POPULATION BIOLOGY AND MOVEMENT BEHAVIOR OF THE NORTHERN SPRING SALAMANDER, *GYRINOPHILUS PORPHYRITICUS*, IN FOUR NEW HAMPSHIRE HEADWATER STREAMS

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Abstract. Demography and dispersal of *Gyrinophilus porphyriticus* (Plethodontidae), the Northern spring salamander, were investigated in four fishless headwater streams in the White Mountain National Forest, New Hampshire. Eight mark-recapture surveys were used to sample 125 m sections of Falls, Canyon, Black East, and Black West brooks during June and July 2003. The Jolly-Seber model in Program MARK was used to estimate initial population size, daily survival, and daily population growth rates in three streams. There was an insufficient number of recaptures for mark-recapture analysis in Black East. Population sizes varied among streams with Falls brook having approximately twice as many individuals than any other stream (N[± SE] = 162.6 ± 57.8 versus N = 80.0 ± 32.0, N = 67.2 ± 16.8). Daily survival and population growth rates were remarkably similar among streams (S±SE = 0.96 ± 0.04, 0.96 ± 0.04, 0.96 ± 0.03; λ = 0.96 ± 0.02, 1.00 ± 0.02, 1.00 ± 0.03). Directional bias and probability of movement was estimated in all four streams. The proportion of individuals moving in Black West was the largest (p = 0.52 versus p = 0.32, 0.36, 0.33), and it was the only stream in which individuals did not display a significant upstream bias in movement. All population-level parameters were consistent between life history stages in each study stream. These results can serve as a benchmark for comparison with populations of *G. porphyriticus* and other stream salamanders in streams impacted by human activities, and in streams with fish predators.

INTRODUCTION

An understanding of local population biology is critical in addressing basic and applied questions in ecology. Population dynamics are a function of local demographic rates (i.e., births and deaths) and dispersal (i.e., immigration and emigration), and these two sets of processes are linked by both ecological and evolutionary factors (Wright 1969, Hanski and Gilpin 1997). Consequently, investigations of basic population ecology provide insight on emergent biological properties such as patterns of community structure and local adaptation. In addition, efforts to manage and conserve species, including basic monitoring programs, are greatly improved by an understanding of population biology (Heyer et al. 1994, Biek et al. 2002). This has become especially important in amphibian biology, where such efforts are imperative in dealing with worldwide amphibian declines (Wake 1990, Blaustein et al. 1994, Houlahan et al. 2000).

Amphibian life cycles are marked by a complex ontogenetic niche shift from larvae to adult, where individuals undergo morphological, physiological, and behavioral changes to accommodate new habitats (Wilbur 1980). Such complex life cycles are thought to make amphibians susceptible to perturbations (Vitt et al. 1990, Blaustein et al. 1994, Stebbins and Cohen 1995, Alford and Richards 1999). Stream amphibians, in particular, have highly specialized adaptations for refuge use and foraging, making them vulnerable to a variety of stresses in lotic systems (e.g., sedimentation, change in discharge regime, elimination of riparian vegetation, etc.) (Kerby and Kats 1998, Welsh and Ollivier 1998, Lowe et al. *In press*). Considering the influences on stream amphibian abundance and distribution of both the physical habitat (Hawkins et al. 1983, Corn and Bury 1989, Welsh and Ollivier 1998, Lowe and Bolger 2001, Barr and Babbitt 2002) and local biota (Petranka 1983, Sih et al. 1992, Resetarits 1997, Lowe and Bolger 2002, Barr and Babbitt 2002), one might expect to find natural variation in demography and movement behavior between streams. However, most intensive studies of stream amphibian demography (Burton

and Likens 1975, Bruce 1988, Lowe 2003) and dispersal (Johnson and Goldberg 1975, Bruce 1986, Lowe 2003) have been limited to individual populations. Consequently, little is known about natural variation among populations in these fundamental characteristics.

Gyrinophilus porphyriticus (Plethodontidae) is a common salamander in headwater streams of the northeastern U.S. In an intensive three-year study of one population, Lowe (2003) showed that upstream-biased dispersal contributed to the equality of population growth rates in upstream and downstream sections of a 1000 m stretch of stream. He also showed that population growth rates were relatively stable over time, and that survival probabilities were similar for adults and larvae. However, the generality of these patterns is unknown. The goal of this study was to assess among-stream variability in *G. porphyriticus* population biology. To meet this goal, I used mark-recapture methods to quantify daily *G. porphyriticus* survival and population growth rates in four fishless headwater streams in central New Hampshire and to estimate total population sizes in the study sections of these streams. To assess variability in the dispersal behavior of *G. porphyriticus* individuals, I analyzed the directional bias and frequency of movement using data from recaptured individuals in the study streams.

METHODS

Study species and site

G. porphyriticus is a member of the family Plethodontidae (lungless salamanders) and is distributed throughout the Appalachian mountains from southern Quebec to central Alabama (Petranka 1998). It is a large salamander (up to 112 mm snout-vent length [SVL]) and is often found at high elevation in cool, well oxygenated, headwater streams. Oviposition occurs from May through September in the northeastern part of its range (Bishop 1941) and the larval period is typically 3-4 years, but can be up to 6 years (Bishop 1941, Bruce 1980, Reseterits 1995). In the northeast, adults mainly forage just outside the stream for terrestrial insects while larvae forage within the stream, although adults take aquatic insects as well (Burton 1976).

This study was carried out in four streams in the White Mountain National Forest, New Hampshire. Falls Brook and Canyon Brook are second-order streams in the Hubbard Brook Experimental Forest, Thornton, New Hampshire. Black West Brook and Black East Brook are first-order streams in Lincoln, New Hampshire. I established 125 m-long study sections in each stream. All four streams had natural barriers to brook trout (Salvelinus fontinalis). Electrofishing surveys of the study reaches of Black West and Black East conducted in August 2000 and 2001 confirmed that these streams were fishless (Lowe et al. In press). Minnow traps were used to confirm that Falls and Canyon were fishless. I placed thirteen traps in the study sections of these streams for two days and nights. No fish were found in the traps at the end of this sampling period. In a previous study (Hogan 2000), minnow traps were found to be an accurate method of assessing brook trout occurrence and abundance in small streams.

The tree stratum in the study drainages is dominated by Acer saccharum, Fagus grandifolia, Betula alleghaniensis, Picea rubens, Abies balsamea, and Betula papyrifera (Bormann et al. 1970). Headwater streams in New Hampshire have low conductivity (12.0 – 15.0 μS), slight acidity (pH of 5.0 – 6.0), high dissolved oxygen content (80-90% saturation), and moderate midday summer temperatures ($13.0^o – 17.0^o$ C) (Lowe and Bolger 2002). The study streams were dominated by run-riffle-pool reach types (Montgomery and Buffington 1997), and all had moderate gradients (2 – 4% slopes).

Field methods

In 2003, eight mark-recapture surveys were conducted in each study section between June 26 and July 17. Surveys took place on two subsequent days, followed by a four-day interval. Sampling ended after the fourth two-day period due to the onset of a period of intense rain and high-flow events. I used a cover-controlled active

search sampling method (Heyer et al. 1994). Moving upstream, I turned over 125 cover objects (rocks between 64-256 mm diameter) from within the main channel and along the bank and edge of the stream, maintaining a constant effort of one rock per meter of stream length. I used an aquarium dip net to capture salamanders, including those flushed downstream by the current. All unmarked G. porphyriticus larvae and adults captured were individually marked by a subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). I also recorded the longitudinal position (distance upstream from the start of the study section in meters), length (SVL, mm), and mass (mg) for each captured individual. Other amphibians encountered were Eurycea bislineata (Plethodontidae), Desmognathus fuscus (Plethodontidae), Rana melanota (Ranidae), and Bufo americanus (Bufonidae).

Mark-recapture analysis

The Jolly-Seber model (Seber 1973) in the MARK computer program (White and Burnham 1999) was used to estimate daily survival (S, probability that an animal alive at time t will be alive at time [t + 1]), daily population growth rate (λ, population growth from time t to time [t + 1]), initial population size (N), and daily recapture probability (p, probability of recapturing a marked animal at time t) in the study reaches. Jolly-Seber models an open population, thus incorporating births, deaths, immigration, and emigration. This model is based on the following assumptions: (1) every individual has the same probability of being captured in the tth sample, whether marked or unmarked, (2) every marked individual has the same probability of surviving from the *t*th to the (t + 1) sample, (3) individuals do not lose their marks, (4) marks are not overlooked at capture and (5) sampling time is negligible in relation to the intervals between samples.

Program MARK uses maximum likelihood analysis to identify best fitting models from a set of models varying in complexity (White and Burnham 1999). Daily survival, daily population growth, and initial population size were modeled as either variable by life-history stage or the same for both stages (larva v. adult). Daily recapture probabilities were set as variable by stage to control for the possibility that larvae are more difficult to capture than adults due to their small size, ability to dart under adjacent cover objects during sampling, and potential of becoming concealed in sediment that is released when rocks are lifted (B.J. Cosentino, personal observation).

Akaike's information criteria (AIC; Akaike 1973, Burnham and Anderson 1998) was used to identify models that best represented the data with as few parameters as possible. A trade-off is thus made between potential bias caused by having too few parameters and poor precision of parameter estimates caused by having too many parameters. Second-order AIC (AIC_c) differences (ΔAIC_c; Burnham and Anderson 1998) were used to rank candidate models. ΔAIC_c represents the difference between AIC_c for each model and the best fitting model, the model with the lowest observed AIC_c. AIC_c weights are used to estimate the relative likelihood of each model in a candidate set (Buckland et. al. 1997), with the AIC_c weights for models within a set summing to 1.

Movement analysis

Movement was measured as the distance in meters from the point of last capture. I quantified movement by constructing frequency distribution histograms, where positive values represented upstream moves and negative values represented downstream moves. I then tested for skewness in the movement distribution to assess directional bias (Zar 1984) and calculated the probability of movement as the proportion of individuals that moved one meter or more, pooling recaptured animals across all recapture intervals.

RESULTS

Demography

In the best-fitting Jolly-Seber model, daily survival, daily population growth rate, and initial population size of G. porphyriticus individuals were consistent between life-stages in Falls, Black West, and Canyon (Table 1). There were an insufficient number of recaptures in Black East for mark-recapture analysis of this population. Estimated recapture probability of individuals was greater for larvae than adults in Falls but was not different between life-stage in Black West and Canyon (Table 2). Daily survival and daily population growth rates were consistent across streams (Table 2). Initial population sizes were similar in Black West and Canyon, but approximately 50% greater in Falls (Table 2).

Movement

I found that movement by *G. porphyriticus* individuals was biased in the upstream direction in three of four streams - Falls, Canyon, and Black East (Fig. 1, Table 3). In Black West there was no bias in the movement distribution. The movement distributions of larvae and adults did not differ in the four streams (Kolmolgorov-Smirnov tests, $P > 0.05$). Probability of movement was similar in Falls, Canyon, and Black East (Table 3), and considerably higher in Black West (approximately 55%).

DISCUSSION

My study is the first to document consistent demographic rates and movement patterns among stream salamander populations. Given the variety of abiotic and biotic factors shaping stream salamander abundance (Bruce 1972, Hawkins et al. 1983, Corn and Bury 1989, Barr and Babbitt 2002, Lowe and Bolger 2002, Lowe et al. *In press*), it is surprising that *G. porphyriticus* populations exhibited only slight variation in demography and dispersal. Daily population growth and survival rates were similar among streams. In addition, individuals in Falls, Canyon, and Black East demonstrated a consistent upstream-bias in movement, and similar overall proportions of individuals moved. These population-level parameters were also consistent in the two life history stages, which is surprising considering the basic morphological and ecological differences between the stages.

What explains the remarkable demographic consistency observed among *G. porphyriticus* populations and life stages? In 15 New Hampshire populations, Lowe et al. (*In press*) found that the abundance of *G. porphyriticus* larvae was negatively related to brook trout abundance and unrelated to substrate embeddedness, while adult abundance was primarily related to substrate embeddedness. Larval and adult abundances were not correlated in these streams, which the authors interpreted as a possible indication of donor stage density-independent recruitment. In my study, however, daily survival, daily population growth rates, and population sizes were consistent between life stages. In the fishless and relatively undisturbed streams I sampled, where *G. porphyriticus* larvae are not affected by the predatory and competitive pressures of brook trout (Resetarits 1991, 1995), larval and adult populations may be regulated by similar density dependent factors, resulting in the observed demographic consistency. Interference or exploitative competition (Petranka and Sih 1986, Buskirk and Smith 1991, Hixon et. al. 2002) for limiting resources such as food and refuge, in addition to the impacts of non-fish predators and disease (Blaustein and Kiesecker 2002, Hixon et. al. 2002), may affect larval and adult stages similarly when stage-specific factors (i.e., brook trout and sedimentation) are removed.

Whereas previous studies have examined long-term population dynamics in stream amphibians (e.g., Tilley 1980, Hairston 1987), this is the first to offer a perspective on population dynamics within a single season of sampling. My mark-recapture surveys of *G. porphyriticus* within the stream channel suggest that the Black West and Canyon populations are relatively stable ($\lambda \approx 1$) over the study period. Conversion of daily to monthly survival rates ($S^{30} = 0.29$ in Black West, Canyon, and Falls) indicates that stability was maintained even in light of high monthly mortality. In a 3-yr study of one stable population ($\lambda = 1.01$), Lowe (2003) found monthly survival estimates for

G. porphyriticus individuals to be between 0.94 and 0.97. However, because the data set used to derive these estimates spanned multiple years, with just three surveys occurring between June and August of each year, these estimates do not represent variation among seasons in survival probabilities. In Black West and Canyon, dispersal from nearby populations (Lowe 2003) in combination with recruitment and high winter survival rates, may compensate for high summer mortality to maintain population stability. The slightly lower population growth rate in Falls may be a consequence of its large population size. In populations regulated by density-dependent negative feedback mechanisms (Hixon et. al. 2002), population growth rates can vary according to local population size. Population size variation in the study streams may reflect differences in the biotic and abiotic composition of these streams, including aspects of habitat size that I did not measure (e.g., the fluctuating size of the hyporheic zone and the width of the stream channel).

Movement of *G. porphyriticus* larvae and adults exhibited upstream bias in three of the four streams I sampled. Although the skewness of movement in Black West was not significant, its positive value is indicative of a tendency for individuals to move upstream. This adds to the evidence that upstream dispersal is a general trend for *G. porphyriticus* larvae and adults (Lowe 2003). In each population with a significant upstream bias, the proportion of individuals moving was approximately 0.33. This surprising consistency in movement probability across the streams may suggest that there is a genetic basis for the movement behavior of this species. More specifically, the consistent proportion of "movers" in the three populations may be indicative of a genetically-based polymorphism in movement behavior resulting in sub-populations of "movers" and "stayers" (Skaliski and Gilliam 2000, Lowe 2003). When movement data from all individuals was pooled across the four streams, the probability of adult movement was negatively related to their size (B.J. Cosentino, W.H. Lowe, and G.E. Likens, *unpublished data*), suggesting that movement behavior may also be related to individual characteristics. Research on the genetic structure of *G. porphyriticus* populations and the heritability of movement, in addition to identifying phenotypic characteristics of "movers" and "stayers" within populations, is needed to better understand the proximate and ultimate causes of dispersal behavior.

G. porphyriticus is sensitive to land-use in headwater drainages (Lowe and Bolger 2002), suggesting that it may be a useful indicator for the management of these systems. While stream amphibians are long-lived organisms that have relatively stable populations, they are still prone to human-caused disturbances such as sedimentation associated with timber-harvesting (Hawkins et al. 1983, Corn and Bury 1989, Welsh and Ollivier 1998, Lowe and Bolger 2002). My field data indicated that *G. porphyriticus* exhibits consistent patterns of demography and dispersal among both populations and life stages in fishless headwater streams. These data can serve as a benchmark for comparison in both basic and applied research on the population biology of *G. porphyriticus* and other stream salamanders in streams impacted by human activities, and in streams with fish predators.

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APPENDIX

TABLE 1. Jolly-Seber models of daily survival (S), recapture probability (p), daily population growth (λ), and initial population size (N) in Black West Brook, Canyon Brook, and Falls Brook.

Stream	Model	AIC_c	ΔAIC_c	AIC Weight	Model Likelihood	K
Black West	S, p_{stage}, λ, N	193.70	0.00	0.38	1.00	5
	$S, p_{stage}, \lambda, N_{stage}$	195.19	1.49	0.18	0.47	6
	$S_{stage}, p_{stage}, \lambda, N_{stage}$	195.42	1.73	0.16	0.42	7
	$S_{stage}, p_{stage,}, \lambda, N$	196.08	2.38	0.12	0.30	6
	$S_{stage}, p_{stage}, \lambda_{stage}, N$	197.23	3.53	0.07	0.17	7
	$S, p_{stage}, \lambda_{stage}, N_{stage}$	197.63	3.93	0.05	0.14	7
	$S_{stage}, p_{stage}, \lambda_{stage}, N_{stage}$	197.73	4.04	0.05	0.13	8
Canyon	S, p_{stage}, λ, N	158.57	0.00	0.30	1.00	5
	$S, p_{stage}, \lambda_{stage}, N$	158.98	0.41	0.25	0.82	6
	$S_{stage}, p_{stage}, \lambda, N$	160.49	1.92	0.12	0.38	6
	$S, p_{stage}, \lambda, N_{stage}$	160.74	2.17	0.10	0.34	6
	$S, p_{stage}, \lambda_{stage}, N_{stage}$	161.01	2.44	0.09	0.30	7
	$S_{stage}, p_{stage}, \lambda_{stage}, N$	161.27	2.70	0.07	0.26	7
	$S_{stage}, p_{stage}, \lambda, N_{stage}$	163.01	4.44	0.03	0.11	7
	$S_{stage}, p_{stage}, \lambda_{stage}, N_{stage}$	163.67	5.09	0.02	0.08	8
Falls	S, p_{stage}, λ, N	196.93	0.00	0.89	1.00	5
	$S, p_{stage}, \lambda_{stage}, N$	201.14	4.21	0.11	0.12	6

Notes: Second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), AIC_c weights, model likelihood, and number of estimable parameters (K) are provided for all models. Subscripts give parameterization for S, p, λ, and N: no subscript = constant over stage; "stage" = variation by life-history stage (larva and adult).

TABLE 2. Daily survival (*S*), recapture probability (*p*), daily population growth(λ), and initial population size (N) estimates for *Gyrinophilus porphyriticus* populations in Black West Brook, Canyon Brook, and Falls Brook from the best-fitting Jolly Seber models (Table 1).

| Stream	Parameter	Estimate	1 SE	95% CI Lower	Upper
Black West	*S*	0.96	0.03	0.83	0.99
	p_{larvae}	0.10	0.03	0.05	0.19
	p_{adults}	0.18	0.05	0.10	0.29
	λ	1.00	0.02	0.97	1.03
	N	33.6	8.39	21.2	55.2
Canyon	*S*	0.96	0.04	0.70	1.00
	p_{larvae}	0.09	0.04	0.04	0.20
	p_{adults}	0.10	0.04	0.04	0.22
	λ	1.00	0.02	0.96	1.03
	N	40.0	16.0	19.7	86.6
Falls	*S*	0.96	0.04	0.74	1.00
	p_{larvae}	0.11	0.04	0.05	0.21
	p_{adults}	0.04	0.02	0.02	0.10
	λ	0.96	0.02	0.93	1.00
	N	81.3	28.9	42.4	161.5

Notes: Standard errors (SE) and 95% confidence intervals (CI) are provided for all estimates.

TABLE 3. Estimates of the skewness of movement distribution (frequency distribution of meters moved) and the probability of movement ($p_{movement}$, proportion of individuals moving ≥ 1 m) in Black West, Black East, Canyon, and Falls brooks.

Stream	*N*	Skewness†	*P* (skewness = 0)	$p_{movement}$
Black West	25	0.90	< 0.10	0.52
Black East	22	1.14	< 0.05	0.32
Canyon	24	3.60	< 0.002	0.33
Falls	28	1.08	< 0.02	0.36

Notes: *N* represents the number of individuals (larvae and adults) recaptured in each stream.

† Positive values represent upstream bias in the movement distribution.
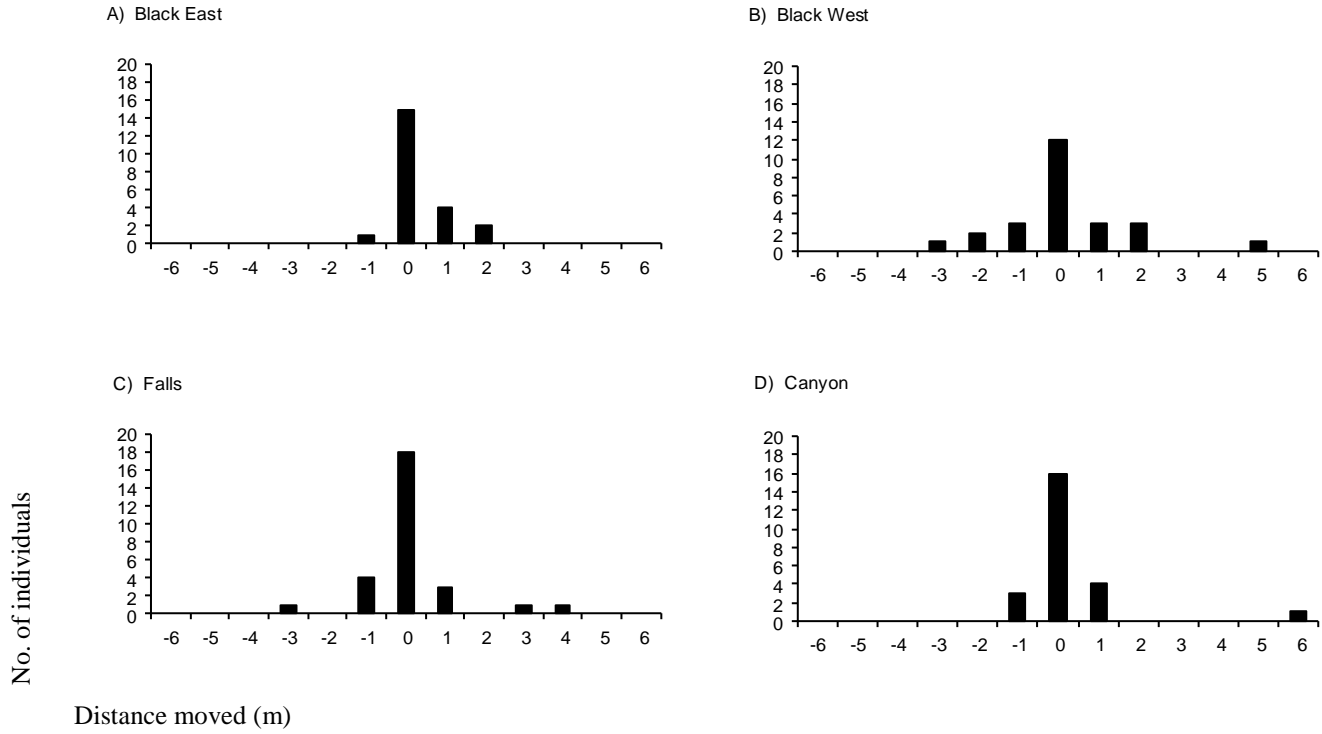
FIGURE 1. Movement distribution of *Gyrinophilus porphyriticus* individuals recaptured in Black East ($N = 22$), Black West ($N = 25$), Falls ($N = 28$), and Canyon ($N = 24$) brooks. Positive values represent upstream moves, and negative values represent downstream moves.