstream of the flow controller. During measurements the concentration of O_2 in the chamber never fell below 20.5% and CO_2 concentration never exceeded 0.45%. All data were recorded, stored, and analyzed on a computer. Each measurement of $\dot{V}_{O_2}$ or $\dot{V}_{CO_2}$ is the mean of at least 20 sequential samples taken at intervals of 20 s. For all $\dot{V}_{O_2}$ measurements the standard deviation was <5% of the mean (the S.D. was slightly greater for $\dot{V}_{CO_2}$ data).

Measurement accuracy and statistical procedures. The accuracy of gas exchange calculations varied with body mass. For snakes larger than 100 g, the maximum cumulative error (primarily due to resolution limits and calibration errors of the flow controllers) was 2–3% for both $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$. At smaller body sizes the potential errors increased because the gas analyzer resolution limits (roughly 0.001% for O_2 and 0.001–0.005% for CO_2, depending on which analyzer was used) became more significant than errors in flow rate measurements. For the smallest animals measured (~2 g), we estimate the maximum

cumulative error to be 8–10% for $\dot{V}_{O_2}$ and 15–20% for $\dot{V}_{CO_2}$. For several 2–10 g animals $\dot{V}_{CO_2}$ data were discarded because the potential error exceeded 20%.

Data analysis was based on analysis of variance (ANOVA) and on least-squares and stepwise multiple regressions of $\log_{10}$-transformed mass and gas exchange data. We computed regressions only for data sets containing five or more individuals and at least a 3.2-fold mass range ($>0.5 \log_{10}$ units). In a small number of cases involving rapidly growing animals, a single individual was run more than once. We accepted multiple data points from individuals in the final analyses only if (1) the different points represented mass increases of at least 50%, and (2) regression slopes and intercepts for data sets including multiple data points for an individual were not significantly different when these points were excluded. In no case did multiple samples from the same individual comprise more than 20% of the data points for a particular species. Covariance analysis (ANCOVA; Sokal and Rohlf 1981) was used to examine slopes and intercepts. For comparisons between phylogenetic and ecological groupings, we used standardized residuals (SR) derived from regression equations (SR = [observed Y value − predicted Y value]/S_y, where S_y is the standard error of predicted Y at a given X). The SR is independent of the absolute magnitude of an observation (thereby allowing meaningful comparisons between groups of different mass) and indicates the magnitude and direction (positive or negative) of deviations from expected values.

Data are presented as mean ± 2 SEM. Unless otherwise indicated, the significance level was 0.05.

Results

Temperature effects and respiratory exchange ratios

The Q_{10} data (Fig. 1) were not normally distributed, so they were log-transformed to remove skewness. When data from all species were combined, there was no significant difference between mean values of Q_{10} between 20 and 30 °C and between 30 and 34 °C (2.61 ± 0.06 ($n = 232$) and 2.65 ± 0.10 ($n = 229$), respectively). A regression of $\log Q_{10}$ against log mass was significant ($P = 0.002$) for the 20–30 °C data, but the relationship was weak ($r^2 = 0.04$). A similar regression for the 30–34 °C data was also significant ($P = 0.003$), but again the relationship was weak ($r^2 = 0.04$). Significant within-species regressions between $\log Q_{10}$ and log mass were not observed in the 14 species which met our criteria for regression (see Methods). No interspecific differences in Q_{10} were observed in the 30–34 °C data, and interspecific differences in the 20–30 °C data were slight and of marginal significance ($P = 0.046$; ANOVA).

Regressions of the respiratory exchange ratio (RE; $= \dot{V}_{CO_2}/\dot{V}_{O_2}$) against log mass were significant at 30 and 34 °C, but in both cases the relationship was weak ($r^2 = 0.059$ and 0.121, respectively), and no significant relationship existed at 20 °C (Fig. 2). There were no significant regressions between RE
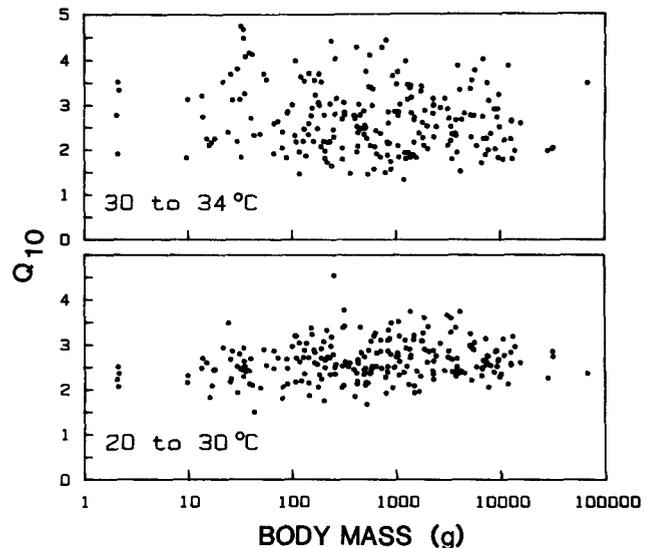

Fig. 1. Temperature coefficient (Q_{10}) of oxygen consumption as a function of mass over two ambient temperature ranges: 20 to 30 °C (bottom) and 30 to 34 °C (top)
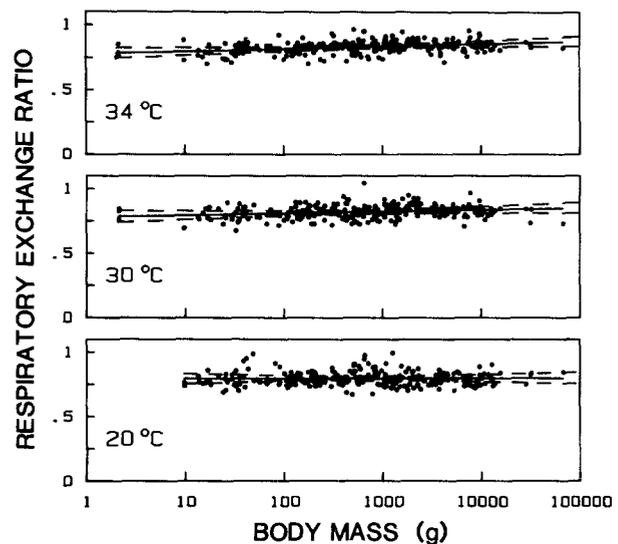

Fig. 2. Respiratory exchange ratio (RE, $= \dot{V}_{CO_2}/\dot{V}_{O_2}$) as a function of mass at three ambient temperatures

and log mass for individual species at any T_a. When data from all species were combined, slight but significant differences in RE were observed at different T_a's (RE = 0.795 ± 0.007 at 20 °C ($n = 232$); RE = 0.819 ± 0.007 at 30 °C ($n = 239$); RE = 0.834 ± 0.006 at 34 °C ($n = 240$); $P \ll 0.001$; ANOVA). Among the 16 species represented by 5 or more individuals, there were slight differences in RE at 20 and 34 °C ($P = 0.0006$ and 0.027, respectively), but no differences were observed at 30° C (ANOVA).

Table 1. Mass coefficients (a) and mass exponents (b) for intraspecific regressions of metabolic rate $(\dot{V}_{O_2})$ and body mass. Units are ml/h for $\dot{V}_{O_2}$ and g for mass. Last two columns show probabilities that the computed mass exponent (b) equals 0.67 and 0.75, respectively (NS indicates no significant difference)

Species	T_a (°C)	Mass coefficient	Mass exponent	r^2	n	Mass range (g)	Prob. b= :	
							0.67	0.75
Python curtis	20	−1.742	0.886	0.96	8	502–4245	0.022	NS
	30	−1.256	0.864	0.96	8	502–4245	0.037	NS
	34	−0.978	0.828	0.97	8	502–4245	0.040	NS
P. regius	20	−0.828	0.575	0.83	23	43–1531	NS	0.007
	30	−0.579	0.640	0.92	29	43–1724	NS	0.005
	34	−0.467	0.658	0.94	27	43–1618	NS	0.010
P. reticulatus	20	−1.245	0.807	0.96	15	152–28500	0.008	NS
	30	−0.601	0.752	0.96	15	152–28500	NS	NS
	34	−0.438	0.752	0.96	15	152–28500	NS	NS
P. sebae	20	−1.244	0.783	0.98	10	100–32180	0.020	NS
	30	−0.728	0.757	0.99	10	100–32180	0.008	NS
	34	−0.497	0.735	0.99	10	100–32180	0.032	NS
P. molurus	20	−1.108	0.736	0.96	20	109–67800	NS	NS
	30	−0.577	0.714	0.95	20	109–67800	NS	NS
	34	−0.460	0.726	0.96	20	109–67800	NS	NS
Morelia spilota	20	−1.243	0.772	0.76	8	108–2023	NS	NS
	30	−0.944	0.835	0.90	8	108–2023	NS	NS
	34	−0.517	0.738	0.87	8	108–2023	NS	NS
Epicrates cenchria	20	−0.770	0.562	0.87	11	35–797	NS	0.029
	30	−0.408	0.570	0.90	11	35–797	NS	0.014
	34	−0.174	0.558	0.90	11	35–797	NS	0.008
Boa constrictor	20	−1.234	0.748	0.97	35	31–15600	0.001	NS
	30	−0.792	0.743	0.97	35	31–15600	0.001	NS
	34	−0.961	0.836	0.92	35	31–15600	0.001	NS
Corallus caninus	20	−1.123	0.661	0.92	7	219–893	NS	NS
	30	−1.244	0.879	0.96	7	219–893	0.039	NS
	34	−0.958	0.817	0.98	7	219–893	0.033	NS
C. enhydris	20	−1.565	0.847	0.82	7	214–1390	NS	NS
	30	−0.965	0.771	0.95	7	214–1390	NS	NS
	34	−1.101	0.872	0.91	7	214–1390	NS	NS
Lichanura trivirgata	20	−1.009	0.613	0.87	12	16–348	NS	NS
	30	−0.716	0.663	0.95	12	16–348	NS	NS
	34	−0.576	0.699	0.96	12	16–348	NS	NS
Acrantophis dumerili	20	−1.291	0.757	0.83	7	1071–4026	NS	NS
	30	−0.415	0.616	0.82	7	1071–4026	NS	NS
	34	−0.470	0.689	0.82	7	1071–4026	NS	NS
Candoia carinatus	20	−1.232	0.668	0.96	14	9.8–1034	NS	NS
	30	−0.912	0.710	0.98	14	9.8–1034	NS	NS
	34	−0.681	0.697	0.98	14	9.8–1034	NS	NS
Eryx colubrinus	20	−1.249	0.700	0.95	9	9.7–162	NS	NS
	30	−0.949	0.762	0.96	9	9.7–162	NS	NS
	34	−0.799	0.766	0.98	9	9.7–162	NS	NS

Interspecific metabolic allometry

A multiple regression incorporating mass (M, grams) and T_a explained 96.7% of the variance in our 723 measurements of metabolic rate $(\dot{V}_{O_2}$, ml/h). The most important predictor was mass, which accounted for 86.4% of the variance. Temperature explained an additional 10.3%. After log transformation of M and $\dot{V}_{O_2}$ to linearize these data, the regression equation was:

$$\log \dot{V}_{O_2} = 0.8060 \log M + 0.0415\, T_a - 2.229 \qquad (1)$$

$(r^2 = 0.967,\ F_{2,720} = 10600,\ P \ll 0.0001)$

or,

$$\dot{V}_{O_2} = 0.0059 M^{0.8060} \times 10^{0.0415 T_a} \qquad (2)$$

The mass exponent 'b' equals 0.8060 ± 0.0117, which is significantly different from both 0.67 and 0.75 ($P < 0.0001$, t-test), but does not differ from the 'b' of 0.80 reported by Andrews and Pough (1985) for squamates. The overall Q_{10} for our data (2.60 ± 0.107) is slightly but significantly higher than the value of 2.4 reported by Andrews and Pough.

To eliminate any bias caused by unequal sample sizes among species or by the inclusion of data from both adult and young animals, we computed two additional regressions. When only the largest individual of each species is included (regardless of age), the equation was:

$$\dot{V}_{O_2} = 0.0043 M^{0.8329} \times 10^{0.0414 T_a} \qquad (3)$$
$$(r^2 = 0.972, \; F_{2,99} = 1736, \; P \ll 0.0001).$$

If the data set was further restricted to include only the largest adults (i.e., snakes large enough to be reproductively competent), the equation became:

$$\dot{V}_{O_2} = 0.0047 M^{0.8305} \times 10^{0.0416 T_a} \qquad (4)$$
$$(r^2 = 0.962, \; F_{2,72} = 922, \; P \ll 0.0001).$$

The mass exponents for equations 3 and 4 (0.8329 ± 0.0296 and 0.8305 ± 0.0408, respectively) both differ significantly from 0.67 and 0.75 ($P < 0.001$, t-test). The mass exponent for equation 3 differs slightly from 0.80 ($P = 0.044$), but the mass exponent for equation 4 does not. There are no significant differences in slope or intercept among equations 2, 3, and 4 (ANCOVA). However, the mass coefficients from these equations (0.0059, 0.0043, and 0.0047, respectively) are less than half that reported for squamates (0.013) by Andrews and Pough (1985).

Intraspecific metabolic allometry

Mass coefficients and mass exponents for the 14 intraspecific data sets containing adequate sample sizes and mass ranges are given in Table 1, and regression lines are shown in Fig. 3. Mean values of the mass exponent at 20, 30 and 34 °C (0.723 ± 0.052, 0.734 ± 0.048, and 0.740 ± 0.044, respectively) did not differ significantly (one-way ANOVA). The overall mean for all T_a combined (0.732 ± 0.027) was significantly different from 0.67 ($t = 4.78$, $P < 0.0001$, $n = 42$), but was not different from 0.75 ($t = -1.31$, $P = 0.098$, $n = 42$).

Although 'b' values for individual species ranged from 0.570 to 0.864, covariance analysis revealed no significant differences among slopes for the 30 °C data ($F_{13,165} = 1.59$, $P = 0.09$). Signif-
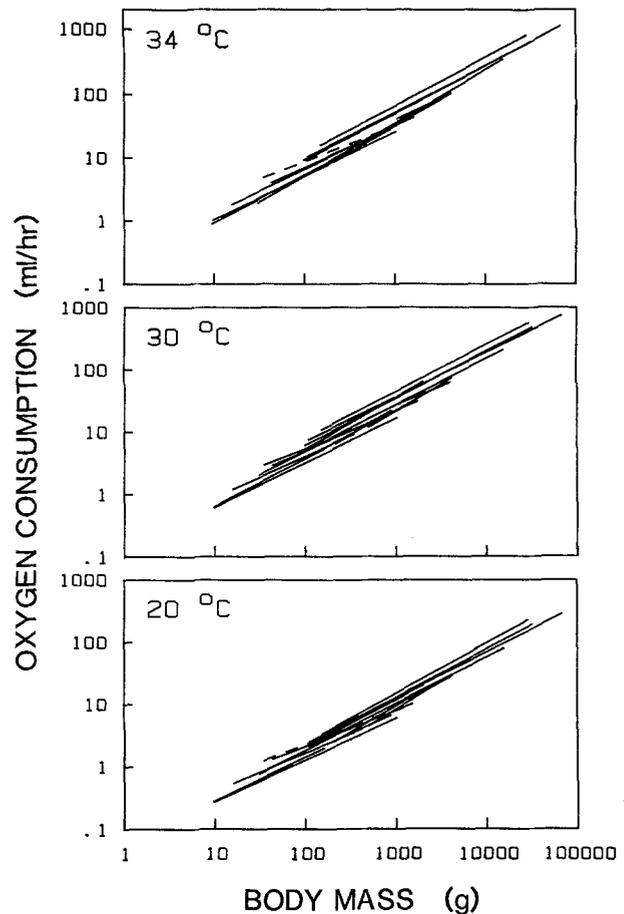

Fig. 3. Within-species regression lines for oxygen consumption ($\dot{V}_{O_2}$) as a function of mass for 14 species of boids at three ambient temperatures. In each plot, solid lines do not differ significantly from each other in slope. Lengths of regression lines indicate the mass ranges for particular species

icant differences were present among the 20 and 34 °C data ($F_{13,158} = 1.93$, $P = 0.03$ at 20 °C; $F_{13,163} = 1.98$, $P = 0.03$ at 34 °C). However, removal of the most divergent species (*Epicrates cenchria*) from the data set eliminated significant differences in slope among the remaining 13 species at both 20 and 34 °C.

Subsequent covariance analysis revealed highly significant differences in intercepts (i.e., mass coefficients, 'a') at all three T_a ($F_{12,161} = 7.42$, $P \ll 0.0001$ at 20 °C; $F_{13,178} = 13.82$, $P \ll 0.0001$ at 30 °C; $F_{12,165} = 8.64$, $P \ll 0.0001$ at 34 °C). Heusner (1982, 1984) and Feldman and McMahon (1983) imply that 'a' should increase with increasing mass in a series of species of different size. We examined this possibility at each of the three T_a's by regressing the adjusted mean Y's for each of the different species (from ANCOVA) against two indices of size: the log of the mean mass of our sample of each species, or the log of the mass

of the biggest specimen we measured (Fig. 4). Both indices yielded significant regressions with positive slopes at all T_a's, but values of r^2 were higher when maximum mass (M_{max}) was used as the predictor (slope $= 0.106 \pm 0.049$, $r^2 = 0.63$, $t_{DF=11} = 4.33$, $P = 0.0011$ at 20 °C; slope $= 0.128 \pm 0.054$, $r^2 = 0.66$, $T_{DF=12} = 4.79$, $P = 0.0004$ at 30 °C; slope $= 0.100 \pm 0.059$, $r^2 = 0.51$, $t_{DF=11} = 3.37$, $P = 0.0062$ at 34 °C). A multiple regression incorporating both M_{max} and T_a was highly significant:

$$\text{adjusted mean } Y = 0.1119 \log M_{max} + 0.0426 \, T_a - 0.353 \tag{5}$$

$(r^2 = 0.934, F_{2,37} = 260, P \ll 0.0001)$.

The ANCOVA results indicated that intraspecific 'b' values are generally similar among different species. Accordingly, to examine metabolic scaling in species which did not meet our criteria for intraspecific regression, we estimated adjusted mean Y values at each T_a by extrapolating from the species means for log mass and log $\dot{V}_{O_2}$, using the common slope and grand mean of log M_{max} obtained from ANCOVA. The regression combining these data with the adjusted mean Y's obtained directly from ANCOVA (less the *Epicrates cenchria* data for 20 and 34 °C) is:

$$\text{adjusted mean } Y = 0.0998 \log M_{max} + 0.0426 \, T_a - 0.280 \tag{6}$$

$(r^2 = 0.899, F_{2,98} = 438, P \ll 0.0001)$.

The slopes and intercepts for equations 5 and 6 do not differ significantly.

Taxonomic and ecological relationships

Andrews and Pough (1985) analyzed the effects of taxonomic and ecological groupings by examining standardized residuals (SR's) from a multiple regression of MR against mass, T_a, and metabolic state (active or resting). Mean SR's from each species were used for comparisons. This procedure is not valid, at least for the Boidae, because within-species slopes are generally similar among species but are significantly lower than the combined slope for all interspecific data, and because the mass coefficient 'a' (indicated by the adjusted mean Y from ANCOVA) increases as a function of log mass. Accordingly, we feel that a more reasonable index for intergroup comparisons is the regression predicting adjusted mean Y as a function of mass and T_a (Eq. 6). The mean SR's (average of the SR's from 3 T_a; Table 2) indicate how much the adjusted mean Y (and hence the $\dot{V}_{O_2}$) of different species deviate from predicted values based on
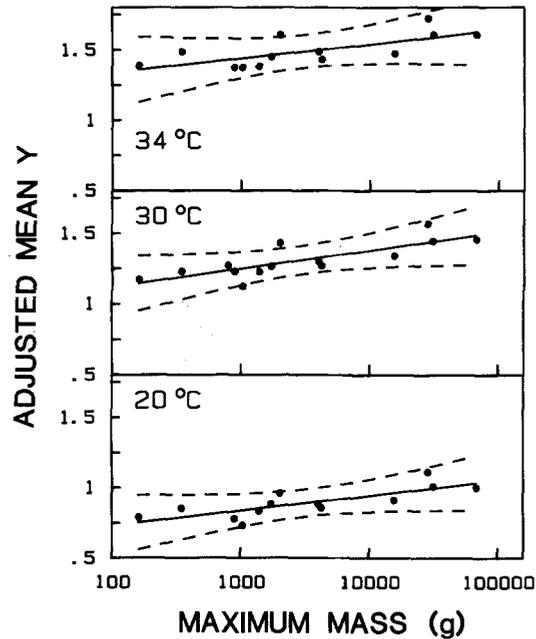

Fig. 4. Regressions of the adjusted mean Y (obtained from ANCOVA) as a function of mass (see text for details). Dashed lines are 95% confidence intervals for the regression line. Slopes are significantly different from zero at all T_a
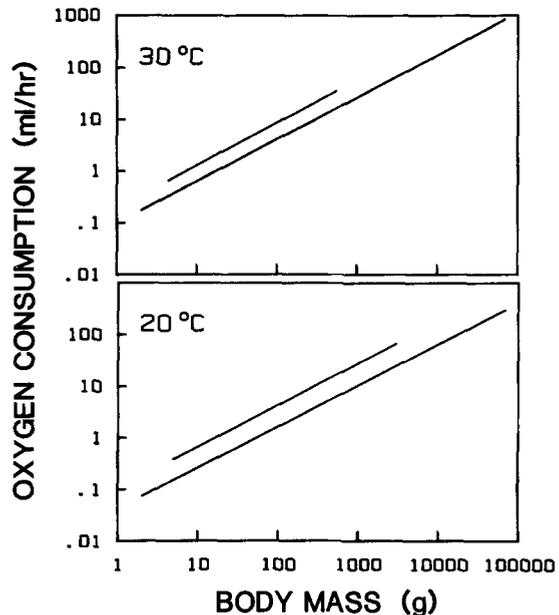

Fig. 5. Comparisons between metabolic rates ($\dot{V}_{O_2}$) of boids (this study) and other non-boid snakes (data from Andrews and Pough 1985). For both T_a, the upper line is for non-boids and the lower line is for boids. Line lengths indicate mass ranges. Slopes are parallel but intercepts differ significantly at both T_a

M_{max} and T_a. Differences in SR were analyzed with t-tests, or with the Kruskal-Wallis rank-order test if sample sizes were < 5 or if there were large differences in sample sizes.

Table 2. Metabolic rates (measured as oxygen consumption) expressed as standardized residuals (SR) from the multiple regression of adjusted mean Y vs T_a and the log of maximum mass (Eq. 6 in the text). The SR values are means for three T_a's; numbers of samples and individuals refer to the original data set. The ecological categories are: T terrestrial; F fossorial; A arboreal; S semiaquatic

Species	SR	n (samples)	n (individuals)	Ecological category
Pythons				
Python regius	−0.41	79	35	T
Python reticulatus	1.24	45	15	T
Python sebae	−0.09	30	10	T
Python molurus	−0.46	60	20	T
Python curtis	−1.00	24	8	T
Morelia spilota	1.00	24	8	T
Liasus amethistina	0.37	3	1	T
Liasus olivaceous	1.44	3	1	T
Liasus childrensii	0.36	18	6	T
Liasus fuscus	−0.15	6	2	T
Liasus albertsi	0.36	3	1	T
Aspidites melanocephalus	0.31	15	5	T
Calabaria reinhardtii	0.40	2	1	F
Bothrocheilus boa	1.80	9	3	T
Chondropython viridis	0.34	9	3	A
Boas				
Corallus enhydris	−0.88	21	7	A
Corallus caninus	−0.88	21	7	A
Boa constrictor	−1.01	105	35	T
Acrantophis dumerili	−0.54	21	7	T
Candoia carinatus	−1.53	42	14	T
Epicrates cenchria	0.26	35	12	T
Epicrates subflavus	−0.52	12	4	T
Epicrates chryogaster	−0.45	3	1	T
Epicrates fordi	−1.41	6	2	T
Epicrates striatus	−0.40	12	4	T
Eunectes notaeus	0.74	6	2	S
Eunectes murinus	0.86	6	2	S
Eryx colubrinus	−0.18	27	9	F
Eryx conicus	−2.59	9	3	F
Eryx miliaris	1.32	9	3	F
Lichanura trivirgata	0.26	35	12	T
Charina bottae	0.63	7	3	F
Tropidophis melanurus	0.41	12	4	T
Taxonomy uncertain				
Loxocemus bicolor	−0.03	3	1	F

As a group, pythons have significantly higher $\dot{V}_{O_2}$ than boas (mean SR = 0.368 ± 0.125 vs −0.298 ± 0.142, P = 0.0008, t-test). Significant differences in SR also occur among the 7 genera of pythons (P = 0.015, Kruskal-Wallis test) and among the 10 genera of boas (P = 0.004, Kruskal-Wallis test). [The taxonomic affinities of *Loxocemus bicolor* are uncertain, so we did not include it in these analyses. However, inclusion of *L. bico-*

lor into either the boas or the pythons has insignificant effects on the results.] Large differences in SR can be found within a single genus. For example, for 5 species in the genus *Python* the mean SR's range from −1.00 to 1.24 (P = 0.012, Kruskal-Wallis test) and for 3 species in the specialized fossorial genus *Eryx* the range is −2.59 to 1.32 (P = 0.027, Kruskal-Wallis test). In contrast, some equally large genera are relatively uniform; significant differences in SR were lacking among 5 species in the genus *Epicrates* and 5 species in the genus *Liasus* (P = 0.16 and 0.20, respectively; Kruskal-Wallis test).

Analysis of the influence of ecological factors on boid metabolic rates is hampered by poor knowledge of the natural history of most species. We divided the species in our sample into 4 ecological categories based on morphological and behavioral characters: fossorial (*Eryx, Calabaria, Charina, Loxocemus*), arboreal (*Corallus, Chondropython*), semiaquatic (*Eunectes*), and terrestrial (all other genera). The mean SR's from these groups (−0.10, −0.48, 0.80, and 0.02, respectively) differ significantly (P = 0.032, Kruskal-Wallis test). However, we also noted large and significant differences among the 6 fossorial species (mean SR's from −2.59 to 1.32, P = 0.02, Kruskal-Wallis test) and the 23 terrestrial species (mean SR's from −1.38 to 1.78, P = 0.0002, Kruskal-Wallis test).

Morphological factors may also influence metabolic rates. We investigated this possibility by dividing the species which satisfied our regression requirements (Table 1) into three classes based on a qualitative judgement of body form: heavy-bodied (*Python curtis, P. regius, P. molurus, Boa constrictor, Acrantophis dumerili*), slender (*Morelia spilota, Corallus caninus, C. enhydris*), and intermediate (all other species in Table 1). No significant differences were observed at any T_a among these classes in either the mass coefficient or the mass exponent.

Discussion

Temperature effects and respiratory exchange ratios

In terms of their basic thermal physiology, boids (even very large individuals) are typical ectotherms. Within the 20–34 °C temperature range, the Q_{10}'s and respiratory exchange ratios of boid snakes closely resembled those of other reptiles. Little or no change in Q_{10} was observed at high (30–34 °C) versus low (20–30 °C) temperatures. Respiratory exchange ratios were indicative of me-

tabolism based on fat and protein substrates. The cause of the small but significant increase in RE with increasing T_a is unclear. It may reflect slow changes of CO_2 concentration in tissue fluid following temperature changes. Stinner (1982) reports rapid changes in the RE of gopher snakes (*Pituophis melanoleucus*) during equilibration to increased T_a, followed by slightly but significantly elevated RE for at least 6 days. These shifts were due to changes in $\dot{V}_{CO_2}$, rather than $\dot{V}_{O_2}$ (which stabilized relatively quickly).

Allometric data

Our analyses of pooled interspecific data yielded results (Eq. 2) remarkably similar to those of several previous investigations of other reptilian groups (Bennett and Dawson 1976, all reptiles; Nagy 1982, iguanid lizards; Andrews and Pough 1985, squamates). For all four studies, the value of 'b' in the equation $MR = aM^b$ was within the range 0.77–0.83. We found no evidence to support the contention of Vinegar et al. (1970) and Dmi'el (1972) that 'b' is temperature dependent in snakes, at least within the range of T_a used here.

It should be emphasized that while Eq. (2) is useful for comparisons with large intergroup differences compared to within-group variation (e.g., boids vs lizards), it is not appropriate for comparisons within the Boidae. Here, within-species slopes are lower than the interspecific slope and mass coefficients differ significantly, partly as a function of mass.

Based on a small sample of boids, Andrews and Pough (1985) tentatively concluded that this family has unusually low resting metabolic rates relative to those of squamates in general. Our results confirm this suggestion. We calculate that boids as a group have resting metabolic rates 62% lower than those of other squamates, based on our Eq. (2) and Eq. (2) of Andrews and Pough (1985). Bennett and Dawson (1976), again working with a limited data set, did not believe that resting metabolism in boids differed from that of other snakes. Using covariance analysis, we compared our results for boids to 26 measurements on 25 species of non-boid snakes (mass range 5.0–2680 g, data from Andrews and Pough 1985). All data were obtained at 20 °C. The regression slopes do not differ (Fig. 4a), but at any mass the metabolic rates of boids are about 56% lower than those of other snakes ($F_{1,259} = 201$, $P \ll 0.0001$). A similar comparison using data taken at 30 °C indicates that boid metabolism is reduced by 39%

($F_{1,252} = 57$, $P \ll 0.0001$, Fig. 4b), but the data set for non-boids is small ($n = 11$, mass range 4.4–548 g).

Several aspects of allometric comparisons and metabolic scaling are controversial. Currently, considerable attention is focused on two major treatments of the theoretical relationship between mass and metabolism. The first is the 'elastic similarity' model, proposed by McMahon (1973). He argued that considerations of mechanical support (especially during locomotion) and muscle biophysical properties require that metabolism increase as the 0.75 power of mass. The second model of 'mass-independent' scaling was developed by Heusner (1982). Heusner worked from principles of dimensional analysis and proposed that in physiologically 'similar' animals, metabolism should scale as the 0.67 power of mass. Departure from a slope of 0.67 is indicative of 'non-similarity'. Empirical observations that the mass exponent approximates 0.75 for a number of interspecific data sets are (according to Heusner 1982) statistical artifacts derived from improperly forcing a regression through a number of independent within-species data sets. He suggests that the within-species slope is in fact 0.67, but that large species have higher intercepts than small species. Feldman and McMahon (1983) reanalyzed empirical data and concluded that 0.67 and 0.75 are both statistically valid mass exponents: the former for within-species slopes and the latter for interspecific comparisons. Dmi'el (1986), using his own measurements on a colubrid (*Spalerosophis diadema*) and published data on 9 other species, suggested that both the intra- and interspecific mass exponents are similar in snakes (0.65 and 0.67, respectively).

Our data on the Boidae do not completely conform to either theoretical prediction, or to Dmi'el's (1986) analysis. The overall mass exponent for boids of 0.806 (Eq. 2) is significantly greater than both 0.67 and 0.75. The mean of within-species 'b' values was 0.732, which is significantly different from 0.67 but not from 0.75. The latter observation is most consistent with McMahon's original 'elastic similarity' model (McMahon 1973). However, our results confirm two important suggestions of Heusner (1982): (1) mass exponents within species are lower than those for interspecific comparisons, and (2) regression equations for different species have common slopes but different intercepts, with larger species having larger intercepts. With the exception of one of 14 species at two of three T_a (i.e., 2 of 42 regressions), all of our within-species 'b' values did not differ significantly, and the mean intraspecific 'b' value was significantly

less than the interspecific 'b'. Perhaps more importantly, values of the adjusted mean Y (an index of the mass coefficient "a") in a covariance analysis of log-transformed data show significant increases of approximately 10–11% for every 10-fold increase in M_{max} (Fig. 4, Eqs. 5 and 6). This is equivalent to a 25–29% change in 'a' for every 10-fold change in M_{max}.

Our results are perhaps the best currently available evidence for similar within-species slopes but different mass coefficients among a variety of species showing large ranges of body mass. Nevertheless, for several reasons we urge that our conclusions be interpreted cautiously. First, we were able to perform regression analysis on only a modest number of species. Second, sample sizes and mass ranges were relatively small for some of the species that did meet our criteria for use in the analysis. Third, even though covariance procedures did not indicate significant differences in slope, the mass exponents of different species showed considerable variation (from 0.56 to 0.89). We suspect that some of this variation may reflect real differences in slope that might be revealed if additional data were available for some of the species with small sample sizes and/or mass ranges. Finally, the regressions showing significant increases in adjusted mean Y with increasing mass were based on a mass index that was selected somewhat arbitrarily as the mass of largest specimen we handled of a given species. Conceivably, other indices of mass might be more appropriate; for example, the largest mass known to be attained by a species, or the mean mass of reproductive adults.

In their extensive review of resting metabolism in squamates, Andrews and Pough (1985) emphasized the importance of ecological factors, such as foraging mode and food type, as opposed to phylogenetic relationships in determining metabolic rates. Within the Boidae, we found few indications that ecological considerations were more important than phylogeny, or vice versa, in determining metabolism. The four ecological groups we defined did differ metabolically, according to our analysis. However, as much or more variance occurred within ecological categories as between them (see Table 2). We were particularly impressed with the degree of metabolic divergence that can occur even within genera that appear to be ecologically homogeneous. For example, considerable variation was found among three species in the specialized fossorial genus *Eryx,* and among five species in the genus *Python.* It is possible that some of the metabolic differences within ecological categories may reflect underlying ecological or behavioral diver-

gence, but this hypothesis cannot be tested with available data.

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