Variation in metabolic rates of a lizard: use of SMR in ecological contexts

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Summary

Standard metabolic rates (SMR) are frequently used to estimate the maintenance costs of free-ranging ectotherms. Ecologically relevant sources of variation in the rate of metabolism not accounted for by SMR (e.g. nutritional status, time of day) can significantly affect estimates of the maintenance costs of free-ranging ectotherms. This study reports the effects of temperature, sex, population and time of day on the rate of oxygen consumption of resting *Sceloporus merriami*. The rate of oxygen consumption of fasted lizards (standard conditions) was strongly dependent on temperature, sex and population, and it was not constant over the inactive period (scotophase). Average rates of oxygen consumption were as much as four times higher than the minimal rate (SMR) for all individuals. Our results indicate that the cost of maintenance of *S. merriami* calculated using SMR is from two to four times lower than the cost estimated from the average rates of oxygen consumption of fasted lizards. These results have important implications for ecologists interested in comparing lizard productivity with similarly sized endotherms. Rates of oxygen consumption at 32 and 37°C increased by as much as 37% after lizards were fed 10–15% of their live mass in crickets. This effect was not observed at 25°C. Because oxygen consumption is not constant over the scotophase and because free-ranging lizards usually have food in their guts, we conclude that when estimating the energy budgets of free-ranging lizards ecologists should use the rate of oxygen consumption averaged over the scotophase of fed animals, not SMR.

Key-words: Ecological energy budget, maintenance metabolism, oxygen consumption, *Sceloporus merriami*

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Introduction

The metabolic rate of reptiles is affected by a number of extrinsic and intrinsic factors including temperature, diel and seasonal rhythms, level of activity and sex. The magnitude of these effects and others has been quantified in physiological laboratory studies for a variety of reptiles (see review in Bennett & Dawson 1976). Due to the variation in metabolic rate introduced by these factors, physiologists have found it useful to compare the metabolic rates of reptiles measured under a set of standard conditions. The standard metabolic rate (SMR), as it has come to be known, is defined as the minimal rate of metabolism of a post-absorptive (fasted), resting animal measured in a dark chamber during the inactive portion of its diel cycle (Kleiber 1975). It has been suggested that SMR is indicative of maintenance costs and that it is the most useful measure for the comparison of basal metabolic rates between different animals (Bennett & Dawson 1976). There is no doubt that SMR is a valuable tool when making taxonomic and physiological comparisons (Bennett 1982). However, regardless of the value of SMR in those contexts, we believe that SMR provides an unrealistic estimate of the cost of 'maintenance' for free-ranging ectotherms. Indeed, Bennett & Dawson (1976) emphasized that the particular question posed by any given study should dictate the conditions under which metabolism is measured.

SMR is a poor estimator of resting maintenance expenditure because the conditions under which it must be measured are unlikely to be representative of the conditions experienced by inactive, free-ranging lizards (Waldschmidt, Jones & Porter 1987). In ecological studies, maintenance costs of free-ranging lizards (e.g. ecological maintenance costs) usually refer to the metabolic expenditure of an inactive animal during the inactive portion of its diel cycle (scotophase). This is the component of total energy

expenditure that Congdon, Dunham & Tinkle (1982) refer to as the resting maintenance expenditure. We follow the terminology of Congdon *et al.* (1982) in defining the resting maintenance expenditure as the metabolic expenditure of free-ranging animals during the scotophase. Thus to measure the resting maintenance expenditure of *Sceloporus merriami* Stejneger our experiments must attempt to mimic the ecological conditions of free-ranging animals. Furthermore the variation in metabolic rate that SMR was designed to avoid must be included when estimating the ecological maintenance costs. For example, SMR is measured not on fed, but on post-absorptive animals. Free-ranging lizards, however, usually have food in their guts (e.g. Tinkle 1967; Parker & Pianka 1975; Best & Gennaro 1984). The absorptive state (i.e. fasted or fed) has been shown to significantly increase metabolic rate in at least two species of lizard (Roberts 1968; Cragg 1978) as well as in other reptiles (Rapatz & Musacchia 1956; Coulson & Hernandez 1973; Gatten 1980). Although not common, some ecologists have recognized the importance of using non-fasted animals in metabolic experiments (e.g. Anderson & Karasov 1981). Finally, because SMR is defined as the minimal rate of metabolism during the scotophase, it will poorly estimate the resting maintenance expenditure to the extent that the metabolic rate of lizards during the scotophase varies above its minimum value.

Conditions under which free-ranging lizards are found are different from the conditions under which SMR is measured, and variation in metabolic rate during the scotophase are sources of variation in metabolic rate relevant to ecological studies which attempt to partition total expenditure into 'maintenance' or 'resting' *vs* 'active' components. For example, Bennett and Gleeson (1979), Congdon, Ballinger & Nagy (1979) and Bennett & Gleeson (1976) measured the energetic costs of specific activities (i.e. foraging, locomotion) in free-ranging reptiles and compared them with maintenance costs estimated from SMR. These comparisons of 'resting' *vs* 'active' expenditure do not reflect the true relative expenditure when laboratory conditions under which SMR is measured are not the same as those of free-ranging animals. In spite of the advances made in the measurement of total energy expenditure by free-ranging animals using the doubly labelled water technique (e.g. Nagy 1982), our ability to reliably partition total expenditure is still limited by the methods involved in estimating maintenance expenditure.

In this paper, we describe an experiment in which we measured the effects of several ecologically relevant variables on the metabolic rate of the lizard *S. merriami*. We then integrate the metabolic rate of fed animals over the scotophase to estimate the resting maintenance expenditure. Our estimate of the cost of maintenance is then compared with an estimate of the cost of maintenance calculated using SMR. Specifically, our experiment addressed the following questions:

1. Are there differences in metabolic rates among ecologically distinct populations of a single species of lizard?
2. Does the metabolic rate differ between the sexes which often exhibit different behaviours?
3. Are the effects of feeding on oxygen consumption temperature dependent?

Table 1. Average SVL and masses of animals used in experiments. Variances are in parentheses and *n* is the sample size

Site	Sex	SVL	Mass	*n*
BOQ	F	51 (0·5)	3·43 (0·31)	4
	M	52 (4·5)	4·50 (0·55)	4
GVH	F	50 (0·7)	3·33 (0·22)	4
	M	53 (1·2)	4·68 (0·58)	4

Materials and methods

ANIMALS AND MAINTENANCE

During the summer of 1986, we measured the metabolic rates of Canyon lizards *(S. merriami)* from two sites in Big Bend National Park, Texas. During a single day, eight adult lizards (four male and four non-gravid female) were captured in the Grapevine Hills (elevation 1036 m) and a second group of four males and four non-gravid females were taken from a side canyon near Boquillas Canyon [elevation 560 m; see Dunham (1978) and Dunham, Grant & Overall (1989) for details about the sites]. The average body mass of the male lizards we captured was slightly larger than that of the females (Table 1). Males were significantly heavier than females at each site (two-way ANOVA, $P<0·01$), but the lack of a significant interaction between site and sex ($P>0·6$) indicates that differences between male and female mass were comparable between sites. Each lizard was housed individually in one of four equally sized compartments within four 24×12 inch (approx. 609×305 cm) aquaria, which were partially filled with sand. The sand substrate was kept moist by periodically sprinkling with water.

Metabolic and feeding experiments were conducted in a research facility in Big Bend National Park. There was only a 2-day delay between capture and testing. Ambient temperatures inside the facility varied daily from highs of 37·0 °C to lows of approximately 28·0 °C. These temperatures are within the range of body temperatures selected by active *S. merriami* in the field (Grant & Dunham 1988). Lizards were maintained under their natural photoperiod without artificial illumination.
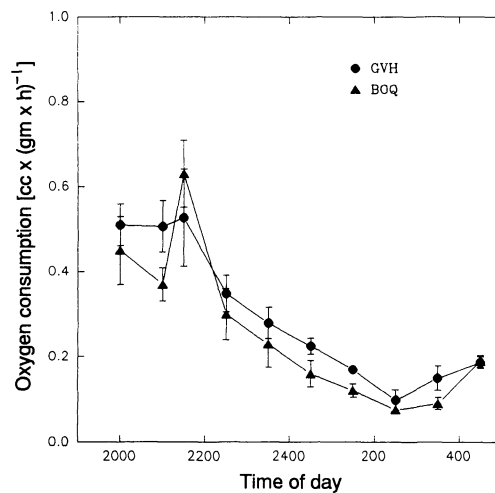
Fig. 1. Mass specific oxygen consumption during the scotophase of fasted male *Sceloporus merriami* from Boquillas and Grapevine at 32 °C: circles, Grapevine males; triangles, Boquillas males.

EXPERIMENTAL DESIGN

We used a repeated measures ANOVA (Winer 1971) to determine the effects of body temperature, site, time, sex and diet on oxygen consumption. We tested male and female lizards from both sites (Grapevine and Boquillas) at three temperatures (25, 32 and 37 °C), at hourly intervals between 21.30 and 05.30 h, under both fed and fasted conditions. Free-ranging lizards from both sites were inactive (i.e. they were in crevices or burrows) after approximately 21.00 h: they typically emerged between 07.30 and 10.00 h during the summer (Grant 1988). Also, during this time of year, the average night-time crevice temperature is approx. 31·5 °C (B. Grant, unpublished data). In preparation for the experiments, all lizards were fasted for 2 days so that most food would be cleared from their digestive tracts (Waldschmidt, Jones & Porter 1986). After fasting for 2 days, one-half of the lizards were randomly assigned to a fasting treatment and the other half to a feeding treatment. We then measured the metabolic rates of fasted lizards on the evening of their second day of fasting. Lizards in the feeding treatment were allowed to consume freely a single cricket at midday each day for 2 days after the initial 2-day fasting period. Each cricket weighed 10–15% of the lizard's live mass and was always consumed immediately. We measured the metabolic rates of lizards in the feeding treatment on the evening of their second day of feeding. Therefore, we measured rates of oxygen consumption of lizards under not only standard conditions (fasted and resting in dark chambers during their scotophase), but also under conditions resembling those of free-ranging lizards. The metabolic rates of fed lizards are hereafter referred to as the maintenance metabolic rates (MMR; Anderson

& Karasov 1988) to distinguish them from standard metabolic rates. These data were analysed using the statistical software BMDP2V (Brown 1977).

After measuring metabolic rate, lizards were returned to their aquaria and immediately cycled to the alternative feeding treatment. In this way, each lizard was tested at each of the three temperatures both in a fasted and fed condition in a randomly assigned order.

To measure oxygen consumption we used a closed manometric, constant pressure system with vertical manometers as null indicators (McDonald 1976; Williams & Prints 1986). Ascarite and Drierite absorbed CO_2 and water vapour, respectively. Lizards were placed into metabolic chambers at 18.00 h to allow time for temperature equilibration. We measured the amount of oxygen consumed by injecting just enough oxygen into the closed chambers to equalize the height of fluid in the manometers. Although this technique is sensitive to small-scale temperature fluctuations (McDonald 1976), the chamber temperatures never fluctuated by more than ±0·1 °C. Chamber temperature was controlled with a circulating water-bath and was measured with a thermocouple connected to an Omega model 871 digital thermocouple reader (accurate to ±0·1 °C). All oxygen consumption rates were corrected to STP using temperatures and barometric pressures measured in the research facility during the experiment. Barometric pressure was measured with a Selsi compensated barometer.

Results

The oxygen consumption of both fed and fasted lizards was variable during the scotophase, regardless of the site of origin, sex, or temperature. For example, the oxygen consumption of males from Grapevine and Boquillas at 32 °C (Fig. 1) was initially high and then steadily declined to a minimum approximately 2 h before the end of scotophase. Then near dawn, lizards exhibited an increase in oxygen consumption even though they were sealed inside dark metabolic chambers and were motionless. The shape of this profile of oxygen consumption *vs* time of day was representative for both sexes from both sites and is responsible for the highly significant time effect in the overall analysis (Table 2, $P < 0.001$).

Although oxygen consumption tended to decrease to a minimum and then increase during the scotophase the rate of oxygen consumption and the rate of decrease and increase in consumption with time depended upon sex, site and temperature. For example, Figs. 2 and 3 show that at 25 °C males and females at both sites exhibited similar rates of oxygen consumption at every time interval. But, at 37 °C (Fig. 3) GVH males and females have indistinguishable rates while at BOQ (Fig. 3), male oxygen
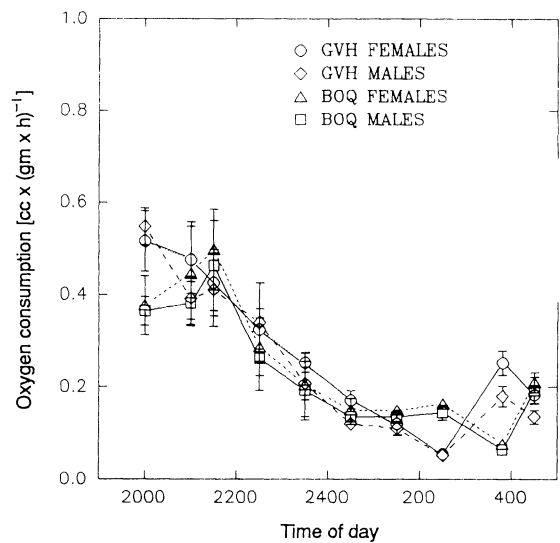
Fig. 2. Mass specific oxygen consumption during the scotophase of fasted male and female *Sceloporus merriami* from Boquillas and Grapevine at 25 °C: circles, Grapevine females; diamonds, Grapevine males; triangles, Boquillas females; squares, Boquillas males. Note that differences in rates of oxygen consumption are indistinguishable for most time intervals. Error bars are ±1 SE.

consumption was higher than female oxygen consumption at every time interval >21.00 h. This site-, sex- and temperature-dependent response in the rate of oxygen consumption during the scotophase explains the significant two-, three- and four-way interaction terms (Table 2). Obviously, males and females from either within or among populations do not necessarily respond similarly to temperature.

Table 2. Results of a repeated measures ANOVA on SMR

Source	df	Mean square	F	P†
Site	1	0·082	0·61	NS
Sex	1	0·005	0·04	NS
Site×sex	1	0·007	0·05	NS
Error	12	0·135		
Temp	2	0·533	23·92	***
Temp×site	2	0·002	0·11	NS
Temp×sex	2	0·073	3·29	NS
Temp×site×sex	2	0·010	0·45	NS
Error	24	0·022		
Time	9	1·116	106·11	***
Time×site	9	0·026	2·49	NS
Time×sex	9	0·012	1·22	NS
Time×site×sex	9	0·003	0·33	NS
Error	108	0·010		
Temp×time	18	0·027	7·70	***
Temp×time×site	18	0·016	4·63	***
Temp×time×sex	18	0·005	1·68	NS
Temp×time×site×sex	18	0·007	2·24	*
Error	216	0·003		

$*P<0.05$; $***P<0.001$. $r^2=0.759$.

†P-values for factors involving repeated measures are determined using the Huynh-Feldt correction.

Furthermore, male and female lizards from BOQ and GVH did not necessarily respond to feeding in the same way. In order to assess directly the effects of feeding on metabolic rates we subtracted each lizard's oxygen consumption under fasted conditions from its corresponding oxygen consumption under fed conditions at a given time and temperature. The results of these calculations were then analysed with the repeated measures ANOVA described above. A plot of these differences (Fig. 4) shows that females at both sites exhibited the greatest response to feeding; the magnitude of the response was temperature dependent and greatest at 37 °C. Males at both sites also showed the greatest increase in oxygen consumption over fasted levels at 37 °C. However, the total increase in oxygen consumption (over the whole scotophase) of fed males above fasted males at 37 °C was only half that for females ($1·2$ cc O_2 $gm^{-1}\pm0·3$ GVH male *vs* $2·45$ cc O_2 $gm^{-1}\pm0·1$ GVH female). Significant higher-order interactions (Table 3) indicate that the difference in oxygen consumption between fed and fasted *S. merriami* cannot be understood from a consideration of main effects alone.
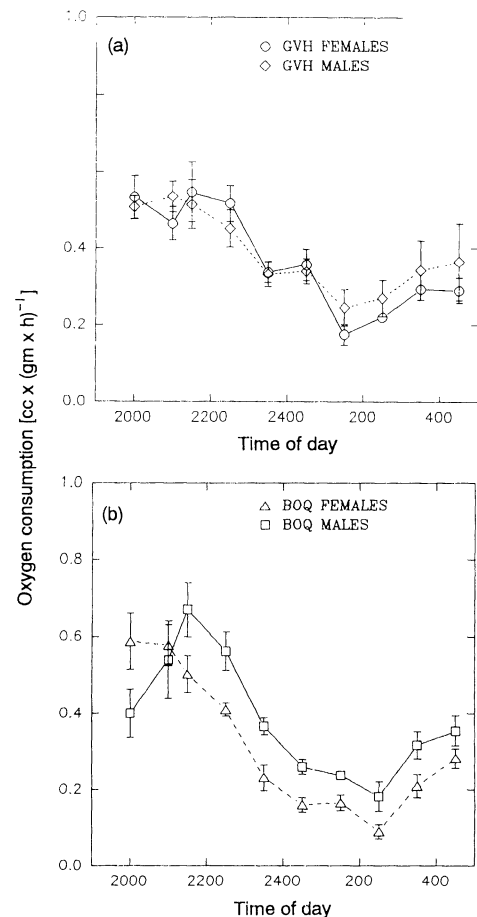
Fig. 3. Mass specific oxygen consumption during the scotophase of fasted male and female *Sceloporus merriami* (a) Grapevine and (b) Boquillas at 37 °C. Symbols as in Fig. 2. Error bars are ±1 SE.
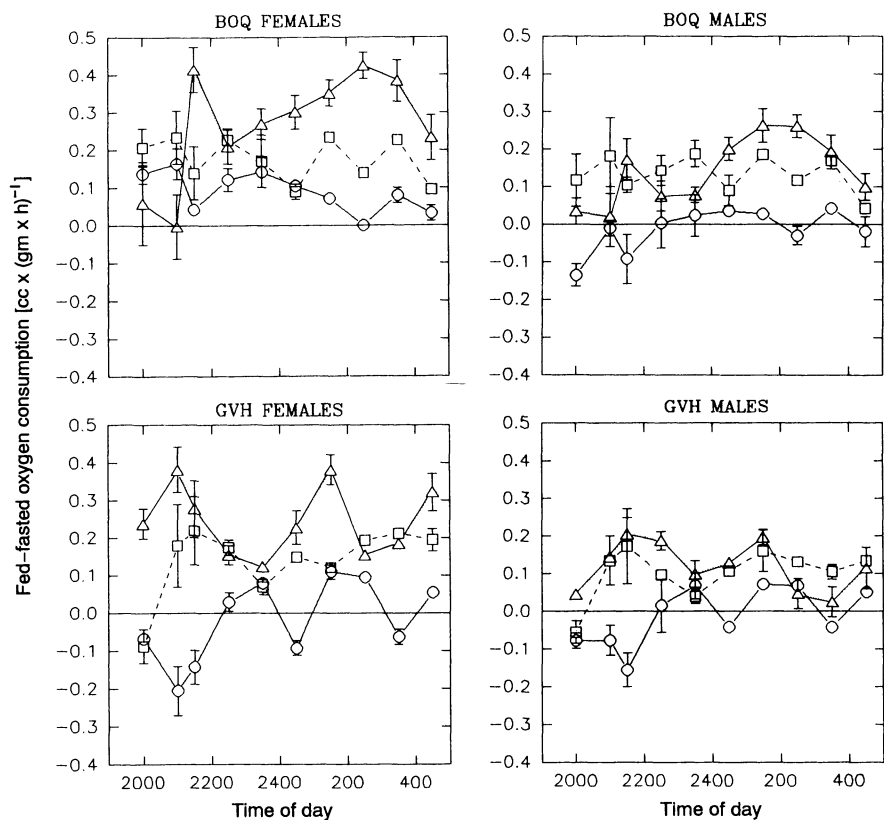
Fig. 4. Mass specific oxygen consumption of fasted animals subtracted from mass specific oxygen consumption of fed animals at 25, 32 and 37°C: circles, 25°C; squares, 32°C; triangles, 37°C. Error bars are ±1 SE.

Population- and sex-specific oxygen consumption rates averaged over the entire scotophase are shown for both fed and fasted lizards in Table 4. Notice that for a given temperature and nutritional status, the average rates of oxygen consumption over the scotophase are often indistinguishable among male and female lizards from the two different sites.

Discussion

We have demonstrated that oxygen consumption by *S. merriami* is a complex function of temperature, time, site, sex and nutrition. At least three of the above results have potentially important consequences for ecologists interested in partitioning the energy budgets of free-ranging lizards. First, oxygen consumption of *S. merriami* is not constant over the scotophase (Fig. 2). Second, there is often a strong, temperature-dependent increase in oxygen consumption for fed lizards (Fig. 4). Finally, interactions among the main effects in our experiment (e.g. site, sex, temperature) indicate that the oxygen consumption of a particular group of *S. merriami* cannot be predicted by a single additive combination of those variables.

Below, we discuss these consequences in detail and then identify the variables ecologists must measure in order to estimate realistically the maintenance costs of free-ranging lizards.

Table 3. Results of a repeated measures ANOVA on MMR−SMR

Source	df	Mean square	F	P†
Site	1	0·148	8·19	*
Sex	1	0·621	34·19	**
Site×sex	1	0·045	2·50	NS
Error	12	0·018		
Temp	2	1·399	55·64	***
Temp×site	2	0·011	0·44	NS
Temp×sex	2	0·086	3·42	*
Temp×site×sex	2	0·042	1·67	NS
Error	24	0·025		
Time	9	0·062	8·32	***
Time×site	9	0·026	3·55	***
Time×sex	9	0·003	0·43	NS
Time×site×sex	9	0·004	0·65	NS
Error	108	0·007		
Temp×time	18	0·035	4·33	***
Temp×time×site	18	0·064	8·03	***
Temp×time×sex	18	0·005	0·73	NS
Temp×time×site×sex	18	0·015	1·89	*
Error	216	0·008		

$*P<0.05$; $**P<0.01$; $***P<0.001$. $r^2=0.673$.
†P-values for factors involving repeated measures are determined using the Huynh-Feldt correction.

VARIABLE O_2 CONSUMPTION RATES

SMR is the minimal rate of oxygen consumption measured during the scotophase; when a circadian

Table 4. Mass specific oxygen consumption rates $[cc \times (gm \times h)^{-1}]$ averaged over the scotophase for lizards under standard conditions and those with food in their guts

Fasted											
BM25	GM25	BF25	BM32	GF25	GM32	BF32	BF37	GF32	GF37	BM37	GM37
0·234	0·249	0·256	0·261	0·277	0·300	0·303	0·322	0·332	0·373	0·389	0·391

Fed											
BM25	GM25	GF25	BF25	BM32	GM32	GF32	BF32	GM37	BM37	BF37	GF37
0·218	0·238	0·257	0·346	0·395	0·403	0·475	0·480	0·510	0·531	0·587	0·681

B, Boquillas; G, Grapevine; M, Male; F, Female; numbers indicate the temperature treatment. Underlined means are indistinguishable at $P < 0·05$ (Ryan's test, Day & Quinn 1989).

cycle is present, as was evident in this study, SMR will underestimate the total expenditure during the scotophase. The average rate of oxygen consumption of a lizard during its scotophase (obtained by averaging oxygen consumption measured at regular intervals throughout the scotophase) is therefore a more useful measure for ecologists interested in calculating metabolic expenditure during the scotophase. Ecologists could simply multiply the average consumption rate for the scotophase by its length and obtain the total expenditure for the period.

Obviously, the discrepancy between SMR and the average rate of oxygen consumption will depend entirely upon the strength of the circadian cycle. For *S. merriami*, the discrepancy is rather large. For example, fasted BOQ males averaged $0·24 \pm 0·082$ cc O_2 $(gm \times h)^{-1}$ over their 10-h scotophase (25°C); during the same period, the minimal rate (SMR) was only $0·065 \pm 0·018$ cc O_2 $(gm \times h)^{-1}$. The difference between SMR and the average rate of oxygen consumption rate in this case is approximately 370%. Clearly, a large difference between SMR and the average rate will affect estimates not only of the total oxygen consumption for the scotophase, but also of the partition of total metabolic expenditure into resting and active components. We compared estimates of the total oxygen consumption during scotophase of an average-size male from GVH obtained from its predicted SMR (from an interspecific regression; e.g. Andrews & Pough 1985), from its measured SMR (this study) and from the measured values (Table 5). Estimates based on SMR (whether from a regression or measurement) are from two to four times lower than the actual total consumption obtained by summing the hourly consumption rates measured during the scotophase. If the diel cycle in oxygen consumption is a general phenomenon in lizards (see Waldschmidt *et al.* 1987), our data suggest that studies that relied on SMR to predict oxygen consumption during the scotophase have underestimated maintenance costs by a factor of two to four.

To demonstrate how a diel cycle in oxygen consumption can affect estimates of the maintenance components of lizard energy budgets derived from SMR, we estimated the maintenance costs of *S. merriami* during its scotophase using measured values from our study and compared it with a published estimate based on the predicted SMR for this species (Congdon *et al.* 1982). Congdon *et al.* (1982) constructed a 3-year energy budget for several species of lizard including *S. merriami*. We recalculated their estimate of resting maintenance expenditure assuming the same activity season length, and time- and temperature-specific schedules of activity (Congdon *et al.* 1982, appendix iii). Congdon *et al.* (1982) calculated the resting maintenance expenditure of *S. merriami* to be 60–78 kJ year^{-1}. When we substituted the average oxygen consumption for fasted Grapevine males for the SMR in the calculation, the total resting expenditure we calculated was 151 kJ year^{-1} approx. 1·9–2·5 times the published values based on SMR. In our calculation we assumed, as did Congdon *et al.* (1982) for SMR, that average oxygen consumption rates did not vary

Table 5. Comparison of total oxygen consumption rates (over the 10-h scotophase) based upon measured SMR (this study), predicted SMR based upon Andrews & Pough (1985) (4·65-g lizard) and actual total consumption for an average size male lizard from the GVH site. All values are cc $O_2 \times gm^{-1}$

Temperature (°C)	Predicted total* (regression)	Predicted total using SMR*	Actual total†
25	0·880	0·650	2·439
32	1·630	0·750	3·003
37	2·530	1·780	3·904

*Total calculated as the SMR×10h (scotophase length).
†Actual total is the sum of the measured hourly consumption rates for the 10-h scotophase of fasted male GVH lizards.

seasonally. This assumption needs to be tested because studies that have examined seasonal variation in the metabolic rate of reptiles show that winter metabolism may be higher, lower or unchanged from summer metabolism (Waldschmidt *et al.* 1987).

We believe that the difference between the estimate of maintenance expenditure based upon average oxygen consumption *vs* SMR, argues strongly against the use of SMR in this ecological context. This is especially evident when we consider that 151 kJ is roughly equal to published estimates of *S. merriami's* total maintenance budget (resting plus activity expenditure) (Table III, Congdon *et al.* 1982).

THE EFFECT OF DIGESTION

The average oxygen consumption of fasted *S. merriami* during their scotophase is often substantially below the average O_2 consumption of fed *S. merriami* (Table 4). Therefore, if *S. merriami* usually have food in their guts during inactivity, then the oxygen consumption averaged over the scotophase of fed lizards would provide a better estimate of the cost of maintenance during inactivity. Using the same assumptions as in the above calculations, fed Grapevine males would have a seasonal expenditure of about 147 kJ for resting maintenance. This value is very similar to the estimate for fasted Grapevine males (151 kJ) and reflects a slightly negative though insignificant response in oxygen consumption to feeding for male *S. merriami* from the Grapevine population at 25 °C (Fig. 4). We emphasize, however, that the effect of feeding is population and sex dependent and that the same comparison for fasted BOQ females *vs* fed BOQ females would result in 143 kJ year^{-1} (fasted) *vs* 223 kJ year^{-1} (fed) — an increase of 56%.

INTERACTIONS AMONG FACTORS

The previous example clearly illustrates how a complex interaction between sex, population and food consumption can significantly affect estimates of maintenance costs in *S. merriami*. Specifically, the effect of feeding on oxygen consumption in *S. merriami* cannot be predicted from the average responses of *S. merriami* at 25 °C; one must consider the sex and population as well. It is clear from Tables 2 and 3 that there are many statistical interactions among the main effects in our analyses of SMR and fed–fasted rates of oxygen consumption. Consider the significant interaction among population, time, sex and temperature for SMR (Table 2). This interaction indicates that there are differences in time- and temperature-dependent oxygen consumption between sexes within one site (BOQ at 37 °C, Fig. 3a) and not the other (GVH at 37 °C, Fig. 3b) illustrating

that oxygen consumption may be highly variable within a single species and population. The statistical significance of these interactions among time, population, sex and temperature, make the use of interspecific regressions of SMR on body size (Bennett & Dawson 1976; Andrews & Pough 1985) of questionable value to ecologists interested in ecological energy budgets. To the extent that interactions among time, population, sex, temperature and nutritional status exist in other species, these effects will have to be measured; a single regression equation may no longer be sufficient to estimate the differences between populations.

IMPLICATIONS FOR ECOLOGISTS

Comparisons of SMR are of general interest in physiological studies and have been used frequently to identify variation in basal levels of aerobic metabolism among species and higher taxa (e.g. Bennett & Dawson 1976). Furthermore, several ecological correlates of this variation have been identified (Andrews & Pough 1985). Because SMR has been measured for a wide variety of species, it is often used by ecologists to partition energy budgets into resting and active components. However, we believe that the results of our experiment argue strongly against this use. The two most important results of our experiment are that a diel cycle in oxygen consumption and a significant increase in oxygen consumption due to feeding can lead to large underestimates of the costs of maintenance of *S. merriami*.

We recognize at least two areas where these potential underestimates can lead to erroneous conclusions. First, in studies that utilize isotopes to measure field metabolic rates (FMR), subtraction of SMR from the total measured expenditure may severely overestimate the amount of energy lizards spend on activity. Second, when energy budgets are partitioned so that patterns of expenditure can be compared between animals with widely different strategies (i.e. ectotherms *vs* endotherms; e.g. Turner, Medica & Kowalewsky 1976), differences will be severely exaggerated.

While we are critical of the use of SMR in these ecological contexts, we do believe that the comparisons described above can be meaningfully made. In the most cases, we believe that substituting the average oxygen consumption over the scotophase of fed lizards for SMR will lead to much more realistic estimates of the cost of maintenance of free-ranging lizards. The results shown in Table 4 support this conclusion because, within any of the three temperatures tested, average oxygen consumption rates of fed male and female lizards from both sites are usually indistinguishable. However, we advocate detailed studies that examine the effects of temperature, sex and feeding on metabolic rates through the scotophase. We believe that ecologists

must measure the effects of variables that significantly influence metabolic rate to estimate realistically the resting metabolic expenditure of free-ranging lizards.

References

Anderson, R.A. & Karasov, W.H. (1981) Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* **49**, 67–72.

Anderson, R.A. & Karasov, W.H. (1988) Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecological Monographs* **58**, 79–110.

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

Bennett, A.F. (1982) The energetics of reptilian activity. *Biology of the Reptilia*, vol. 13(D) (eds. C. Gans & F.H. Pough), pp. 155–199. Academic Press, London.

Bennett, A.F. & Dawson, W.R. (1976) Metabolism. *Biology of the Reptilia*, vol. 5 (eds. C. Gans & W. Dawson), pp. 127–223. Academic Press, London.

Bennett, A.F. & Gleeson, T.T. (1976) Activity metabolism in the lizard *Sceloporus occidentalis. Physiological Zoology* **49**, 65–79.

Bennett, A.F. & Gleeson, T.T. (1979) Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus. Copeia* **1979**, 575–577.

Best, T.L. & Gennaro, A.L. (1984) Feeding ecology of the lizard, *Uta stansburiana*, in Southeastern New Mexico. *Journal of Herpetology* **18**, 291–301.

Brown, M.B. (1977) *Biomedical Computer Programs.* University of California Press, Berkeley.

Congdon, J.D., Ballinger, R.E. & Nagy, K.A. (1979) Energetics, temperature and water relations in winter aggregated *Sceloporus jarrovi. Ecology* **60**, 30–35.

Congdon, J.D., Dunham, A.E. & Tinkle, D.W. (1982) Energy budgets and life histories of reptiles. In: *Biology of the Reptilia*, vol. 13 (D) (eds. C. Gans & F.H. Pough), pp. 155–199. Academic Press, London.

Coulson, R.A. & Hernandez, T. (1973) Increase in metabolic rate of the alligator fed proteins or amino acids. *Journal of Nutrition* **109**, 538–550.

Cragg, P.A. (1978) Oxygen consumption in the lizard genus *Lacerta* in relation to diel variation, maximum activity and body weight. *Journal of Experimental Biology* **77**, 33–56.

Day, R.W. & Quinn, Q.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecology* **59**, 433–463.

Dunham, A.E. (1978) Food availability as a proximate factor influencing individual growth rate in the iguanid lizard *Sceloporus merriami. Ecology* **59**, 770–778.

Dunham, A.E., Grant, B.W. & Overall, K.L. (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial ectotherms. *Physiological Zoology* **62**, 335–355.

Gatten, R.E., Jr. (1980) Metabolic rates of fasting and recently fed spectacled caimens *(Caiman crocodilus). Herpetologica* **36**, 361–364.

Grant, B.W. (1988) *The thermal biophysical ecology of the desert lizard* Sceloporus merriami. PhD dissertation, University of Pennsylvania, Philadelphia.

Grant, B.W. & Dunham, A.E. (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami. Ecology* **69**, 167–176.

Kleiber, M. (1975) *The Fire of Life.* Krieger Publishing Co. Inc., New York.

McDonald, H.S. (1976) Methods for the physiological study of reptiles. *Biology of the Reptilia,* vol. 5 (eds. C. Gans & W. Dawson), pp. 127–223. Academic Press, London.

Nagy, K.A. (1982) Energy requirements of free-living iguanid lizards. *Iguanas of the World: Behaviour, Ecology and Evolution* (eds. G. M. Burghardt & A.S. Rand). Garland STPM Press, New York.

Parker, W.S. & Pianka, E.R. (1975) Comparative ecology of populations of the lizard *Uta stansburiana. Copeia* **1975**, 615–632.

Rapatz, G.L. & Musacchia, X.J. (1957) Metabolism of *Chrysemys picta* during fasting and during cold torpor. *American Journal of Physiology* **188**, 456–460.

Roberts, L.A. (1968) Oxygen consumption in the lizard *Uta stansburiana. Ecology* **49**, 809–818.

Tinkle, D.W. (1967) The life and demography of the side-blotched lizard, *Uta stansburiana.* Miscellaneous Publications Museum of Zoology **132**, 1–182.

Turner, F.B., Medica, P.A. & Kowalewsky, B.W. (1976) Energy utilization by a desert lizard *(Uta Stansburiana).* US/IBP Desert Biome Monograph No. 1. Utah State University Press, Logan.

Waldschmidt, S.R., Jones, S.M. & Porter W.P. (1986) The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard, *Uta stansburiana. Physiological Zoology* **59**, 376–383.

Waldschmidt, S.R., Jones, S.M. & Porter, W.P. (1987) Reptilia. *Animal Energetics,* vol. 2 (eds. T. J. Pandian & F. J. Vernberg), pp. 553–619. Academic Press, London.

Williams, J.B. & Prints, A. (1986) Energetics of growth in nestling Savannah Sparrows: a comparison of doubly labelled water and laboratory estimates. *Condor* **88**, 74–83.

Winer, B.J. (1971) *Statistical Principles in Experimental Design,* 2nd edn. McGraw-Hill, New York.