

# The metabolic cost of reproduction in an oviparous lizard

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## Summary

1. Studies of reproductive effort in ectotherms have focused primarily on the energetic investment in gamete production; much less is known about the indirect energetic costs of reproduction, such as increased metabolic costs of maintenance or activity.
2. The metabolic cost of reproduction in the oviparous lizard, *Sceloporus undulatus*, was investigated by measuring the metabolic rate of females prior to and following oviposition.
3. The metabolic rates of gravid females were adjusted for embryonic metabolism by subtracting the metabolic rate of egg clutches, measured immediately after oviposition.
4. The metabolic rate of females when gravid was elevated by 122% compared with that when non-gravid. The difference was not detected until the metabolic rates of gravid females were adjusted for the metabolic rates of the embryos.
5. The increment in metabolic rate associated with reproduction was not correlated with clutch mass or body mass, indicating that different components of reproductive effort (i.e. metabolism vs gametic investment) may not covary in a predictable fashion.
6. Indirect energetic costs of reproduction constitute a substantial portion of the reproductive effort of female *S. undulatus*, and should be incorporated into theoretical considerations of life history.

*Key-words:* Metabolism, reproductive effort, *Sceloporus*

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## Introduction

The 'cost of reproduction' has been an influential concept in the development of life-history theory (Bell 1980; Stearns 1992; Jonsson & Tuomi 1994). In general, it is assumed that the energy allocated to current reproduction leads to a reduction in future survival and fecundity, via trade-offs with activity, growth or storage (Stearns 1989). Recent empirical studies have identified some of the physiological and behavioural mechanisms that may result in the 'costs of reproduction' considered by life-history theory (e.g. Landwer 1994; Marler *et al.* 1995; Sorci, Clobert & Michalakis 1996; Wernham & Bryant 1998). Of these potential mechanisms, the energy invested in reproduction, often expressed as reproductive effort, has been the most frequently investigated. Individuals incur a direct energetic cost of producing gametes, which will reduce the amount of energy available for other functions. Furthermore, if reproducing individuals feed more frequently to offset the increased expenditure (Jonsson, Tuomi & Jaremo 1995), they may experience greater exposure to predators. For many organisms, the direct energetic cost associated with reproduction is a major portion of the energy used for production (Congdon, Dunham & Tinkle 1982).

Reproducing individuals experience other energetic costs besides the energy invested in gametes. Increased metabolic rates may result from the maintenance or activity associated with reproduction. In many species, males expend energy on mate searching, territorial defence or courtship (Duvall, Schuett & Arnold 1993; Marler *et al.* 1995; Michener 1998), and females expend energy to carry and maintain embryos for some or all of embryonic development (Guillette 1982; Beuchat & Vleck 1990). Also, the metabolic cost of gamete synthesis is incurred by both males and females. Each of these indirect costs will increase the level of reproductive effort, and may reduce future survival and fecundity. Unfortunately, much less is known about the contribution of indirect energetic costs to reproductive effort than the direct cost of gamete production. Activities such as mate acquisition (Madsen & Shine 1993; Marler *et al.* 1995) and parental care (Chappell *et al.* 1993; Poppitt, Speakman & Racey 1993) can be energetically expensive, but the consequences of reproduction for the metabolic cost of maintenance are not well known.

Is the metabolic cost associated with reproduction a substantial portion of the total reproductive effort? Is this cost proportional to the energy allocated to gametes? In viviparous lizards, the increment in

metabolic rate during pregnancy is largely determined by offspring mass (Guillette 1982; Beuchat & Vleck 1990). However, gravid females may incur a metabolic cost of reproduction above that required to meet the energetic demands of developing embryos (Beuchat & Vleck 1990). One complicating factor has made it difficult to provide a clear demonstration of a metabolic cost of reproduction in gravid females. Unless the mass-specific metabolic rate of embryos is identical to that of adult females, increased metabolic costs may not be detected in comparisons of metabolic rate in gravid and non-gravid individuals. To determine if gravid females have a higher metabolic rate than non-gravid females, one must identify the portion of metabolic rate that is due to the metabolism of maternal tissue *vs* that that is due to the metabolism of embryonic tissue (Demarco & Guillette 1992).

Oviparous species provide an ideal opportunity to investigate the metabolic cost of reproduction. Because females lay eggs in the early stages of embryonic development, the metabolic rates of embryos can be measured in order to calculate the metabolic rate of maternal tissue during pregnancy. We compared the metabolic rate of the oviparous lizard *Sceloporus undulatus* Latrielle in a gravid and non-gravid state, to determine whether reproduction results in an elevated maintenance metabolism. By adjusting metabolic rate of gravid females for the metabolic rate of embryos, we were able to demonstrate that a significant energetic cost is associated with reproduction in *S. undulatus*, which could not be detected without data on embryonic metabolism.

## Materials and methods

### STUDY ANIMALS

Sixteen gravid females were collected in May of 1998 from a population in Burlington County, New Jersey. Females were transported to the University of Pennsylvania where they were maintained in 6–1 terraria at a constant temperature of 30 °C and a light cycle of 14L:10D. A temperature of 30 °C was chosen because it maximized survival in previous laboratory studies of hatching success (Sexton & Marion 1974; Angilletta, Winters & Dunham, *in press*). The substrate consisted of moist sphagnum moss, to prevent eggs from dehydrating before they were discovered. Lizards were offered crickets (*Acheta domestica* Linnaeus) daily, except the days on which metabolic rates were to be measured (see below). Water was provided at feeding by misting the walls of the terraria.

### MEASUREMENT OF METABOLIC RATE

For each female, metabolic rate was determined prior to oviposition, hereafter referred to as gravid metabolic

rate (GMR), and following oviposition, hereafter referred to as non-gravid metabolic rate (NGMR). All measurements were made in the dark at 30 °C using a flow-through respirometry system (TR3, Sable Systems, Las Vegas, NV). Respirometry procedures are described in Angilletta (1998). Lizards were fasted 36 h prior to measurement of metabolic rate to ensure that they were in a postabsorptive state. Individuals were weighed to the nearest 0.1 mg and placed in 120-ml chambers. Animals entered the chambers during the afternoon ( $\approx$  1600 h), to allow them to adjust to the experimental conditions. All measurements of metabolic rate were made between 2000 and 0200 hours. Within this time, the CO<sub>2</sub> production and O<sub>2</sub> consumption of each female were recorded for a continuous period of 20 min. Measurements of GMR were repeated weekly, to obtain metabolic rates close to oviposition dates. On average, the last measure of GMR was  $5 \pm 1.5$  days before oviposition. Immediately following oviposition, females were fed once and then fasted for 36 h. After this period, NGMR was measured by the procedure described above.

The metabolic rate of a gravid female consists of gas exchange by maternal and embryonic tissue. To determine the portion of GMR that was accounted for by the metabolism of embryos, the metabolic rate of the clutch of eggs produced by each female was measured. Within 24 h of oviposition, all eggs in a clutch were weighed to the nearest 0.01 mg, and placed in a 30-ml respirometry chamber at 30 °C. The CO<sub>2</sub> production of each clutch was recorded for a 20-min period.

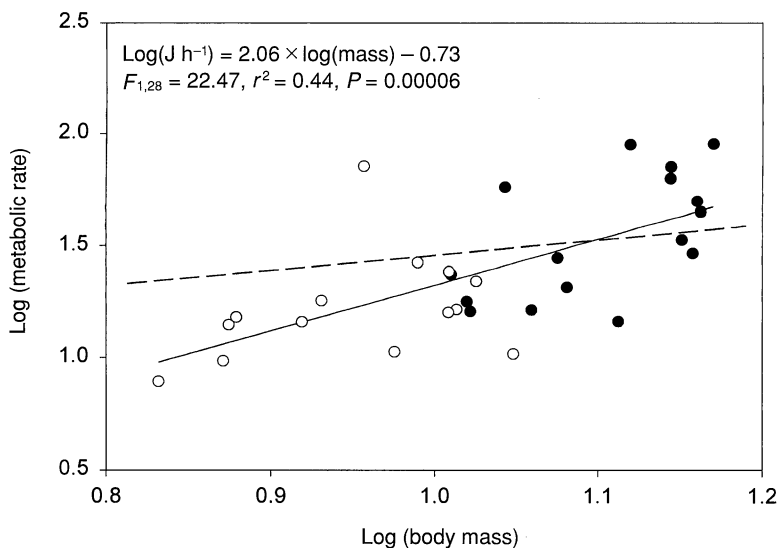
The data analysis program DAN (Sable Systems) was used to calculate rates of CO<sub>2</sub> production and O<sub>2</sub> consumption from each recording. Because the chambers were too small to permit activity and lizards appeared to rest while inside, the entire 20 min of each recording was averaged to obtain a metabolic rate. Volumes of O<sub>2</sub> consumption and CO<sub>2</sub> production (ml h<sup>-1</sup>) at standard temperature and pressure (STP) were calculated and converted to energy use (J h<sup>-1</sup>) with the conversion factors provided by Nagy (1983). Data on CO<sub>2</sub> production of egg clutches were treated identically to those for females. Carbon dioxide production was converted to energy expenditure by assuming that energy was derived equally from protein and lipid (Thompson & Stewart 1997; Thompson & Russell 1998, *in press*), which yield 23.1 and 27.7 J ml<sup>-1</sup>, respectively (Nagy 1983). All data were log-transformed for statistical analyses, but descriptive statistics are reported as mean  $\pm$  95% confidence interval of untransformed data.

### EVALUATION OF REPRODUCTIVE COSTS

Metabolic rates of females when gravid and non-gravid were compared by two means. First, analysis

**Table 1.** Metabolic rates of gravid females (GMR) and non-gravid females (NGMR) of *Sceloporus undulatus*, as well as metabolic rate of gravid females minus that of their respective egg clutch (AGMR). Predicted NGMR is the metabolic rate determined by a regression equation for males of *S. undulatus*, reported by Beyer & Spotila (1994). Data are means  $\pm$  95% confidence intervals

Measure	Metabolic rate ( $\text{J g}^{-1} \text{h}^{-1}$ )	<i>n</i>
GMR	$3.19 \pm 0.89$	16
NGMR	$2.18 \pm 0.91$	14
Predicted NGMR	2.83	16
Clutch	$1.18 \pm 0.17$	12
AGMR	$4.37 \pm 1.58$	13
AGMR-NGMR	$2.67 \pm 1.25$	11



**Fig. 1.** Allometry of metabolic rate in gravid (●) and non-gravid (○) females of *Sceloporus undulatus*. Mass-specific metabolic rate did not differ significantly between the two groups. The solid line is the metabolic rate predicted by the linear regression model for combined data (NGMR and GMR). The dashed line is the metabolic rate predicted for male lizards from the source population of females used in this study (Beyer & Spotila 1994).

of covariance with repeated measures was used to compare GMR to NGMR. Body mass at the time of each measurement was used as a covariate in the analysis. However, this comparison does not control for the metabolic rate of embryos carried by gravid females. Therefore, the metabolic rate ( $\text{J h}^{-1}$ ) of each female's clutch was subtracted from her GMR. The difference, hereafter referred to as adjusted gravid metabolic rate (AGMR), was considered an estimate of the true metabolic rate of gravid females. Analysis of covariance with repeated measures was used to compare AGMR with NGMR. Body mass was used as a covariate, but the mass used for AGMR, the mass of maternal tissue, was calculated as the difference between body mass of the gravid female and her clutch mass. Finally, a paired *t*-test was used to compare GMR and NGMR to metabolic

rate predicted by a regression equation reported for male *S. undulatus* from the source population of the females used in this study (Beyer & Spotila 1994).

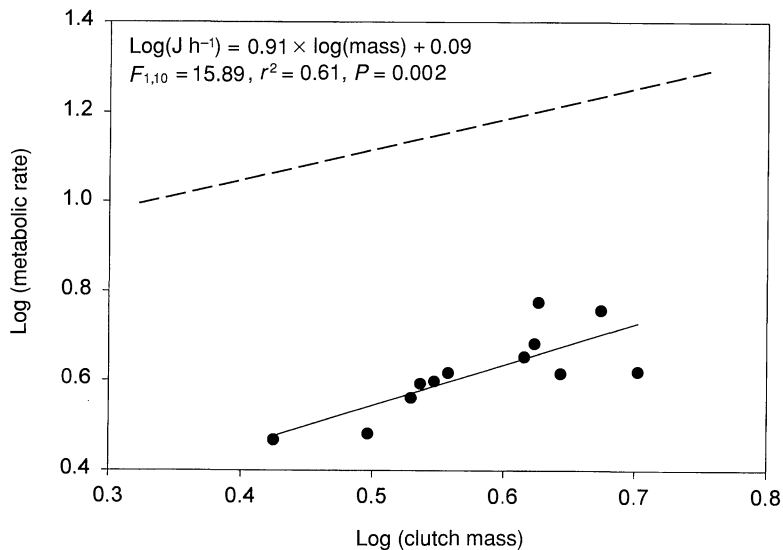
The metabolic cost of reproduction was defined as the difference between the AGMR ( $\text{J g}^{-1} \text{h}^{-1}$ ) and the NGMR ( $\text{J g}^{-1} \text{h}^{-1}$ ). This definition should accurately reflect the increment in metabolic rate associated with reproduction, because metabolic rates used in this calculation were determined from repeated measures of individuals. Linear regression analysis was used to determine if metabolic cost of reproduction was positively related to clutch mass or maternal mass.

## Results

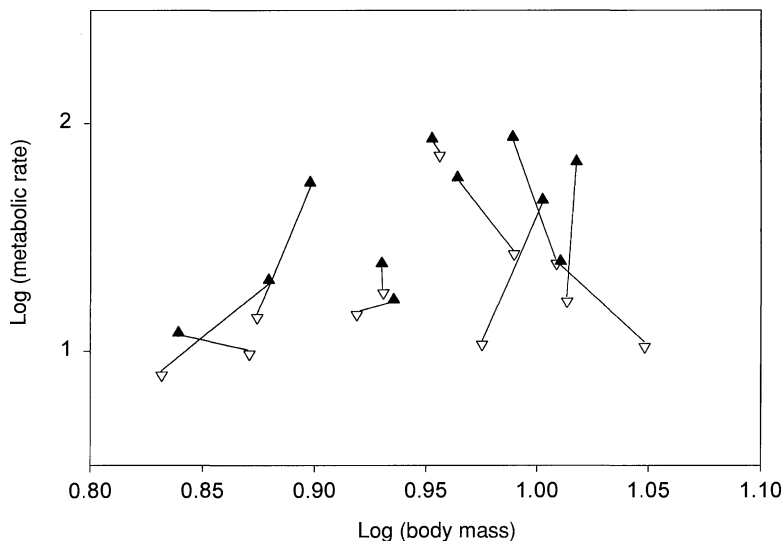
GMR, NGMR and clutch metabolism were obtained for 11 of the 16 females. Partial data obtained from the other five females were included in descriptive statistics, but not in statistical analyses. Respiratory exchange of gravid females was  $1.33 \pm 0.13$  and that of non-gravid females was  $1.39 \pm 0.18$ . Therefore, metabolism of carbohydrate was assumed and a conversion factor of  $20.9 \text{ J ml}^{-1} \text{ O}_2$  was used to calculate metabolic rate. Carbohydrate metabolism at  $30^\circ \text{C}$  is consistent with previous measures of respiratory exchange in non-gravid females of *S. undulatus* (Angilletta 1998).

No detectable effect of reproductive state on female metabolic rate was observed from measurements of GMR and NGMR, except that caused by greater mass of gravid females ( $F_{1,12} = 0.88$ ,  $\text{MS} = 0.02$ ,  $P = 0.37$ ). Although GMR was positively related to body mass ( $F_{1,14} = 7.80$ ,  $r^2 = 0.36$ ,  $P = 0.01$ ), NGMR was not significantly related to body mass ( $F_{1,12} = 1.56$ ,  $r^2 = 0.11$ ,  $P = 0.24$ ). Gravid metabolic rate did not differ from NGMR, after controlling for greater body mass of females when gravid (Table 1). Values of GMR and NGMR were significantly less than those predicted by the regression equation reported for metabolic rate of male lizards in the same population ( $t = -2.79$ ,  $\text{df} = 29$ ,  $P = 0.009$ ; Fig. 1). The difference between GMR and NGMR was not significantly related to clutch mass ( $F_{1,10} = 1.74$ ,  $r^2 = 0.15$ ,  $P = 0.22$ ).

Adjustment of GMR for embryonic metabolism revealed a significant difference in metabolic rate when gravid vs non-gravid ( $F_{1,9} = 25.73$ ,  $\text{MS} = 0.68$ ,  $P = 0.0007$ ). Metabolic rate of egg clutches was positively related to clutch mass (Fig. 2), but mass-specific metabolic rate of embryos was much lower than that of females (Table 1). Consequently, all of the 11 females exhibited a greater metabolic rate when gravid than when non-gravid (Fig. 3). Metabolic rate of females when gravid was approximately twice that when non-gravid. Metabolic cost of reproduction (AGMR-NGMR) was estimated to be a 122% increase in metabolic rate compared to NGMR



**Fig. 2.** Allometry of metabolic rate in egg clutches of *Sceloporus undulatus*. The solid line is the metabolic rate predicted by the linear regression model for the data. The dashed line is the metabolic rate predicted for male lizards from the source population of females used in this study (Beyer & Spotila 1994). Mass-specific metabolic rate of embryos is only 20% of that of gravid females (Table 1).



**Fig. 3.** Metabolic cost of reproduction in *Sceloporus undulatus*. For each female, the gravid metabolic rate adjusted for embryonic metabolism (▲) is paired with the non-gravid metabolic rate (△). After adjusting for embryonic metabolism, metabolic rate of females was significantly higher when gravid.

(Table 1). This cost was not related to clutch mass or maternal mass (Fig. 4).

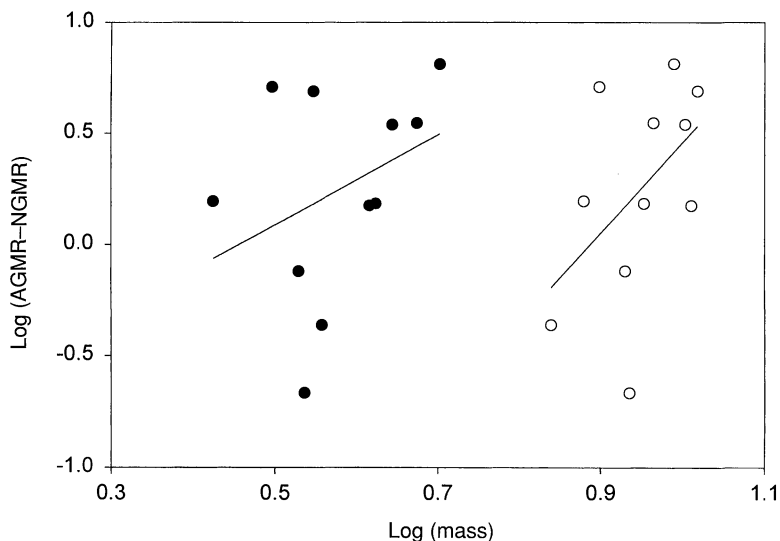
### Discussion

Gravid females incurred a substantial metabolic cost as a result of pregnancy. Adjusted gravid metabolic rate of females was higher than metabolic rate predicted for male lizards (Beyer & Spotila 1994), while NGMR was not. On average, AGMR was 200% of NGMR (Table 1), resulting in an average metabolic

cost of reproduction of  $2.67 \text{ J g}^{-1} \text{ h}^{-1}$ . This increment appears to be greater than that experienced by viviparous lizards. Guillette (1982) observed an increment of  $0.24 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  in gravid *S. aeneus bicanthalis*, and estimated that 45.5% of the 66.5% increase in metabolic rate was caused by a change in maternal metabolic rate. Beuchat & Vleck (1990) considered a 21% increase in metabolic rate of *S. jarrovi* during pregnancy to be caused by changes in maternal metabolism, but Demarco & Guillette (1992) used measures of embryonic metabolism to conclude that metabolic rate in this species increased by only 10%. It appears that *S. undulatus* exhibits a greater metabolic cost of reproduction than viviparous lizards. However, individual variation in metabolic cost of reproduction is unknown for viviparous lizards, because other investigators did not use repeated measures to correct for embryonic metabolism. Therefore, we are unable to determine whether the 122% increment in maternal metabolism observed in our study is statistically greater than increments observed in viviparous lizards.

Importantly, the increment in maternal metabolic rate would not have been detected without data on embryonic metabolism. Mass-specific metabolic rates of gravid and non-gravid females were not significantly different. If one assumes that the mass-specific metabolic rate of eggs is the same as that of adults, then one would conclude that there is no additional metabolic cost of reproduction above that required to sustain the metabolism of embryos. However, the mass of metabolically active tissue in an egg is only a small portion of the total egg mass at the time of oviposition (Deeming & Ferguson 1991). It is not surprising then that the mass-specific metabolic rate of eggs ( $1.18 \pm 0.17 \text{ J g}^{-1} \text{ h}^{-1}$ ) was much lower than that predicted for adult lizards (see Fig. 2). Consequently, a significant metabolic cost of reproduction was missed by simply comparing the metabolic rates of gravid and non-gravid females. Most of the difference between GMR and NGMR was the result of increased metabolism of maternal tissue. In fact, the apparently greater metabolic cost of reproduction in *S. undulatus*, compared with that of the viviparous lizards studied previously (Guillette 1982), may be explained by the fact that an interspecific regression equation for the metabolic rate of adult lizards (Bennett & Dawson 1976) was used to calculate embryonic metabolism.

Although it seems certain that a metabolic cost of reproduction exists, our estimate of the magnitude of this cost is sensitive to the accuracies of metabolic rates of both adult females and embryos. An error in metabolic rate can arise from an incorrect assumption about the respiratory quotient. To convert oxygen consumption of adult females to energy expenditure, it was assumed that females metabolized carbohydrate. Not only is this assumption supported by previous study (Angilletta 1998), but it



**Fig. 4.** Allometry of metabolic costs associated with reproduction in *Sceloporus undulatus*. Neither clutch mass ( $\circ F_{1,9} = 1.26, r^2 = 0.12, P = 0.29$ ) or maternal mass ( $\bullet F_{1,9} = 2.90, r^2 = 0.24, P = 0.12$ ) were significantly related to metabolic cost of reproduction (AGMR – NGMR).

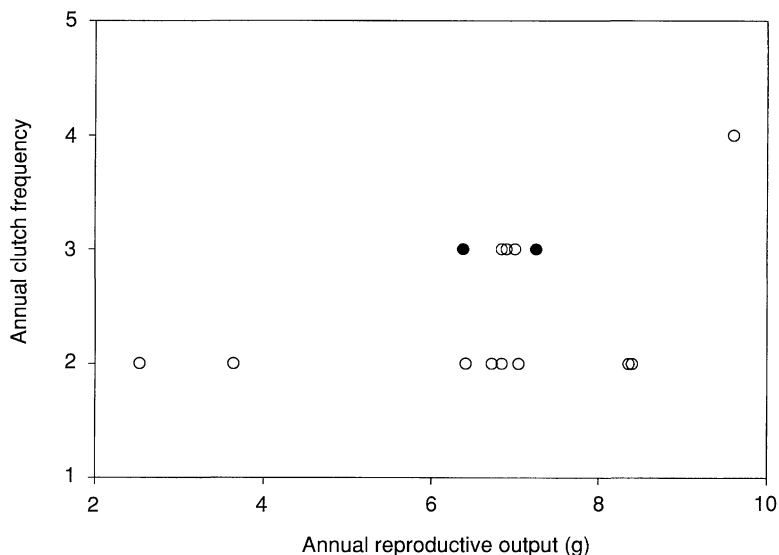
results in the lowest estimate of energy expenditure for a given rate of oxygen consumption by gravid and non-gravid females. Thus, our choice of respiratory quotient for adult females favours a conservative estimate of the metabolic cost of reproduction. The respiratory quotient assumed for embryonic metabolism is well supported by data on metabolism of lizard embryos (Thompson & Stewart 1997; Thompson & Russell 1998, in press).

Because the proportion of GMR that was accounted for by metabolism of embryos was estimated by subtracting clutch metabolism measured after oviposition, a change in metabolic rate of embryos after oviposition would affect our estimate of the metabolic cost of reproduction. Such a change might be caused by an increase in oxygen demands during ontogeny or a difference between environmental conditions experienced inside and outside a female lizard. The former cause is not a concern because metabolic rate of *S. undulatus* embryos does not increase significantly during the first 20 days of incubation ( $0.03 \text{ ml CO}_2 \text{ h}^{-1}$ ; M. J. Angilletta & M. W. Sears, unpublished data). The latter cause is of much more concern because it is evident that the environment experienced by embryos does differ inside and outside a gravid female. However, metabolic rate of embryos within a female may be lower than that of embryos that have been oviposited, because of relatively low oxygen concentration of maternal tissue. In fact, eggs that are retained in females for extended time periods are thought to arrest development until oviposition (Vleck & Hoyt 1991). Embryonic metabolism may have been underestimated by measuring metabolic rates after oviposition. Moreover, the metabolic cost of reproduction is less sensitive to error in embryonic metabolism

than error in adult metabolism, because the metabolic rate of embryos ( $1.18 \text{ J g}^{-1} \text{ h}^{-1}$ ) was only 37% of the metabolic rate of gravid females ( $2.67 \text{ J g}^{-1} \text{ h}^{-1}$ ) and clutch mass was only 30% of gravid female mass. For example, a 20% error in embryonic metabolism would yield less than 4% error in the metabolic cost of reproduction. Therefore, it is likely that the metabolic cost of reproduction observed is close to the actual cost incurred by gravid females.

What is the source of increased metabolic costs during pregnancy? In the viviparous lizard *S. jarrovi*, the difference between GMR and NGMR is positively related to offspring number (Beuchat & Vleck 1990). This result indicates that the metabolic requirement of developing embryos is a major component of the metabolic costs associated with reproduction in viviparous animals. In *S. undulatus*, the difference between GMR and NGMR was not related to clutch mass. The lack of a relationship is not surprising considering that embryonic metabolism accounts for only 17% of the average increase in the metabolic rate of gravid females ( $4.1 \text{ J h}^{-1}$  out of  $24.5 \text{ J h}^{-1}$ ). Therefore, most of the increment in metabolic rate of gravid females is maternal metabolism. This increment in maternal metabolic rate, which we termed the metabolic cost of reproduction (AGMR–NGMR), was highly variable among females. However, the variation was not explained by embryonic mass or maternal mass (Fig. 4). Although it is clear that reproducing females experience some metabolic cost, the factors that determine the magnitude of this cost are unknown.

It is hypothesized that the metabolic cost of reproduction is a by-product of an overall increase in metabolic intensity (i.e. mass-specific rate of metabolism) of maternal tissue. Metabolic costs in gravid females may be incurred through a variety of sources, including an increase in cardiac output to deliver oxygen to embryos, greater resting metabolic rates associated with enhanced aerobic capacity, and proliferation and maintenance of oviductal tissue (Demarco & Guillelte 1992). For instance, gravid females must transport substantially more mass during locomotion, raising the metabolic cost of locomotion. Although females may reduce locomotion during pregnancy, they may require brief periods of activity to evade predators. If females undergo physiological adjustments to accommodate greater energy expenditure during this activity, a change in resting metabolism may be an unavoidable by-product. This argument is the basis of the aerobic capacity model for the evolution of endothermy (Bennett & Ruben 1979), and has some empirical support among amniotes (Hayes & Garland 1995; Ricklefs, Konarzewski & Daan 1996). In fact, standard metabolic rate (SMR) was positively correlated with maximal metabolic rate in *S. undulatus* (Hayes & Garland 1995). Because differences in body mass among individuals or species were removed before statistical analysis, the positive



**Fig. 5.** The relationship between reproductive output (g wet mass) and the number of clutches produced for females in 16 populations of *Sceloporus undulatus* (●, two data points). Data are from Niewiarowski (1994) and Smith, Rowe & Ballinger (1996). The relative magnitude of reproductive investment by females in most populations is uncertain, given the difference in clutch frequency among populations with similar levels of gametic investment.

correlation between SMR and maximal metabolic rate implies that a need for greater levels of sustained metabolic activity requires an enhanced state of metabolic readiness, which is thought to be achieved through an increase in the metabolic intensity of tissues (Ricklefs *et al.* 1996). Additionally, metabolic intensity of other tissues may be affected by the reproductive state of females. Specifically, support and movement of eggs by smooth muscle of the oviduct and synthesis of eggshells probably contribute to the metabolic cost of reproduction in *S. undulatus*. A comparison of maximal metabolic rates of gravid females and non-gravid females or direct measurement of metabolic rates of tissues would identify sources of increased metabolism in gravid females.

In *S. undulatus*, the metabolic cost of reproduction is an important component of reproductive effort. An average female from New Jersey produces a total of 17 eggs in two clutches, containing about 78 kJ (Derickson 1976; Niewiarowski 1994). The metabolic cost of reproduction for the same female would be at least 25 J h<sup>-1</sup> of activity at 30 °C (or higher). Assuming an activity time of 11 h per day (Niewiarowski & Roosenburg 1993) for 14 days (average duration from capture to oviposition in the laboratory), a female would expend 4 kJ per clutch on indirect costs associated with reproduction. Therefore, the metabolic cost of reproduction accounts for at least 10% of energy expended on reproduction annually by females in this population, or the energy equivalent of about two eggs.

Furthermore, the metabolic cost of reproduction has important consequences for studies of intraspecific variation in reproductive effort. Throughout

the geographic range of *S. undulatus*, the number of clutches produced annually by females varies from two to four. Individuals that produce three or four clutches per year instead of two will have a greater reproductive effort, despite an equivalent energetic investment in gametes. Of 16 populations for which data on reproduction have been collected, females in 11 populations vary in clutch number with relatively little variation in annual reproductive output (Fig. 5). Without factoring in the metabolic cost of reproduction it is impossible to rank reproductive effort of females from these populations. Thus, an understanding of the factors that determine the metabolic cost of reproduction will enhance efforts to interpret intraspecific variation in life history. A consideration of indirect energetic costs of reproduction may alter the hypothetical relationship between an organism's age-specific reproductive effort and its fitness, thereby influencing the 'cost of reproduction'. Both empirical and theoretical treatments of reproductive effort should incorporate indirect energetic costs of reproduction, such as the one identified in this study.

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