Demography and movement of the northern spring salamander in four New Hampshire headwater streams

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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 and movement, and these two processes are linked by both ecological and evolutionary factors. Consequently, investigations of basic population ecology provide insight into emergent biological properties such as patterns of community structure and local adaptation. Likewise, efforts to manage and conserve species, including monitoring programs, are greatly improved by a comprehensive understanding of population biology (BIEK et al. 2002).

Empirical study on the relative contributions of local demographic rates and dispersal to population dynamics is especially critical to amphibian conservation, where this information is necessary for assessing both the validity and causes of population declines (WAKE 1990). In an intensive 3-yr study on the northern spring salamander (*Gyrinophilus porphyriticus*), LOWE (2003) showed that upstream-biased movement contributed to the equality of population growth rates in upstream and downstream sections of a 1000-m stretch of stream in northern New Hampshire, USA. 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. We used mark-recapture methods to assess natural variation in the population biology of the spring salamander in multiple headwater streams.

Key words: amphibian dispersal, demography, *Gyrinophilus porphyriticus*, headwater streams, population biology

Methods

This study occurred in 4 fishless and undisturbed streams in the White Mountain National Forest, New Hampshire, USA. Falls Brook and Canyon Brook are second-order streams in the Hubbard Brook Experimental Forest, Woodstock, New Hampshire. Black West Brook and Black East Brook are first-order streams in Easton, New Hampshire. The vegetation in the study drainages was dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), and paper birch (*B. papyrifera*) (BORMANN et al. 1970).

We established 125-m long study sections in each stream. Eight mark-recapture surveys were conducted in each study section between 26 June 2003 and 17 July 2003. Surveys occurred on 2 successive days, followed by a 4-day interval. We used a cover-controlled, active-search sampling method (HEYER et al. 1994). Moving upstream, we turned 125 cover objects (rocks between 64 and 256 mm diameter) from within the main channel and along the bank and edge of the stream, maintaining a constant effort of 1 rock/m of stream length. All unmarked individuals were uniquely marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). We also recorded the longitudinal position (distance upstream from the start of the study section, m), length (SVL, mm), and mass (mg) for each captured individual.

The Jolly-Seber model in program MARK version 4.1 (WHITE & BURNHAM 1999) was used to estimate daily capture probability (p_t), daily apparent survival (S), daily population growth rate (λ), and initial population size (N_1) in the study reaches. The Jolly-Seber model applies to "open" populations, thus incorporating births, deaths, immigration, and emigration. Program MARK was used to assess relative support for different models in a predefined set of candidate models. Daily survival, daily population growth, and initial population size were modeled as either variable or constant across life history stages (larva or adult). Daily capture probabilities were modeled to vary by stage based on the observation that larvae were more difficult to capture than adults due to their smaller size. We also made the *a priori* decision not to model parameters as variable over time based on the short duration of the sampling period. Small sample Akaike's Information Criteria (AIC; BURNHAM & ANDERSON 1998) were used for model selection.

Movement was measured as the distance (m) from the point of last capture. We quantified movement in each stream by constructing frequency distribution histograms, where positive values represented upstream moves and negative values represented downstream moves. We then tested for skewness

Table 1. Ranking of Jolly-Seber models for capture probability (p_t), daily survival (S), daily population growth (λ), and initial population size (N_1) in Black West, Canyon, and Falls brooks. Small sample correction of AIC 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 p_t, S, λ, and N_1: no subscript = constant over stage; "stage" = variation by life-history stage (larva and adult).

Stream	Model	AIC_c	ΔAIC_c	AIC weight	Model likelihood	K
Black West	$p_{t,stage}$, S, λ, N_1	193.70	0.00	0.38	1.00	5
	$p_{t,stage}$, S, λ, $N_{1,stage}$	195.19	1.49	0.18	0.47	6
	$p_{t,stage}$, S_{stage}, λ, $N_{1,stage}$	195.42	1.73	0.16	0.42	7
	$p_{t,stage}$, S_{stage}, λ, N_1	196.08	2.38	0.12	0.30	6
	$p_{t,stage}$, S_{stage}, λ_{stage}, N_1	197.23	3.53	0.06	0.17	7
	$p_{t,stage}$, S, λ_{stage}, $N_{1,stage}$	197.63	3.93	0.05	0.14	7
	$p_{t,stage}$, S_{stage}, λ_{stage}, $N_{1,stage}$	197.73	4.04	0.05	0.13	8
Canyon	$p_{t,stage}$, S, λ, N_1	158.57	0.00	0.30	1.00	5
	$p_{t,stage}$, S, λ_{stage}, N_1	158.98	0.41	0.25	0.82	6
	$p_{t,stage}$, S_{stage}, λ, N_1	160.49	1.92	0.12	0.38	6
	$p_{t,stage}$, S, λ, $N_{1,stage}$	160.74	2.17	0.10	0.34	6
	$p_{t,stage}$, S, λ_{stage}, $N_{1,stage}$	161.01	2.44	0.09	0.30	7
	$p_{t,stage}$, S_{stage}, λ_{stage}, N_1	161.27	2.70	0.08	0.26	7
	$p_{t,stage}$, S_{stage}, λ, $N_{1,stage}$	163.01	4.44	0.03	0.11	7
	$p_{t,stage}$, S_{stage}, λ_{stage}, $N_{1,stage}$	163.67	5.09	0.02	0.08	8
Falls	$p_{t,stage}$, S, λ, N_1	196.93	0.00	0.89	1.00	5
	$p_{t,stage}$, S, λ_{stage}, N_1	201.14	4.21	0.11	0.12	6

of the movement distribution to assess directional bias (ZAR 1984) and calculated the probability of movement as the proportion of individuals that moved 1 m or more, pooling recaptured animals across all recapture intervals.

Results

A total of 48 salamanders were captured in Black West Brook (n_{larvae} = 18, n_{adults} = 30), 38 in Black East Brook (n_{larvae} = 14, n_{adults} = 24), 48 in Canyon Brook (n_{larvae} = 23, n_{adults} = 25), and 57 in Falls Brook (n_{larvae} = 41, n_{adults} = 16). In the most parsimonious Jolly-Seber model, S, λ, and N_1 were consistent between life-stages in Black West, Canyon, and Falls brooks (Table 1). Recaptures in Black East were insufficient for mark-recapture analysis. Daily S and λ were consistent across Black West, Canyon, and Falls brooks (Table 2). Initial population sizes were similar in Black West and Canyon brooks and approximately 100% greater in Falls Brook (Table 2), although confidence intervals overlapped.

Spring salamander movement was biased in the upstream direction in 3 of the 4 streams: Black East, Canyon, and Falls (Fig. 1, Table 3). In Black West, no significant bias was found in the movement distribution (Fig. 1; Table 3). The movement distributions of larvae and adults did not differ in the 4 streams (Kolmolgorov-Smirnov tests, $P > 0.05$). Probability of movement was similar in

Black East, Canyon, and Falls brooks (Table 3), and approximately 53% higher in Black West Brook.

Table 2. Capture probability (p_t), daily survival (S), daily population growth (λ), and initial population size (N_1) estimates for spring salamander populations in Black West, Canyon, and Falls Brooks from the best-fitting Jolly Seber models (Table 1). Standard errors (SE) and 95% confidence intervals (CI) are provided for all estimates.

| Stream	Parameter	Estimate	1 SE	95% CI Lower	95% CI Upper
Black West	$p_{t,larvae}$	0.10	0.03	0.05	0.19
	$p_{t,adults}$	0.18	0.05	0.10	0.29
	S	0.96	0.03	0.83	0.99
	λ	1.00	0.02	0.97	1.03
	N_1	33.6	8.39	21.2	55.2
Canyon	$p_{t,larvae}$	0.09	0.04	0.04	0.20
	$p_{t,adults}$	0.10	0.04	0.04	0.22
	S	0.96	0.04	0.70	1.00
	λ	1.00	0.02	0.96	1.03
	N_1	40.0	16.0	19.7	86.6
Falls	$p_{t,larvae}$	0.11	0.04	0.05	0.21
	$p_{t,adults}$	0.04	0.02	0.02	0.10
	S	0.96	0.04	0.74	1.00
	λ	0.96	0.02	0.93	1.00
	N_1	81.3	28.9	42.4	161.5
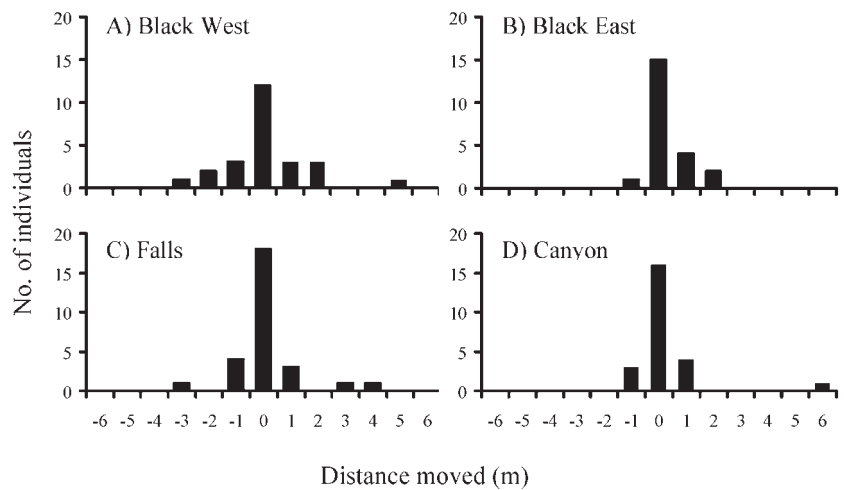
Fig. 1. Movement distribution of spring salamanders recaptured in (A) Black West (n = 25), (B) Black East (n = 22), (C) Falls (n = 28), and (D) Canyon (n = 24) brooks. Positive values represent upstream moves, and negative values represent downstream moves.

Table 3. Estimates of the skewness of movement distribution and the probability of movement (p_m) in Black West, Black East, Canyon, and Falls brooks. The number of individuals recaptured (n; larvae and adults) and the skewness of movement (frequency distribution of meters moved) are included.

Stream	n	Skewness*	P (skewness = 0)	p_m
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

* Positive values represent upstream bias in the movement distribution.

Discussion

This study documents generally consistent demographic rates and movement patterns among streams over a relatively short period of intense sampling. In spite of fundamental morphological and ecological differences, S, λ, N_1, and directional bias in movement were also similar across life-history stages. What explains this demographic consistency? In 15 New Hampshire streams, Lowe et al. (2004) found that spring salamander larval abundance was negatively related to brook trout abundance and unrelated to substrate embeddedness (a measure of sediment accumulation around substrates within the stream bed), while adult abundance was primarily related to substrate embeddedness. In the fishless and relatively undisturbed streams we sampled, where spring salamander larvae are not affected by the predatory and competitive pressures of brook trout (e.g., Resetarits 1995), larval and adult populations may be regulated by similar density dependent factors, resulting in the observed demographic consistency.

Movement of spring salamander larvae and adults exhibited significant upstream bias in 3 of the 4 streams we sampled. Although skewness of movement in Black West Brook was not statistically significant, its positive value is indicative of a tendency for individuals to move upstream. This result adds to the evidence that upstream-biased movement is a general trend for larvae and adults of the spring salamander (Lowe 2003). Additionally, proportions of individuals moving 1 m or more in the 3 streams where significant upstream bias was documented were between 0.32 and 0.36. The consistent proportion of "movers" in the 3 populations may be indicative of a genetically-based polymorphism in movement behavior, resulting in subpopulations of "movers" and "stayers" (Skalski & Gilliam 2000). However, while these movement results were relatively consistent among populations, they are based on a short period of sampling. Further research on the genetic structure of spring salamander populations and the heritability of movement behavior, in addition to identifying phenotypic characteristics of "movers" and "stayers" within populations (e.g., Lowe et al. 2006), is needed to better understand the proximate and ultimate causes of these patterns.

Given that sampling took place at a time of the year when spring salamanders are most active (B. Greene, pers. comm.), we believe the lack of variation in daily demographic rates and movement patterns is surprising, probably reflecting the lack of biological and physical factors with known stage-specific effects in the study

streams (e.g., brook trout presence and harvest-induced sedimentation). Long-term studies are clearly needed that compare spring salamander demography and movement across multiple streams in disturbed and undisturbed ecosystems, and in the presence and absence of brook trout. Until those studies occur, our data can serve as a benchmark for comparison of the population biology and conservation requirements of the spring salamander and other headwater stream salamanders. More specifically, the low variance among fishless and undisturbed streams in survival rates, population growth rates, and movement probabilities suggests that these may be especially accurate and useful indicators of land-use impacts.

Summary

- Spring salamander populations exhibited minor variation in survival and population growth rates, and individuals demonstrated a consistent upstream bias in movement.
- In spite of basic morphological and ecological differences, daily survival, daily population growth, population size, and an upstream-bias in movement were consistent between life history stages.
- In the fishless and undisturbed study streams we sampled, the observed consistency in demography and movement likely reflects a lack of biotic and abiotic factors with stage-specific effects (e.g., brook trout presence and substrate embeddedness).
- Our results provide an empirical context for demographic and behavioral patterns observed both in streams impacted by human activities and in streams with different community compositions.

Acknowledgements

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