

Life-history costs of reproductive behaviors in a wetland-breeding amphibian

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Studies examining the association between life-history strategies and behavior can help inform our understanding of the fitness consequences of reproductive behaviors. Breeding migrations are common in numerous taxa and often represent an important reproductive cost. We examined body mass changes of spotted salamanders (*Ambystoma maculatum*) during their seasonal breeding migrations to determine the influence of breeding behaviors on reproductive costs. We sampled salamanders entering and exiting a 0.92-ha ephemeral wetland in the North Carolina Piedmont using a 400-m drift fence completely encircling the wetland. Traps were checked daily during annual breeding migrations in mid-January to early March of 2013 and 2014. The relationship between body mass changes and explanatory factors including sex, duration of stay at wetland, and distance between site entrance and exit were examined using a set of candidate linear mixed models selected a priori and compared using Akaike's information criterion. Female salamanders lost a greater percentage of body mass during the time in the wetland than males as a result of oviposition. Model selection identified duration of stay as the most important predictor of female body mass change with greater duration of stay associated with lower mass loss. In males, percentage mass loss was most closely associated with site entrance–exit correspondence with greater distance between entrance and exit sites associated with greater mass loss. These data demonstrate both the importance of wetland entrance–exit sites and duration of stay at the wetland in determining mass change during spotted salamander reproduction and also that these relationships can differ as a function of sex. Taken together, our findings provide a potential link between behavior, life-history cycles, and costs experienced during reproduction.

Keywords: life history; migration; reproductive cost; wetland; *Ambystoma maculatum*

Introduction

Life-history theory posits that natural selection tends to favor traits that maximize lifetime production of offspring (Cole 1954). Traditionally, life-history studies have examined demographic traits intimately tied to fitness such as body size, age at maturity, and number of offspring (e.g., Stearns 1983, 1984; Roff 1992; Bernardo 1996; Wallace et al. 2007; Lee et al. 2012). Such factors are major components of life-history theory; however, a focus on these demographic traits means less attention has been paid to the relationship between reproductive behaviors (e.g., reproductive migrations) and life-history theory. Life-history traits evolve within and under the direction of a particular ecological context and an organism's behavioral responses to environmental influences can serve to

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maximize the likelihood of reproductive success (Wilbur et al. 1974; Resetarits 1996). Therefore, the study of behavior is important to understanding life history because an organism's behavior can influence the evolution of life history just as life history can influence the evolution of behavior.

Traditionally, studies of reproductive costs have examined the delayed, post-breeding outcomes including the reproducing organism's growth and reproductive output in later breeding seasons (e.g., Bernardo 1996; Lee et al. 2012). However, pre-breeding costs of parental investment (e.g., costs incurred through mating behavior, migration movement, increased foraging for resources) are also a significant component of an organism's life history (Jonsson et al. 1998). The pre-breeding period can exert a critical influence on animal survival as upregulation of stress hormones and metabolic rates can leave the reproducing organism more susceptible to predation, starvation, or disease (Jones & Ward 1979; Birchard et al. 1984; Angilletta & Sears 2000; Homan et al. 2003; Moore & Jessop 2003). Pre-breeding costs may include the loss of body mass or decreased body condition from the reproductive event (Ryser 1989; Lemckert & Shine 1993). These changes can have an important effect on current and future reproductive behaviors and may influence the evolution of an organism's life-cycle history. For example, the evolution of larger clutch sizes and multiple reproductive events in a single year has resulted in increased body mass loss observed in common eastern frogs (*Crinia signifera*, Lemckert & Shine 1993). Behavioral response during reproduction can also modify the costs of a breeding event, such as changes in relative clutch mass or body condition (Brodie 1989). For example, in the European common frog (*Rana temporaria*), increased time spent in breeding ponds is associated with greater mass loss in males and females as a consequence of reduced feeding (Ryser 1989). Links between life-history strategies and behavior can help inform our understanding of the fitness consequences of reproductive behaviors and evolution of life-cycle history and associated behaviors.

Breeding migrations are observed in a variety of taxonomic groups and these migrations can incur reproductive costs for the migrating animal, such as decreased body condition (Alerstam et al. 2003; Dingle & Drake 2007; Crossin et al. 2009; Rittenhouse et al. 2009). Pond-breeding amphibians participate in predictable and directed breeding migrations and are a taxonomic group with important ecological and conservation implications (for details on the importance of pond-breeding amphibians, see Semlitsch & Bodie 1998; Wake & Vredenburg 2008). One such amphibian with a well-described breeding migration is the spotted salamander (*Ambystoma maculatum*). Spotted salamanders migrate to ephemeral wetlands for breeding (Freda 1983), where larvae hatch and grow within the aquatic environment (Figiel & Semlitsch 1995; Petranka 1998). The breeding migration of spotted salamanders is influenced by a variety of environmental factors, and several studies have provided the detailed descriptions of these migration movement patterns. Namely, high site fidelity (i.e., return to the same wetland location) is observed during spotted salamander annual migrations with males arriving earlier than females and females traveling a greater distance than males (Whitford & Vinegar 1966; Regosin et al. 2003; Tennessen & Zamudio 2003; McDonough & Paton 2007). During the time spent in the breeding pond, spotted salamanders are thought to consume little prey (Smallwood 1928; Petranka 1998), thereby making body mass changes a potential correlate of reproductive effort. Although several studies have examined environmental factors influencing spotted salamander breeding migrations, these studies seldom examined the energetic costs related to breeding site selection and the role of other behavioral responses in determining the costs of reproduction. For example, high concordance in wetland entrance and exit sites (i.e., entrance–exit fidelity) is observed in migrating spotted salamander (Shoop

1965, 1968; Phillips & Sexton 1989); however, it is unknown if this behavioral response has developed as a result of the associated reproductive costs.

The purpose of this study was to examine behavioral factors influencing spotted salamander reproductive costs (i.e., body mass and body condition changes) including entrance–exit site fidelity and time spent in the breeding pond. We hypothesized that behaviors commonly observed in spotted salamander breeding would be associated with lower reproductive costs. Therefore, we predicted that spotted salamanders that moved the greatest distances between pond entrance and exit (an indirect measure of energetic concerns related to increased movement for breeding site selection in the pond) and that stayed longer would show the largest decreases in percentage body mass and body condition. Additionally, we predicted that females would show a larger decrease in percentage body mass than males as a result of oviposition. To test these hypotheses, we conducted a mark–recapture study of spotted salamanders during their annual breeding migration using a drift fence completely encircling an isolated, ephemeral wetland.

Methods

Study site

Our study site consisted of a 0.92-ha isolated, ephemeral wetland at the Cowan's Ford Wildlife Refuge in Mecklenburg County, NC, USA (35° 22' 48.659" N, 80° 58' 6.710" W; Steelman & Dorcas 2010). The wetland is bordered by an area of mixed hardwood and pine forest, and contains wetland vegetation of tall grasses and shrubs. During 2013 and 2014, a drift fence 400 m long, 50 cm high, and buried 10–15 cm deep completely encircled the wetland (Gibbons & Semlitsch 1981). Thirty-eight pairs of pitfall traps (13-L plastic buckets) were placed every 10 m, one on either side of the fence, and each bucket included a moist sponge to prevent animal desiccation.

Data collection and measures

Daily surveys were conducted from mid-January to early March of 2013 and 2014. Each fence trap was checked for spotted salamanders entering and exiting the ephemeral pond. All spotted salamanders captured in fence traps were given a unique identification code using visible implant elastomer injected subcutaneously (VIE; Northwest Marine Technologies, <http://www.nmt.us>; Grant 2010).

After the capture, each salamander was identified and the following measurements were taken: sex (based on secondary sex characteristics such as gravidity and swollen cloacal regions), mass (to the nearest 0.1 g), total length (TTL; mm), and snout–vent length (SVL; mm). All salamanders were released on the day of capture on the opposite side of the fence approximately 2 m from the capture site. The duration of stay was calculated as days from entrance to exit in the wetland. Entrance–exit site fidelity was determined as distance between site entrance and exit (in m). Only salamanders with a complete behavioral history (i.e., entrance and exit data; 141 of the 656 captures; 21.5%) from the 2013 breeding season were included in body mass change analysis. Salamanders with entrance data from the 2013 and 2014 season were used for the entrance-site fidelity secondary analysis.

Data analysis

Body mass change was evaluated as the percentage change in body mass from wetland entrance to exit. Body condition was estimated using scaled mass index (SMI). SMI

offers benefits over traditional measures of body condition (e.g., simple ratios of length to mass) because it accounts for the allometric relationship between body structure and mass. To calculate SMI, we followed Peig and Green (2010) and MacCracken and Stebbings (2012) procedures. Briefly, we (1) fitted a line to the length (TTL) and mass data using an ln-ln scale and used the slope estimate as the power variable in the SMI function, (2) calculated the mean length that is used as a constant in the SMI function, and (3) estimated SMI for each individual using the formula: $SMI = M_i (L_0/L_i)^b$ where M_i is the subject's mass, L_0 is the mean body length of the group, L_i is the subject's length, and b is the slope of the standard major axis (SMA) regression of mass on length.

To determine the influence of sex on body mass change, we conducted an Analysis of Covariance (ANCOVA) with sex as the between-subjects factor, percentage change in body mass as the outcome, and initial mass as a covariate. We also determined the influence of sex on body condition changes using an ANCOVA with sex as the between-subjects factor, change in body condition as the outcome, and initial mass as a covariate. To meet the assumptions of normality and linearity for parametric analyses, all mass measurements were log-transformed.

We assessed the factors influencing body mass and body condition changes using general linear mixed models ranked by Akaike information criteria corrected for small sample sizes (AIC_c ; Burnham & Anderson 2004). General linear mixed models were computed using a Gaussian distribution and AIC_c values calculated using maximum likelihood (ML) estimation. The criterion used was percentage body mass change or change in body condition (i.e., SMI), and candidate models were built from the following predictors: mass at entrance, duration of stay, and distance between site entrance and exit. Interactions were not included in order to minimize possible overfitting models for our sample size (~70 in each group). Because of the inherent sex difference in mass change (i.e., female gravidity), we choose to conduct separate AIC_c analyses for each sex. Models were ranked using weighted AIC_c values and the relative importance of each model determined using ΔAIC_c (Burnham & Anderson 2004). Models with less than a 2.0 difference in ΔAIC_c were averaged and the averaged model was used to estimate the standardized beta values and associated standard errors for each included predictor.

Based on initial evaluation of AIC_c outcomes, a *post hoc* comparison of entrance site fidelity was conducted to evaluate potential sex differences as they related to wetland entrance–exit behavior. Fidelity was measured as a continuous variable representing the distance between entrance sites used by an individual subject in 2013 and 2014. Males and females were compared for entrance fidelity using an independent samples *t*-test. All statistical tests were conducted in R (version 2.15.2, R Development Core Team 2012) with statistical significance set at $p < 0.05$.

Results

We collected complete entrance and exit data for 141 salamanders (77 females and 64 males) during the 2013 breeding migration. During 2013, all salamanders arrived to the wetland on the same date following a large, overnight rainfall. Males tended to be shorter, weigh less, and stay in the wetland longer than females (Table 1). After controlling for initial body mass, female salamanders lost a greater percentage of body mass ($27.97 \pm 0.84\%$) than males ($12.69 \pm 0.66\%$) during the time spent in the wetland (ANCOVA; sex: $F_{1,138} = 113.8$, $p < 0.01$; Figure 1). Female salamanders showed a greater change in SMI than male salamanders (ANCOVA; sex: $F_{1,138} = 75.4$, $p < 0.01$).

For males, AIC_c model selection failed to provide strong support for a single model predicting percentage body mass loss with five models differing by less than 2.0 (Table 2).

Table 1. Characteristics of spotted salamanders marked and recaptured during the 2013 breeding season.

Measure	Males ($n = 64$)	Females ($n = 77$)	95% CI LL	95% CI UL
Mass-enter (g)	19.15 ± 0.46	29.96 ± 0.55	-12.26	-9.36
Mass-exit (g)	16.69 ± 0.40	20.79 ± 0.45	-5.31	-2.89
% mass change	27.97 ± 0.84	12.69 ± 0.66	13.20	17.36
SVL (mm)	95.17 ± 0.79	106.29 ± 0.72	-13.23	-9.00
TTL (mm)	183.3 ± 1.61	197.29 ± 1.47	-18.30	-9.68
Days spent	14.06 ± 0.80	9.42 ± 0.31	3.05	6.23
Distance (m)	29.69 ± 4.44	33.51 ± 3.77	-15.26	7.62

Note: Mass-enter = mass at wetland entrance; Mass-exit = mass at wetland exit; SVL = snout-vent length; TTL = total length; Days spent = days spent in wetland; Distance = distance from site entrance to exit.; LL = lower limit; UL = upper limit. Values represent mean ± standard error of the mean (SEM) and 95% confidence intervals (CI). Bold values indicate significant differences between sexes after correcting for multiple comparisons ($p < 0.05$).

Model averaging of these five models indicated that body mass loss increased with greater distances between site entrance and exit ($\beta = 0.240$, $SE = 0.12$, 95% CI [0.001, 0.479]). This model also indicated that mass loss tended to increase with greater initial mass ($\beta = 0.193$, $SE = 0.122$, 95% CI [-0.046, 0.432]) and days spent in the wetland ($\beta = 0.159$, $SE = 0.122$, 95% CI [-0.080, 0.398]), but neither of these parameters were significant predictors in the averaged regression model as the confidence intervals contained zero.

The best model explaining female spotted salamander body mass loss was one that incorporated only days spent in wetland ($w_i = 0.50$; Table 3). Parameter estimates indicated that female salamanders that stayed for shorter periods tended to lose a greater percentage body mass than those that stayed longer in the wetland ($\beta = -0.259$, $SE = 0.112$, 95% CI [-0.477, -0.04]).

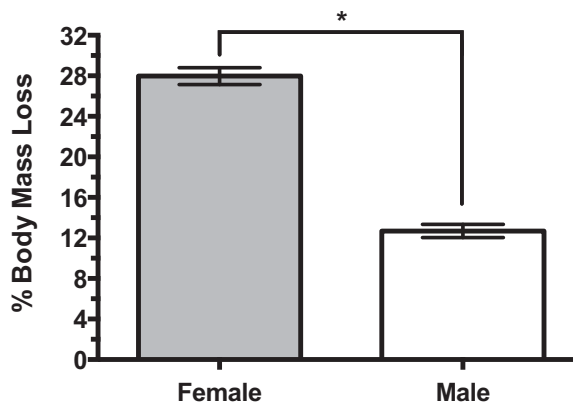


Figure 1. Percentage body mass loss for female and male spotted salamanders during time spent in Cowan's Ford wetland during the 2013 breeding season. Individual salamanders were marked during entrance to and recaptured during exit from an ephemeral wetland at Cowan's Ford using a drift fence encircling the breeding pond. Bars represent mean percentage body mass loss from site entrance to exit for female (gray bar; $n = 77$) and male (white bar; $n = 66$) spotted salamanders. Error bars represent the standard error of the mean (SEM). * $p < 0.05$ after controlling for initial salamander mass.

Table 2. AIC_c model selection for regression of predictor variables (days spent in wetland, mass at site entrance, and distance between site entrance and exit) against percentage mass loss for male spotted salamanders.

Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>
Mass + distance	4	182.72	—	0.23
Distance	3	183.01	0.29	0.20
Mass + days + distance	5	183.30	0.58	0.17
Days + distance	4	183.51	0.79	0.15
Mass	3	184.39	1.67	0.10
Mass + days	4	184.75	2.03	0.08
Days	3	185.10	2.38	0.07

Note: ΔAIC_c = difference in AIC_c relative to top model; *w_i* = AIC_c weight; *K* = number of estimated predictors in model; Mass = mass at site entrance; Days = days spent in wetland; Distance = distance between site entrance and exit. Bold models were model-averaged for parameter estimates.

To explore potential factors mediating the relationship between female body mass and days spent in wetland, secondary correlational analyses of the data were conducted. Females that stayed longer tended to weigh less upon entering the wetland, although this correlation only approached statistical significance ($r = -0.201$, $p = 0.080$, 95% CI [-0.406, 0.025]). In contrast, there was no relationship between male mass at entrance and length of stay ($r = 0.038$, $p = 0.765$, 95% CI [-0.210, 0.281]). The number of days spent in the breeding pond was not related to SVL in either male or female salamanders ($r = 0.014$ and 0.138 , respectively, $p > 0.233$).

Analysis of body condition changes revealed no difference in results for male salamanders. For female salamanders, the best model explaining body condition change was one that incorporated days spent in wetland as well as initial body mass with shorter periods of wetland stay ($\beta = -0.268$, SE = 0.106, 95% CI [-0.475, -0.061]) and higher initial body mass ($\beta = 0.318$, SE = 0.106, 95% CI [0.111, 0.526]) predicting greater decreases in body condition.

Entrance site fidelity in the following breeding season (i.e., 2014) indicated higher entrance site fidelity in males (34.15 ± 8.49 m) than females (61.25 ± 12.45 m);

Table 3. AIC_c model selection for regression of predictor variables (days spent in wetland, mass at site entrance, and distance between site entrance and exit) against percentage mass loss for female spotted salamanders.

Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>
Days	3	218.50	—	0.50
Days + distance	4	220.64	2.14	0.17
Mass + days	4	220.73	2.23	0.16
Mass + days + distance	5	222.93	4.42	0.05
Distance	3	222.93	4.43	0.05
Mass	3	223.60	5.10	0.04
Mass + distance	4	224.98	6.47	0.02

Note: ΔAIC_c = difference in AIC_c relative to top model; *w_i* = AIC_c weight; *K* = number of estimated predictors in model; Mass = mass at site entrance; Days = days spent in wetland; Distance = distance between site entrance and exit.

however, this difference was not statistically significant ($t(41) = 1.835, p = 0.075, 95\% \text{ CI} [-0.275, 5.605]$).

Discussion

Our results indicate that behaviors during spotted salamander reproduction can influence breeding costs and that this association differs as a function of sex. Specifically, we observed greater body mass loss and decrease in body condition in female salamanders compared to males. Mass loss and body condition change in males were most closely associated with entrance–exit site fidelity with greater distance between entrance and exit sites predicting greater decreases in mass loss and body condition. Contrary to expectations, female mass loss and change in body condition were negatively correlated with duration of stay in the wetland potentially as a consequence of egg mass development. Collectively, these findings provide a link between reproductive behaviors and costs, as well as evidence that demographic factors (i.e., sex) can moderate this relationship.

Numerous studies conducted on reproducing salamanders have observed greater mass loss during reproduction in females than males (e.g., Sexton et al. 1986; Windmiller 1996; Gamble et al. 2008; De Lisle & Grayson 2011). Our data are consistent with previous studies conducted with spotted salamanders that indicated mass losses of 4.5%–13% in males and 24.1%–38% in females (Sexton et al. 1986; Windmiller 1996). Sex differences in mass losses are likely a consequence of female gravidity and subsequent oviposition, as well as male's smaller size on entrance. In the current study, wetland behaviors were also dependent on sex as males spent more time in the wetland than females. In contrast to previous studies (Sexton et al. 1986; Tennessen & Zamudio 2003), these findings could not be attributed to arrival date because males did not arrive at the wetland before females in the present study. Although weather pattern could have affected movement patterns, both sexes were present in the pond during the same period of time (i.e., all salamanders arrived on the same date) and as such weather did not differentially affect either sex. Differences in duration of stay could be a result of life-history characteristics, in particular the tendency for females to exit immediately after oviposition and for males to stay in the wetland to maximize potential for multiple mating events (Arnold 1976; Petranka 1998).

Predictors of mass loss and body condition in males supported our hypothesis because the greatest mass loss was associated with greater distances between site entrance and exit and longer stay in the wetland. However, model averaging indicated that the most important predictor was entrance–exit site fidelity and, thus, duration of stay had less of an influence on mass loss. Males tend to deposit spermatophores on multiple occasions, extending males' stay in the wetland (Arnold 1976; Petranka 1998). Numerous studies have also documented high entrance–exit site fidelity in spotted salamanders (Shoop 1965, 1968; Phillips & Sexton 1989). It is possible that greater movement from site entrance to exit could be associated with greater energetic expenditure in the pond as a result of breeding site selection. It is also possible that salamanders that occupied less than optimal overwintering and foraging habitats (and as such were less than optimally fit) prior to breeding would have entered and exited the wetland at further distances to seek out better environments outside the breeding season. Although our findings are only correlational, these data support the importance of energetic considerations in the high fidelity of site entrance to exit. Together, these associations between reproductive behaviors and costs for male salamander reproduction support the multi-dimensional nature of life-history theory wherein behavioral responses, demographic traits, and reproductive

costs interrelate to determine life-cycle characteristics (Zera & Harshman 2001; Sinervo & Clobert 2008).

Our hypothesis that mass loss would be positively correlated with duration of stay within the wetland and the entrance to exit site distance was not supported in females. Instead, the greatest mass loss was observed in females occupying the wetland for the shortest durations. Most females entering the wetland were gravid and, therefore, a significant amount of mass loss can be attributed to oviposition. Because we were unable to distinguish the mass lost as a result of depositing the egg sac from mass lost due to other behaviors, percentage mass loss in females represents both reproductive cost and reproductive output (i.e., egg mass weight). It is possible that females that spent less time in the wetland carried more developed, heavier egg masses and, therefore, were prepared for reproduction and subsequent oviposition sooner upon wetland entrance. Supporting this assertion, we found that salamanders that stayed longer tended to weigh less at entrance. It is not likely that the association between wetland stay and initial mass was a consequence of body size because SVL was not related to duration of stay. Furthermore, male entrance mass was not related to duration of stay providing additional support for the role of egg mass development in the relationship between females' initial mass and length of stay. Alternatively, prey consumption may explain the lower levels of mass loss observed in females staying longer. Although minimal prey consumption has been observed in breeding spotted salamanders (Smallwood 1928; Petranka 1998), females that stayed longer could have also consumed prey, thus losing less body mass during wetland stay.

In contrast to males, site entrance–exit was not an important predictor of mass loss in females. Sex differences in the importance of wetland entrance site were further supported by a trend towards higher entrance–entrance site fidelity observed in male salamanders over two breeding seasons. These results may be a consequence of the greater distances traveled to the wetland by females (Regosin et al. 2003; McDonough & Paton 2007). Males tend to occupy upland sites close to the breeding site where densities are higher and habitat is more limited (Regosin et al. 2003); therefore, males may be more motivated than females to return to the exact home location and site entrance as a result of this 'owner-advantage'. Our findings suggest that these life-history differences may be a consequence of differences in reproductive costs between the sexes.

Several limitations of the present study should be noted. First, our data collected using a drift fence do not provide direct insight into the cost of reproductive migrations, only the costs at the breeding site. Because migration represents a substantial cost of amphibian reproduction, future studies could evaluate how the observed behavioral factors might relate to costs accrued during migration. Second, due to sampling constraints we were unable to incorporate changes in tail length as a dependent variable in our study. Future studies could use tail length change as an indication of reproductive effort that is independent of sex in order to better reveal the possible influence of sex on the observed behavioral factors. Third, we did not examine the direct effects of mass changes on future fitness (e.g., future clutch sizes), limiting the generalization to evolutionary processes. Future investigations could evaluate the outcomes such as egg mass size or years between breeding events in order to further relate behavioral measures with the evolution of life-history cycles.

Taken together, the present findings provide a potential link between life-history cycles, behavior, and the costs observed during reproduction. We identified several behavioral mechanisms that affect reproductive costs in a sex-dependent manner. Our findings highlight the potential importance of behavioral responses to the environment in determining life-history characteristics and cycles.

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