

## Sex-Related Differences in Metabolic Rate and Energy Reserves in Spring-Breeding Small-Mouthed Salamanders (*Ambystoma texanum*)

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**We investigated differences in metabolism and metabolic substrates between male and female small-mouthed salamanders (*Ambystoma texanum*) collected from breeding sites. Resting O<sub>2</sub> consumption rates (VO<sub>2</sub>) of gravid females at 15 C were roughly double those of males and postgravid females. Whole-body triglyceride and glycogen contents were similar among males, gravid females, and postgravid females, but free glucose contents were higher in both gravid and postgravid females than in males. Respiratory quotients for all groups were ~0.9, suggesting a relatively high dependence on carbohydrates to fuel metabolism. Our findings suggest that females have a considerably higher metabolic cost of reproduction than do males. Such differences may be associated with aspects of life history and ecology such as sexual size dimorphism, age of sexual maturity, asynchronous arrival at breeding areas, and differential survival between the sexes.**

INVESTIGATION into “costs” of reproduction has been a cornerstone of life-history research, because the “trade-off” between current reproductive expenditure and possible future reproductive output may have a profound influence on the evolution of life histories (e.g., Stearns, 1992; Bernardo, 1993). Potential costs of reproduction include the allocation of energy for the synthesis of gametes, cost of migration to breeding areas, increased vulnerability to predation caused by changes in behavior, morphology, physiology, or all three (Stamps et al., 1998; Angilletta and Sears, 2000). Such costs may be particularly high for females, because typically larger amounts of energy are invested in their gametes (Pianka, 1978). Moreover, gravidity may be associated with increased costs of maintenance and activity (Ryser, 1989; Angilletta and Sears, 2000) and decreased locomotor performance (Lee et al., 1996; Miles et al., 2000).

Although considerable attention has been given to the energetic cost of reproduction in reptiles (most notably squamates), relatively little research into energetic costs has been conducted on amphibians, and data for nonanuran taxa are especially lacking. Although some investigations have been made into the respiration of reproductive plethodontid salamanders of the genus *Desmognathus* (Fitzpatrick, 1973; Bennett and Houck, 1983), sex-related differences in the energetic cost of reproduction have received minimal attention in other salamander taxa (Ryan and Hopkins, 2000). For terrestrial form salamanders of the genus *Ambystoma* (Ambystomatidae), these energetic costs of reproduction may constitute a considerable encumbrance on the animals’ energy budgets. Many

northern species breed during the late winter or early spring (Petranka, 1998) after a prolonged period of reduced feeding (see Plummer, 1977). Moreover, salamanders may migrate appreciable distances from their overwintering sites to the breeding ponds (Petranka, 1998; Semlitsch, 1998), thus introducing a potentially large transportation cost to the overall cost of reproduction.

Because female ambystomid salamanders produce much larger masses of gametes than do males, the energetic costs of reproduction may be considerably higher in females than in males (Ryan and Hopkins, 2000). Differences in the energetic cost of reproduction, therefore, may contribute to morphological, physiological, behavioral, and demographic differences between males and females. Female ambystomid salamanders are typically larger than male conspecifics (Petranka, 1998). Ryan and Hopkins (2000) found that the scaling of oxygen consumption with body mass in postreproductive, paedomorphic *Ambystoma talpoideum* was greater in females than in males. For terrestrial forms, the two sexes often arrive at breeding sites asynchronously, with males arriving sooner (Petranka, 1998). In addition, some studies have found a shift in demography from roughly equal numbers of males and females at metamorphosis to heavily male-biased sex ratios in adult populations, suggesting higher mortality, less frequent reproduction, or both, in females compared to males (Husting, 1965; Sever and Dineen, 1978; Whiteman, 1997).

The present study investigated potential differences in the energetic cost of reproduction between male and female small-mouthed salamanders (*Ambystoma texanum*). We hypothesized

that reproductive females would have higher resting metabolic rates than would either male or postreproductive females. We also hypothesized that females would have lower stored energy contents (fat and carbohydrates) than would males and that postreproductive females would have lower stored energy contents than would reproductive females.

#### MATERIALS AND METHODS

*Ambystoma texanum* were collected from breeding areas at Salamonie River State Forest, Wabash County, Indiana, and Lost Bridge State Recreation Area, Huntington County, Indiana, during early March of 2000 (males:  $n = 12$ , gravid females:  $n = 5$ , postgravid females  $n = 5$ ) and 2001 (males:  $n = 5$ , gravid females:  $n = 5$ , postgravid females  $n = 5$ ). Animals were weighed to the nearest 0.1 g within 16 h of collection and housed in plastic shoe boxes lined with moistened paper towels. Animals were maintained at 15 C on a 12:12 h light:dark cycle during the study.

Oxygen consumption ( $VO_2$ ) and carbon dioxide production ( $VCO_2$ ) rates were measured within 24 h of collection. For each year, all respirometry measures were conducted within a five-day period. Early measurements within a year included males and gravid females, whereas later measurements included males and postgravid females. Animals were weighed to the nearest 0.1 g and then placed individually into 250 ml sample bottles containing moistened paper towels to avoid dehydration of the subjects. Bottles were connected via plastic tubing to a Micro-Oxymax respirometry system (Columbus Instruments) and then placed into a 15 C water bath and covered to minimize light exposure.  $VO_2$  and  $VCO_2$  were measured automatically by the system at 2 h intervals over a 20–24 h period. Measurements for an individual were averaged to a single value prior to statistical analysis to provide an overall measure of metabolic rate. Because ambystomid salamanders appear to eat little during the reproductive period (Plummer, 1977), we assume that the animals were post-absorptive and that measurements constitute resting metabolic rates. Based upon  $VO_2$  and  $VCO_2$  measured, respiratory quotients (amount of  $CO_2$  liberated/amount of  $O_2$  consumed) were calculated, and from these RQ values, estimates of energy expenditure (cal/h) were derived based upon conversion values from Kleiber (1961) with the assumption that most of the energetic needs of the animals were supported by fat and carbohydrate catabolism.

Following measurement of respiration, the

animals were removed from their respirometry chambers and were anesthetized by submerging them in a 0.67% solution of MS-222. Animals were then measured for snout-vent length and total length, females were dissected to remove any eggs present in the oviducts, and the animals were sacrificed by freezing. Carcasses were stored at -50 C until biochemical assays could be performed. Estimates of clutch mass from gravid females were calculated as the difference between live mass and carcass mass, and relative clutch mass was calculated by dividing clutch mass by carcass mass (see Shine, 1980).

Carcasses were homogenized in 100 ml of distilled water. A 1-ml sample of the homogenate was then added to 2 ml of 0.6 N perchloric acid for deproteinization. After neutralization with 1 ml of 1 M  $KHCO_3$ , the homogenate was analyzed for total triglyceride and free glucose contents using colorimetric assays (Sigma Diagnostic Kits 337 and 510, respectively) performed on a Spectronic Genesys 20 spectrophotometer. Glycogen content was determined by digesting a sample of the deproteinized and neutralized homogenate with amyloglucosidase (Sigma A-3514), measuring total glucose content colorimetrically (Sigma Diagnostic Kit 510), then subtracting the free glucose content. Total caloric contents were calculated based on values for caloric yields from aerobic catabolism of free carbohydrates (4.2 cal/mg) and triglycerides (9.7 cal/mg) as per Kleiber (1961).

In preliminary analyses, we evaluated body size data using multivariate analyses of variance (MANOVA) and biochemical data using multivariate analyses of covariance (MANCOVAs). Because  $VO_2$  data were available for both study years but data on  $VCO_2$  only in 2001, metabolic data ( $VO_2$ ,  $VCO_2$ , and cal/h) were analyzed using univariate analyses of covariance (ANCOVAs). In all three sets of analyses, group (male, gravid female, or postgravid female) and year (2000 and 2001) were fixed effects. Because the contribution of eggs in the oviducts of gravid females to observed changes in respiratory gases is unknown, two ANCOVAs of  $VO_2$  and  $VCO_2$  were conducted: one using carcass mass (i.e., mass after removal of eggs from gravid females) as the covariate and the other using total live mass. Effects found to be significant in MANOVAs and MANCOVAs were subsequently analyzed for each response variable using univariate ANOVAs and ANCOVAs to determine which response variables were significantly influenced by the predictor variables. All initial analyses also included two- and three-way interaction terms of the above factors, but because none of these interaction terms were significant, they were

TABLE 1. SIZE MEASURES, METABOLISM, AND ENERGY RESERVES OF MALE, GRAVID FEMALE, AND POSTGRAVID FEMALE SMALL-MOUTHED SALAMANDERS USED IN THIS STUDY.

Parameter	Gravid females*	Nongravid females*	Males*
<b>Size</b>			
Live mass (g) <sup>a</sup>	11.40 ± 0.70 (A)	9.33 ± 0.70 (AB)	7.71 ± 0.56 (B)
Carcass mass (g) <sup>a</sup>	8.91 ± 0.62 (A)	9.33 ± 0.62 (A)	7.56 ± 0.49 (A)
SVL (mm) <sup>a</sup>	78.40 ± 1.93 (A)	82.60 ± 1.93 (A)	76.54 ± 1.54 (A)
Total length (mm) <sup>a</sup>	131.40 ± 3.94 (A)	141.40 ± 3.94 (A)	131.18 ± 3.15 (A)
<b>Live mass-adjusted respiration</b>			
VO <sub>2</sub> (μl/h) <sup>a</sup>	699.66 ± 44.78 (A)	428.58 ± 38.52 (B)	438.79 ± 33.22 (B)
VCO <sub>2</sub> (μl/h) <sup>b</sup>	718.79 ± 57.56 (A)	439.01 ± 54.30 (B)	437.11 ± 55.98 (B)
RQ <sup>b,c</sup>	0.91 ± 0.03	0.91 ± 0.03	0.87 ± 0.03
Energy expenditure (cal/h) <sup>b</sup>	3.869 ± 0.279 (A)	2.428 ± 0.264 (B)	2.484 ± 0.272 (B)
<b>Carcass mass-adjusted respiration</b>			
VO <sub>2</sub> (μl/h) <sup>a</sup>	764.00 ± 41.34 (A)	407.78 ± 42.39 (B)	417.54 ± 33.77 (B)
VCO <sub>2</sub> (μl/h) <sup>b</sup>	790.91 ± 56.05 (A)	400.02 ± 56.42 (B)	403.97 ± 55.58 (B)
Energy expenditure (cal/h) <sup>b</sup>	4.315 ± 0.272 (A)	2.185 ± 0.274 (B)	2.281 ± 0.270 (B)
<b>Stored energy reserves</b>			
Triglyceride content (mg) <sup>d</sup>	77.91 ± 25.89 (A)	112.41 ± 20.79 (A)	144.21 ± 18.11 (A)
Free glucose content (mg) <sup>a</sup>	4.95 ± 1.04 (A)	5.70 ± 0.83 (A)	1.97 ± 0.72 (B)
Glycogen content (mg) <sup>a</sup>	81.42 ± 17.36 (A)	76.73 ± 13.94 (A)	98.19 ± 12.14 (A)
Energy content (cal) <sup>d</sup>	937.48 ± 280.32 (A)	1423.78 ± 225.10 (A)	18.05.65 ± 196.06 (A)

\* Data are presented as least-squares means ± SEM. Like letters in parentheses indicate no significant difference between paired groups ( $P = 0.017$ , unpaired  $t$ -test).

<sup>a</sup> Based on 2000 and 2001 data combined. Sample sizes: gravid females  $n = 10$ , postgravid females  $n = 10$ , males  $n = 17$ .

<sup>b</sup> Based on 2001 data only. Sample sizes: gravid females  $n = 5$ , postgravid females  $n = 5$ , males  $n = 5$ .

<sup>c</sup> Nearly identical values were obtained for least squares mean RQ using carcass mass as a covariate. As RQ is a ratio of VO<sub>2</sub> and VCO<sub>2</sub>, no formal hypothesis tests were conducted on this parameter.

<sup>d</sup> Based on 2000 and 2001 data combined. Sample sizes: gravid females  $n = 9$ , postgravid females  $n = 10$ , males  $n = 17$ .

collapsed back into the model. Moreover, because year was not a significant effect in any of the analyses, the results of this factor in each model are not reported in the univariate statistical summaries below, although all results reflect models incorporating this factor. Where appropriate, pairwise comparisons of groups were conducted using unpaired  $t$ -tests of least-squares means (i.e., estimated marginal means) evaluated at a Bonferroni-adjusted pairwise error rate of  $\alpha = 0.017$ .

## RESULTS

Body size differed significantly among gravid females, postgravid females, and males (MAN-

OVA Wilkes-lambda  $F_{8,60} = 9.98$ ;  $P < 0.0001$ ) but was not affected by year (MANOVA Wilkes-lambda  $F_{4,30} = 2.02$ ;  $P = 0.12$ ). Gravid females had greater live masses than did males, but there were no significant differences in carcass mass, snout-vent length, or total length among the three groups (Tables 1–2). When gravid and postgravid females were combined, however, carcass mass ( $F_{1,34} = 5.70$ ;  $P = 0.023$ ), was significantly greater for females than for males, whereas neither snout-vent length nor tail length differed significantly between the sexes. Mean relative clutch mass ( $\pm$  SEM) of gravid females was  $0.29 \pm 0.05$  g.

Gravid females had markedly higher rates of

TABLE 2. UNIVARIATE ANOVAS AND ANCOVAS OF SIZE MEASUREMENTS, RESTING METABOLISM, AND ENERGY SUBSTRATE LEVELS IN MALE, GRAVID FEMALE, AND POSTGRAVID FEMALE SMALL-MOUTHED SALAMANDERS.

Parameter	Group (fixed effect)			Covariate		
	F	df	P	F	df	P
Live mass	10.55	2, 33	0.0009	—	—	—
Carcass mass	2.90	2, 33	0.07	—	—	—
Snout-vent length	3.03	2, 33	0.06	—	—	—
Total length	2.38	2, 33	0.11	—	—	—
Live mass-adjusted $VO_2^a$	12.52	2, 32	<0.0001	12.93	1, 32	0.0011
Live mass-adjusted $VCO_2^a$	7.50	2, 13	0.009	7.18	1, 13	0.022
Live mass-adjusted energy expenditure <sup>a</sup>	8.11	2, 13	0.007	11.51	1, 13	0.006
Carcass mass-adjusted $VO_2^b$	26.04	2, 32	<0.0001	7.78	1, 32	0.009
Carcass mass-adjusted $VCO_2^b$	15.90	2, 13	0.0006	6.22	1, 13	0.030
Carcass mass-adjusted energy expenditure <sup>b</sup>	19.34	2, 13	0.0003	10.34	1, 13	0.008
Triglyceride content <sup>b</sup>	2.02	2, 31	0.15	24.19	1, 31	<0.0001
Free glucose <sup>b</sup>	5.31	2, 31	0.010	1.68	1, 31	0.20
Glycogen content <sup>b</sup>	0.71	2, 31	0.50	11.84	1, 31	0.0017
Stored energy content <sup>2</sup>	2.98	2, 31	0.065	25.41	1, 33	<0.0001

<sup>a</sup> Covariate = live mass.

<sup>b</sup> Covariate = carcass mass.

$O_2$  consumption than did either males or postgravid females (Tables 1–2) regardless of whether carcass mass or live mass served as covariates. Oxygen consumption was not significantly influenced by year in either model ( $F_{1,32} = 2.84$ ;  $P = 0.10$ ).  $CO_2$  production and energy expenditure were also significantly greater in gravid females than in either males or postgravid females in 2001 (Tables 1–2). In all three groups, however, respiratory quotients were approximately 0.9, suggesting a relatively high contribution of carbohydrates to overall metabolism.

Energy reserves differed significantly among groups (MANCOVA Wilkes-lambda  $F_{8,56} = 4.01$ ;  $P = 0.0008$ ) once corrected for differences in carcass mass (MANCOVA Wilkes-lambda  $F_{4,28} = 7.58$ ;  $P = 0.0003$ ). Univariate analyses were unable to detect any differences among the three groups in any of the individual measures except free glucose, which was lower in males than in either group of females (Tables 1–2). Stored energy reserves did not differ between the two years (MANCOVA Wilkes-lambda  $F_{4,28} = 1.98$ ;  $P = 0.13$ ).

#### DISCUSSION

Gravid females had resting metabolic rates that were substantially higher than those of both males and postgravid females. Fitzpatrick (1973) also found an elevated metabolic rate in gravid *Desmognathus ochrophaeus* at 15 C compared to nongravid female and male conspecifics, but the proportional increase was much lower (~17% higher  $VO_2$  than nongravid females). This difference may reflect the inclusion of the

mass of the eggs in the gravid females into the mass-specific metabolic rates reported by Fitzpatrick. This method presumes that the eggs have the same metabolic rate as does the female's tissues. Angilletta and Sears (2000) found no significant difference in standard metabolic rate between gravid and postgravid female *Sceloporus undulatus*. However, adjustment of female metabolism after the determination of the mass-specific metabolism of eggs revealed a 122% increase in metabolic rate of gravid females over postgravid females. Similarly, our data shows a considerable difference in mass-adjusted metabolic rate depending on whether gravid mass (58% higher in gravid females compared to postgravid females) or carcass mass (99% higher in gravid females) is used as the covariate. We believe that our model using carcass mass as the covariate is more representative of the true metabolism of the female, because  $VO_2$  of the eggs is likely minimal before oviposition. Regardless, the elevated metabolism of the female likely constitutes a considerable component of the overall energetic cost of reproduction. A variety of factors may contribute to this increase in metabolic rate, including proliferation and maintenance of the oviducts (Demarco and Guillette, 1992), and/or increased cost of locomotion during activity (Olsson et al., 2000), and shifts in metabolic capacity (Bauwens and Thoen, 1981).

In both males and females, metabolism during the reproductive period appears to be fueled primarily through carbohydrate catabolism. In all three groups, respiratory quotients

were approximately 0.9. Although females generally had a higher free glucose level than did males, we were unable to detect a corresponding difference in whole-body glycogen reserves in females relative to males. However, depletion in liver glycogen (the likely source of the free glucose) may have been obscured by variation in muscle glycogen in the whole body homogenates.

The considerable elevation in metabolism by reproductive females compared to males and postreproductive females may be related to important attributes of ambystomid life history. First, elevated resting metabolism may reduce the maximum sustainable level of activity for females (Finkler et al., 2000; but see Angilletta and Sears, 2000), which could increase the duration of the migration to the breeding pools or necessitate that females delay migration until ideal environmental conditions (i.e., warm, wet weather) are available. This may, in part, account for regularly observed asynchronies in the arrival of males and females at breeding pools (Downs, 1989; Petranka, 1998) although other factors such as a propensity for males to maximize chances of reproduction by early arrival at the breeding sites could also account for these asynchronies. Second, the increased energy expenditure by females during reproduction could impact both growth and survival. Energy that could be used for growth may be diverted to reproduction, which may in turn slow growth rates in females compared to males (E. Blackwell, pers. com.), necessitate greater foraging activity, or both, thus increasing potential exposure to predators. Differential survivorship, coupled with females' need to procure greater stored energy to meet higher direct and indirect energetic costs of reproduction (and hence possibly less frequent participation in reproductive events), may account in part for the often male-biased sex ratios observed in some breeding aggregations of ambystomids (Husting, 1965; Flageole and Leclair, 1992; Whiteman, 1997). Third, the increased metabolic cost of reproduction in females may contribute to the selection of larger female body size at reproductive maturity to reduce mass-specific energetic costs or effects on performance (e.g., Shine et al., 1998; Stamps et al., 1998) or to increase fecundity (Reiss, 1991; Stearns, 1992). This may contribute to observed delays in the age of first reproduction (Wilbur, 1977; Marvin, 2001; Morey and Reznick, 2001) as well as the sexual size dimorphism that are commonly observed in ambystomids (see Plummer, 1977; Downs, 1989; Petranka, 1998).

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