

Sex-Related Differences in Metabolic Rate and Locomotor Performance in Breeding Spotted Salamanders (*Ambystoma maculatum*)

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We investigated differences in metabolism and locomotor performance of male and female spotted salamanders (*Ambystoma maculatum*) collected during the breeding season. Male salamanders had faster voluntary crawling speeds than did both gravid and postgravid females. Burst swimming velocity was higher in males than in gravid females but not postgravid females, and there was no difference in burst crawling speeds between the sexes. Oxygen consumption during rest was greater in both gravid and nongravid females than in males, but there was no difference among the three groups in oxygen consumption during locomotion. Both male and postgravid females were able to sustain terrestrial locomotion on the treadmill longer than were gravid females. These findings suggest differences in locomotor performance and energetics between the sexes that may underlie differences in arrival times at breeding sites, frequency of participation in reproductive events, and survival.

A reduction in the locomotor performance of gravid females is frequently observed in studies of the cost of reproduction (e.g., Shine, 1980; Seigel et al., 1987; but see Brown and Weatherhead, 1997). Such reductions in performance may be based on physical hindrance of movements during locomotion (e.g., Sinervo et al., 1991) or physiological changes associated with gravidity (e.g., Bauwens and Thoen, 1981; Birchard et al., 1984; Olsson et al., 2000). This reduction in locomotor performance may form a considerable component of the overall cost of reproduction. Females with reduced locomotor performance may be more susceptible to predation or parasitism (e.g., Bauwens and Thoen, 1981; Sorci et al., 1996; Miles et al., 2000), thus reducing chances of survival to the next reproductive event. Moreover, gravid females may be less capable of foraging (Cooper et al., 1990; but see Shine, 1980), thus reducing energetic intake that would contribute to survivorship and future fecundity. These factors may, in turn, constitute selective pressures for behavioral and morphological characteristics of females that directly or indirectly reduce the cost of reproduction, such as changes in body size or in the relative size of morphological structures that influence locomotor performance (e.g., Shine et al., 1998), and alterations in habitat selection, feeding, and defensive behaviors (Brodie, 1989; Cooper et al., 1990; Charland and Gregory, 1995).

Reductions in locomotor performance associated with gravidity may be of particular importance to salamanders of the genus *Ambystoma* (Caudata: Ambystomatidae). Many members of this genus reproduce in aquatic environments

in late winter or early spring following a prolonged overwintering period. Terrestrial forms of these salamanders may need to migrate considerable distances overland from their overwintering sites to breeding sites (Petranka, 1998; Semlitsch, 1998). Therefore, variation in locomotor performance would influence future chances of reproduction by affecting the ability to evade predators and acquire prey but also by affecting the energetic cost of transport during this migration. Moreover, because the mass of mature gametes carried by a gravid female during migration is considerably greater than that carried by males (Sexton et al., 1986), the cost of transport to the breeding areas may be particularly elevated in females. Gravid females may have reduced maximal locomotor performance because of the physical encumbrance by the eggs and physiological factors associated with gravidity (Seigel et al., 1987; Ryan and Hopkins, 2000; Finkler and Cullum, 2002), and voluntary locomotor activity of females migrating to the breeding ponds may similarly be reduced to minimize the energetic cost incurred. This could, in part, account for observed differences between the sexes in the time of arrival at the breeding pond (reviewed in Downs, 1989), as well as observed male-biased sex ratios during reproductive events via increased susceptibility to predation, delayed sexual maturity, or less frequent reproduction in females (Husting, 1965; Flageole and Leclair, 1992; Whiteman, 1997).

In the present study, we investigated differences in locomotor performance and oxygen consumption in male, gravid female, and postgravid female Spotted Salamanders (*Ambystoma*

TABLE 1. BODY SIZE MEASUREMENTS, SWIMMING AND CRAWLING SPEEDS, OXYGEN CONSUMPTION (VO_2) AT REST AND DURING EXERCISE, AND NONSTOP DISTANCE TRAVELED DURING EXERCISE OF MALE, GRAVID FEMALE, AND NON-GRAVID FEMALE SPOTTED SALAMANDERS AT 15 C.

Parameter	Group	LS Mean \pm SEM*
Live mass (g)	Males	17.536 \pm 0.968 (A)
	Gravid females	31.638 \pm 0.890 (B)
	Postgravid females	24.245 \pm 1.135 (C)
Snout-vent length (mm)	Males	91.0 \pm 1.8 (A)
	Gravid females	106.1 \pm 1.7 (B)
	Postgravid females	104.3 \pm 2.2 (B)
Total length (mm)	Males	172.5 \pm 3.4 (A)
	Gravid females	207.0 \pm 3.1 (B)
	Postgravid females	203.4 \pm 4.0 (B)
Burst crawling speed (cm/sec) ^a	Males	7.36 \pm 1.72 (A)
	Gravid females	8.28 \pm 1.47 (A)
	Postgravid females	6.65 \pm 1.47 (A)
Burst swimming speed (cm/sec) ^a	Males	23.3 \pm 1.8 (A)
	Gravid females	17.6 \pm 1.7 (B)
	Postgravid females	23.0 \pm 1.6 (A)
Voluntary crawling speed (cm/sec) ^b	Males	2.27 \pm 0.19 (A)
	Gravid females	1.20 \pm 0.28 (B)
	Postgravid females	1.62 \pm 0.19 (B)
Resting VO_2 (ml/h) ^c (Model A) ^d	Males	0.448 \pm 0.421 (A)
	Gravid females	0.753 \pm 0.306 (B)
	Postgravid females	0.767 \pm 0.177 (B)
Resting VO_2 (ml/h) ^c (Model B) ^d	Males	0.264 \pm 0.228 (A)
	Gravid females	1.307 \pm 0.178 (B)
	Postgravid females	0.858 \pm 0.203 (AB)
Distance traveled (m) ^c	Males	11.22 \pm 1.67 (A)
	Gravid females	2.43 \pm 1.47 (B)
	Postgravid females	7.62 \pm 1.53 (A)
Exercise VO_2 (ml/h) ^c (Model A) ^d	Males	3.105 \pm 0.586 (A)
	Gravid females	3.489 \pm 0.543 (A)
	Postgravid females	4.348 \pm 0.415 (A)
Exercise VO_2 (ml/h) ^c (Model B) ^d	Males	2.823 \pm 0.473 (A)
	Gravid females	3.819 \pm 0.384 (A)
	Postgravid females	4.200 \pm 0.426 (A)

* Like letters in parentheses indicate no significant difference between groups (Bonferroni test).

^a Sample sizes males $n = 8$, gravid females $n = 8$, postgravid females $n = 8$.

^b Sample sizes males $n = 10$, gravid females $n = 9$, postgravid females $n = 8$.

^c Sample sizes males $n = 11$, gravid females $n = 13$, postgravid females $n = 8$.

^d Model A based on ANCOVA with body mass as the covariate; Model B based on ANCOVA with snout-vent length as the covariate (see Table 2).

maculatum). We hypothesized that male and postgravid female salamanders would have greater voluntary and burst speeds, lower rates of oxygen consumption during both rest and exercise, and greater endurance than would gravid females.

MATERIALS AND METHODS

Male ($n = 11$), gravid female ($n = 13$), and postgravid female ($n = 8$) Spotted Salamanders were collected with dip nets from Indian Creek County Park, Butler County, Ohio, in late February of 1998. Animals were transported to Miami University, Oxford, Ohio, where they were housed in pairs in plastic shoeboxes lined with

moistened unbleached paper towels and acclimated to a 12:12 h light cycle and a temperature of 15 C for 7–12 days prior to testing. Animals were weighed (nearest 0.1g) and measured for total length and snout-vent length (nearest mm) before commencing the experiment (see Table 1).

Voluntary crawling speed measurements (cm/sec) were conducted at 15 C, using a 1.0 m \times 13.5 cm \times 6 cm racetrack partitioned into 0.25-m lengths and lined with moist paper towels. Between 1800 h and 2400 h EST and under dim lighting conditions, animals were individually placed onto the racetrack. A video camera linked to a VCR and monitor was used to observe and record the movements of the animal.

The experimenter moved out of the visual field of the animal, and the animal was allowed to voluntarily traverse the racetrack. Voluntary speed was calculated based on the time required to travel a nonstop 0.25-m distance. Three such measurements were taken per animal, with a 15-min period between trials, and the average of the three values was included in statistical analyses. Runs in which the animal appeared to exhibit burst locomotion (e.g., high degrees of axial flexion during movement, etc.) were not included in determining average voluntary crawling speed for an individual.

Burst speeds (cm/sec) at 15 C were examined using the racetrack described above, which was lined with moist paper towels for crawling speed measurements and filled with 15 C dechlorinated water for swimming speed measurements. Under bright lighting conditions, the animal was placed at the end of the track and coaxed to move as quickly as possible with repeated taps to the tail with the experimenter's finger. The movements of the salamander were recorded with a video camera and VCR. Each animal was tested twice for each measurement, with a 1–2 h interval between measurements. The fastest 0.25 m traversal used as the estimate of burst speed.

For measurement of resting O_2 consumption (ml/h), individual animals were placed into 237-ml chambers constructed from modified canning jars connected via rubber tubing to a pair of 50-ml syringes. The chambers were then placed into a darkened water bath at 15 C. After equilibration for 15 min, the air in the chamber was mixed by alternate depression of the plungers of the two syringes, then a 50-ml air sample was withdrawn from each chamber and injected through a drying tube containing a mixture of Drierite and Ascarite into an Ametek Applied Electrochemistry S-3A/II O_2 analyzer. A second air sample was withdrawn from each chamber and tested for O_2 content after a 4-h period had elapsed. Barometric pressure was recorded during both time intervals. The difference in fractional O_2 concentration of this air sample before and after this 4-h period was used to calculate STPD-corrected O_2 consumption (VO_2) using the following equation:

$$VO_2 = (\Delta O_2\%) \times V_s \times (273^\circ K/T) \\ \times [(P - r)/760 \text{ mm Hg}]$$

where $\Delta O_2\%$ = change in fractional O_2 content between the two samples; V_s = the respiratory chamber volume (237 ml + 50 ml for the syringe—the volume of the salamander in ml, assumed to be equal to the mass of the animal in

grams); T = absolute temperature (288 °K); P = atmospheric pressure (mmHg); and r = vapor pressure at 288 °K (here 13 mmHg).

Measurements of locomotor endurance and respiration during exercise were conducted at 15 C using a 1040-ml respirometry chamber containing a motorized 6 cm × 28 cm treadmill. Between 1800h and 2400h EST and under dim lighting conditions, animals were individually placed into the chamber and allowed to adjust to their surroundings for 30 min. Then, a 50-ml air sample was withdrawn from the chamber and tested for O_2 content using an Ametek Applied Electrochemistry S-3A/II O_2 analyzer as described above. The chamber was sealed, and the treadmill was activated at a speed equal to the mean voluntary crawling speed of gravid females (1.2 cm/sec). Animals were coaxed to walk on the racetrack through gentle taps with an internal prod located at the end of the treadmill. Testing continued until the salamander's tail remained in contact with the back of the treadmill for 5 sec. Upon completion, the duration of sustained movement was recorded, and a 50-ml sample of air in the chamber was analyzed for O_2 content. The difference in relative O_2 concentration before and after exercise was used to calculate STPD-corrected VO_2 . Distance traveled was calculated by multiplying exercise duration by treadmill speed.

Potential differences in body size among the three groups (male, gravid female, or postgravid female) were evaluated using one-way ANOVA. Differences in all measurements of locomotion and O_2 consumption were analyzed using analyses of covariance (ANCOVA) with group as a fixed effect in all models. In analyses of burst swimming velocity, total length was selected as the covariate to account for size differences among animals, as the buoyancy of the animals in the water and the anguilliform swimming patterns of salamanders suggest that burst swimming speed is greatly influenced by total body length (see Weatherhead and Robertson, 1992). Body mass was employed as a covariate in analyses for all other measures. However, a second set of analyses was conducted for resting and exercise VO_2 using snout–vent length (which presumably does not change appreciably with gravidity) as the covariate for two reasons: (1) the mass of gravid female reflected both the masses of tissues and eggs (which was unknown); and (2) the metabolism of unfertilized eggs is presumably much lower than is that of the females' tissues (see Angilletta and Sears, 2000; Finkler and Cullum, 2002). Regressions of snout–vent length with body mass did not differ in slope among the three groups, although the

TABLE 2. ANCOVAs EXAMINING DIFFERENCES IN VELOCITY, OXYGEN CONSUMPTION, AND DISTANCE TRAVELED IN MALE, GRAVID FEMALE, AND NONGRAVID FEMALE SPOTTED SALAMANDERS.

Parameter	Factor	<i>F</i>	df	<i>P</i>
Live mass	Group	57.64	2, 29	<0.0001
Snout-vent length	Group	20.41	2, 29	<0.0001
Total body length	Group	31.21	2, 29	<0.0001
Burst crawling speed	Group	0.59	2, 20	0.56
	Mass	0.46	1, 20	0.51
Burst swimming speed	Group	3.57	2, 20	0.05
	Total length	4.59	1, 20	0.04
Voluntary crawling speed	Group	6.22	2, 23	0.005
	Mass	0.80	1, 23	0.38
Resting VO ₂ (Model A) ^a	Group	3.87	2, 26	0.03
	Mass	0.12	1, 26	0.73
	Group × Mass	4.15	2, 26	0.03
Resting VO ₂ (Model B) ^a	Group	5.06	2, 28	0.01
	Snout-vent length	0.09	1, 28	0.77
Distance traveled*	Group	3.37	2, 28	0.05
	Mass	4.93	1, 28	0.03
Exercise VO ₂ (Model A) ^a	Group	2.51	2, 28	0.10
	Mass	1.28	1, 28	0.27
	Log distance	10.38	1, 28	0.003
Exercise VO ₂ (Model B) ^a	Group	1.99	2, 28	0.16
	Snout-vent length	0.64	1, 28	0.43
	Log distance	9.73	1, 28	0.004

* Values log-transformed prior to analysis.

^a Model A based on ANCOVA with body mass as the covariate; Model B based on ANCOVA with snout-vent length as the covariate.

regression for gravid females had a significantly lower intercept than did those for either males or postgravid females. Distance traveled was not normally distributed, and therefore we log-transformed the data prior to analysis. ANCOVAs of exercise VO₂ included log-distance traveled as a second covariate. Models initially tested for interactions among the main effects. In most cases, however, these interaction terms were not significant and were removed from the model. In no case did removal of a nonsignificant interaction term from the model affect the conclusions drawn regarding the main effects.

RESULTS

Females used in this study were significantly larger than were males in all three measures of body size (Tables 1–2). Gravid females were more massive than were postgravid females but had similar snout-vent lengths and total lengths. We did not measure clutch mass directly for the gravid females, but based upon the difference in mean mass between gravid and postgravid females, we estimate the relative clutch mass to be 23% based upon the gravid mass of the female (per Vitt and Congdon, 1978) and 30% based upon the clutch-free body mass of the female (per Shine, 1980).

There was no significant difference among the three groups in burst crawling speed. However, gravid females swam more slowly than did either males or postgravid females. Males voluntarily crawled at significantly faster speeds than did either gravid or postgravid females.

Males had lower rates of oxygen consumption than did either gravid or postgravid females. Resting VO₂ was significantly correlated with mass in postgravid females ($r = 0.73$, $P = 0.013$) but not in males or in gravid females ($r = 0.39$ and 0.38 , respectively, $P > 0.05$).

Gravid females traveled shorter distances before stopping than did either males or postgravid females. However, there was no significant difference in VO₂ during exercise detected among the three groups. Exercise VO₂ correlated negatively with log-distance traveled.

DISCUSSION

Reductions in burst speed are often, but not always, observed in gravid females. Our findings suggest that changes in performance may differ between terrestrial and aquatic locomotion. Contrary to what we hypothesized, there was no significant difference in burst crawling speed among males, gravid females, and postgravid females, suggesting that gravidity does not inhibit

burst crawling performance in *A. maculatum*. However, swimming speed was reduced with gravidity in accord with our hypothesis. The burst swimming speed of gravid females was ~24% lower than was that of both males and postgravid females. Although we did not attempt to quantify it, the degree of axial flexion during swimming seemed to be reduced in gravid females. This, coupled with presumed elevated drag from the increased girth of gravid females, may have reduced the ability of gravid females to generate high swimming speeds. We are unaware of any other studies of changes in performance associated with gravidity involving more than one mode of locomotion, but such research may reveal important insights into the costs of reproduction in amphibious animals.

As we had hypothesized, male Spotted Salamanders had greater voluntary crawling speeds than did both gravid and postgravid female salamanders, even through maximal terrestrial locomotor performance did not appear to differ between males and females. In contrast to our hypothesis, however, gravid and postgravid females did not differ in their voluntary crawling speeds. This may reflect a tendency for females to reduce activity to conserve energy (e.g., Cooper et al., 1990), both during breeding and during the immediate postreproductive period. Alternatively, it may reflect behavioral changes in the males directed toward reaching the breeding site as quickly as possible (see below).

In accord with our hypothesis, resting oxygen consumption rates of female salamanders were markedly greater than those of males, with gravid females having a mean live mass-adjusted rate 68% higher than that of males. Other studies examining effects of sex and reproductive condition on metabolism in amphibians (Fitzpatrick, 1971, 1973; Finkler and Cullum, 2002) also noted higher metabolic rates in gravid females compared to those in males. Curiously, resting metabolic rates in postgravid *A. texanum* females are much lower than those of gravid females (Finkler and Cullum, 2002), whereas there was no significant difference in oxygen consumption rates between gravid and postgravid female *A. maculatum* in the present study. We are unsure as to why this difference between the two studies exists, but one possibility is that recovery from mating and oviposition may be more prolonged in *A. maculatum* than in other salamander species. The relatively high metabolic rate of female *A. maculatum* compared to males likely reflects a pronounced difference between the sexes in the energetic cost of reproduction. A number of factors could account for these changes, including proliferation of tissues asso-

ciated with gravidity (e.g., Birchard et al., 1984; Demarco and Guillette, 1992) and shifts in metabolic capacity (Bauwens and Thoen, 1981; Birchard et al., 1984).

In contrast to our hypothesis, oxygen consumption during exercise did not differ significantly among males, gravid females, and postgravid females. However, in support of our hypothesis, males and postgravid females were able to crawl longer distances before stopping than were gravid females. It is possible that the level of exercise needed to maintain locomotion at the treadmill speed exceeded the aerobic capacity of the gravid females, whereas exercise in the postgravid females and males could be sustained primarily through aerobic metabolism. Further investigation incorporating measures of anaerobic respiration (e.g., lactic acid concentrations) are needed to fully elucidate the effects of gravidity on the metabolic ability of these salamanders to sustain locomotor activity.

The high resting metabolic rates and reduced locomotor performance of gravid female salamanders compared to males may have important implications for the reproductive ecology and life history of *A. maculatum*. Males voluntarily crawl faster and can sustain locomotion longer than can females. This may enable males to arrive at breeding sites earlier than females, thus increasing the potential number of females the male may encounter during the reproductive season. Asynchronous arrival of the two sexes at the breeding pools is commonly observed in *A. maculatum* and in other ambystomatid salamanders (Douglas, 1979; Hardy and Raymond, 1980; Downs, 1989).

Differences in metabolism and locomotor performance may also account for the often male-biased sex ratio observed at ambystomatid breeding sites (Husting, 1965; Flageole and Leclair, 1992; Whiteman, 1997). The reduced burst swimming performance of gravid females may make them more susceptible to predators while in the breeding pools, which could contribute to lowered survivorship in females compared to males in some populations (Husting, 1965; Flageole and Leclair, 1992). Moreover, the elevated energetic cost of reproduction for females likely requires energy that could be used for growth or future reproductive events, perhaps reducing growth rates (Marvin, 2001; but see Flageole and Leclair, 1992), reducing the frequency by which females participate in breeding events (Flageole and Leclair, 1992; Scott and Fore, 1995), or accelerating reproductive senility (Raymond and Hardy, 1990).

Finally, differences in metabolism and loco-

motor performance between males and females may present a selective force favoring larger body size in females to minimize mass-specific metabolism and cost of transport (Stamps et al., 1998) or to increase fecundity (Kaplan and Salthe, 1979). This may contribute to the sexual size dimorphism observed in this and other species of ambystomatid salamander (Downs, 1989; Flageole and Leclair, 1992; Petranka, 1998) and the delayed sexual maturation of females compared to males (Flageole and Leclair, 1992; Marvin, 2001).

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