
HOMING BEHAVIOR OF THE NORTHERN SPRING SALAMANDER, *GYRINOPHILUS PORPHYRITICUS*, IN A NORTHEASTERN UNITED STATES HEADWATER STREAM

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Abstract.—The ability to home, or to navigate back to a home range after displacement, may offer advantages at both the individual and population levels. Returning to familiar territory may decrease the vulnerability of an individual to predation or food scarcity after displacement, and balance and stabilize population distribution across the landscape. The purpose of this study was to test whether the Northern Spring Salamander, *Gyrinophilus porphyriticus*, exhibits homing behavior when displaced upstream and to examine whether this behavior is stage-specific. We conducted an experiment along a first-order stream in the Hubbard Brook Experimental Forest, New Hampshire, USA. We tagged 60 salamanders (30 adults and 30 larvae) and assigned them to one of three treatments: 0 m, 10 m, and 30 m displacement. We conducted 10 recapture surveys during a one month period, resulting in a total recapture rate of 33%. Of nine displaced and recaptured adult salamanders, six had homed and three had moved toward home. A chi-square analysis showed significant differences among the number of recaptured adults that had homed across the three treatments. Our results suggest that adult *G. porphyriticus* has the ability to return home after displacement, but the stage-specificity of this behavior is still unclear because of low larval recapture rates. The homing ability of *G. porphyriticus* may become increasingly important as changes in climate lead to more unpredictable weather events (e.g. flooding) in the northeastern United States.

Key Words.—amphibian; displacement; homing; life stages; movement behavior; navigation; salamander; stream

INTRODUCTION

Understanding the movement behavior of individual organisms is key to understanding the spatial distribution and dynamics of natural populations (Nathan et al. 2008; Hawkes 2009). Dependent on individual movements, one of three general spatial patterns is likely to emerge at the population level: nomadism, in which there is no clear range; migration, in which travel occurs between seasonal ranges; or sedentary ranges, in which there is a residential home range (Mueller and Fagan 2008). Most research has focused on the movement of an animal within its home range (Wittenberger 1981); however, recent research has expanded our knowledge of the movement of an individual outside of the home range (e.g., Berry et al. 2005; Lowe et al. 2008; Nevoux et al. 2013).

Homing, the ability to navigate back to a home range or territory after intentional or involuntary displacement, is one movement behavior that requires a capacity for navigation across a landscape. The theory of habitat selection predicts that individuals will choose the best habitats available to maximize individual fitness, resulting in a predictable distribution of the population across the landscape (Holt 1985). Green (1971) has

suggested that homing serves to stabilize this distribution, thus decreasing clusters of competition. Therefore, the ability to home should offer an advantage at both the individual and population levels (Twitty 1959). At the individual level, homing behavior can enable more effective use of local resources, such as refuges from predators, feeding sites, and breeding sites (Wittenberger 1981). The cost of relearning such spatial features in a new location may be more costly than the act of homing (Twitty 1959; Twitty et al. 1966). From a population standpoint, homing behavior can act as a compensatory mechanism for density dependent processes (Gill 1979; Carpenter 1984).

Homing behavior after displacement has been observed in most groups of amphibians (Martof 1953; Brattstrom 1962; Rose 1966; Madison 1969; Salvidio 2013), including some semi-aquatic salamander species (Barthalmus and Bellis 1969; Gill 1979; Holomuzki 1982). For example, the Northern Dusky Salamander, *Desmognathus fuscus*, has been found to home up to 30 m along a stream (Barthalmus and Bellis 1972). Though homing behavior of several plethodontid salamanders has been observed, most of these homing studies have not distinguished between life stages and focused primarily on adults (Barthalmus and Bellis 1969;

Barthalmus and Savidge 1974; Holomuzki 1982). Recent work with *Plethodon cinereus* suggests that adults and juveniles can home from short displacement distances, but not from long displacement distances (Ousterhout and Liebgold 2010). It is important to consider multiple life stages because factors affecting survival may act differently on each life stage. For example, survival of juvenile Eastern Newts (*Notophthalmus viridescens*) may be dependent on the ability to disperse from natal ponds, but adult survival and fitness may be dependent on homing ability (Gill 1978, 1979). This is important to consider because Lowe (2012) recently found that a decline in Northern Spring Salamander (*Gyrinophilus porphyriticus*) abundance in one New Hampshire population was linked to stage-specific effects of climate change. Specifically, increases in precipitation and accompanying floods are most detrimental to metamorphosing larvae, causing a decline in adult recruitment. Similarly, stage-specific disparities in homing behavior could have important consequences for the ability of isolated populations to recover from large-scale displacement events (e.g., weather events).

To test for homing behavior in larval and adult *G. porphyriticus* inhabiting a northeastern U.S. stream, we displaced to an upstream location individuals of both life stages. All salamanders were displaced upstream of their initial capture site to increase the likelihood that detected movement was associated with homing behavior, as opposed to natural upstream dispersal tendencies (Lowe 2003; Lowe et al. 2006). We hypothesized that (1) *G. porphyriticus* would exhibit homing behavior, which could be measured as the differences between the control and displacement treatments, (2) the tendency to home would be stronger in individuals displaced shorter distances compared to individuals displaced longer distances, and (3) the tendency to home would be stronger in adults, with more time to establish territories or home ranges, and potentially more experience foraging outside of their home range, than in larvae.

MATERIALS AND METHODS

Study site.—We conducted this study on Bagley Trail Brook in the Hubbard Brook Experimental Forest (HBEF), located within the White Mountain National Forest of central New Hampshire, USA. The 3,160 ha HBEF encompasses most of the Hubbard Brook watershed. Dominant tree species along Bagley Trail Brook (Likens and Buso 2006) include North American Beech (*Fagus grandifolia*), Sugar Maple (*Acer saccharum*), Yellow Birch (*Betula alleghaniensis*), Paper Birch (*Betula papyrifera*), Red Spruce (*Picea rubens*), and Balsam Fir (*Abies balsamea*).

Bagley Trail Brook is a fishless, first-order stream situated in the southeastern portion of HBEF. The stream has a steep gradient and contains a mixture of cobble and small boulders, which provide habitat for spring salamanders. For this study, we surveyed a 260 m section of Bagley Trail Brook, beginning 200 m from its confluence with the second-order Hubbard Brook main stem. We flagged trees every 5 m along the stream for accurate estimation of salamander capture locations.

Study species.—*Gyrinophilus porphyriticus* is in the family Plethodontidae, the lungless salamanders, and occurs primarily in low-order, well-oxygenated streams along most of the Appalachian uplift (Petranka 1998). *Gyrinophilus porphyriticus* has a larval stage of approximately 3–5 y (Bruce 1980) and can live up to an estimated 14 y (Lowe 2012). Both larvae and adults feed primarily on invertebrates (Burton 1976). Adults have the ability to foray outside of streams, but larvae are strictly aquatic (Greene et al. 2008). Both larvae and adults are found in interstitial spaces in the streambed, but microhabitats can be somewhat stage-specific (Bruce 1980; Petranka 1998).

Mark-recapture surveys.—We initially collected salamanders from the study section of Bagley Trail Brook during a three-day period (14–16 July 2012) throughout the entire 260 m study reach. During this initial capture period, we systematically overturned rocks, then returned them to their original positions to minimize habitat disruption. Metal flags that we placed at the edge of the stream identified the particular rocks under which we found each salamander. We assumed that the initial capture location of a salamander was within its home range, which previous studies have estimated to be about 3 m along a stream (Lowe 2003), with conservative estimates of ≤ 5 m according to Lowe (2009). We measured the body mass and snout-vent length (SVL) of each individual. We individually marked salamanders by subcutaneous injection of visual elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA) and then we assigned them haphazardly to one of the three treatments: (1) 0 m displacement, which served as the control; (2) 10 m upstream displacement; and (3) 30 m upstream displacement. The displacement distances for each treatment were based on long-term mark-recapture studies of *G. porphyriticus*, which have found that few individuals move such relatively great distances (Lowe 2003). We captured 10 adults and 10 larvae and marked them for each treatment, yielding 60 total salamanders for this study. We released all salamanders back into the stream on the day of initial capture. We considered 10 individuals per treatment a robust sample for this study because *G. porphyriticus* can be hard to detect in nature (Beachy 2005) and larger samples would have taken

considerably longer than the allotted study period. To accommodate all 60 experimental salamanders and to reduce continued disturbance over a small area, we displaced individuals throughout the entire 260 m study reach.

After the initial capture period (12–14 July) of experimental salamanders, we conducted 10 recapture surveys for three weeks. Survey dates were 17, 19, 21, 23, 25, 27, 29 July and 2, 4, 7 August of 2012. The lead author’s time availability in the field limited the duration of our study to four weeks. We acknowledge that four weeks may not have been enough time to permit homing of some salamanders as other studies have indicated it can take over three months (Cecala et al. 2014). Survey methods consisted of turning over one rock per stream-meter throughout the 260 m study reach, identifying salamanders, and recording their locations before releasing them back to the recapture location. This work is part of a longer-term study on this stream; thus, only one rock per stream-meter was used instead of every rock per meter to minimize disturbance (i.e., rests between sampling events) after initial capture (Hyde and Simons 2001; Marsh and Goicochea 2003). We acknowledge that this method may not fully represent the actual distribution of salamanders in the stream: however, if we lifted every rock per meter during resampling, then we could bias dispersal behavior of salamanders. We considered salamanders recaptured at their home meter ± 2 m in either direction to have homed. We noted unmarked salamanders captured during the surveys, but were not marked or displaced.

Statistical analysis.—To compare the differences between the number of individuals that had homed in each displacement treatment versus the number of individuals that had remained home in control treatments, we used a contingency table analysis with Fisher’s exact test ($\alpha = 0.05$). We used the number of individuals that had homed out of the original 10 that were displaced, because the remaining individuals were not found at home. This is similar to prior studies (Barthalmus and Bellis 1969; Barthalmus and Bellis 1972) that used the number that had homed out of the total displaced. This allowed us to determine if individuals had homed in displacement treatments relative to individuals in the control treatments. For instance, we expected to find a high number of the individuals in the controls repeatedly (i.e., “stayers” staying home). Therefore, if we found an equally high number of individuals in either of the displacement treatments back at their home rock, then we could state that individuals had the ability to home from that particular displacement distance. Only two Fisher Exact tests were conducted for the adult life stage (control vs. 10 m displacement and control vs. 30 m displacement)

because we recaptured too few larvae, which precluded us from analyzing these data.

RESULTS

Of the 60 marked salamanders across life stages, we recaptured 20 (33.3%), consisting of 15 adults and five larvae. Nine of these were in the control group (released at their home meter ± 2 m) and 11 were displaced individuals (Table 1). Of the 11 recaptured, displaced individuals, six homed (54.6%), three moved toward home (27%), and two were found at the release site (18%). No salamanders were detected that had dispersed in the opposite direction of their home (Table 1). For the comparisons of individuals between controls and displacement treatments, we were conservative and considered only the individuals that were found within 2 m of the home area. Individuals that had moved towards home were likely homing, but were not included in the contingency analyses. Adult *G. porphyriticus* from 10 m displacement treatments homed as indicated by the lack of a statistically significant difference between the number of recaptured adult *G. porphyriticus* in control treatments and 10 m displacement treatment ($\chi^2 = 0.20$, $df = 1$, $P = 0.65$). This indicates that a comparable number of individuals were found at home rocks in both the control (six in 10) and 10 m (five in 10) displacement treatments (Table 1). However, there was a non-significant trend for a difference between the number of recaptured adult *G. porphyriticus* in control treatments and the 30 m displacement treatment ($\chi^2 = 4.49$, $df = 1$, P

TABLE 1. Displacement distance, number recaptured, and the number that moved home for 30 larval and 30 adult *Gyrinophilus porphyriticus* displaced 0, 10, or 30 m upstream in Bagley Trail Brook in Hubbard Brook Experimental Forest, New Hampshire, USA. Abbreviations are DD = Displacement Distance, N = number recaptured, NO = number recaptured at original location, NDS = number caught at displacement site, and NMTS = number moved towards home.

Life Stage	DD	N	NO	NDS	NMTS
Larvae	0 m	3	3	-	-
	10 m	2	0	2	0
	30 m	0	0	0	0
Adults	0 m	6	6	-	-
	10 m	7	5	0	2
	30 m	2	1	0	1
Total		20	15	2	3

= 0.047) indicating individuals from the 30 m displacement did not home.

DISCUSSION

Our results indicate that adult *G. porphyriticus* have the ability to home after upstream displacement. Of the 11 displaced salamanders that were recaptured, nine moved toward home and two were caught at the displacement site, but both of the latter were captured during the first survey (only one day after initial displacement). Previous studies indicate that *G. porphyriticus* rarely will disperse from an upstream section to a downstream section (Lowe 2003; Lowe et al. 2006, 2008), thus it is unlikely that the downstream movement was associated with dispersal. It is also unlikely that the observed homing within the 260 m study reach was due to downstream drift, because no recaptured salamanders were found downstream of their original capture site. Based on prior studies with other stream salamanders, we do not expect the ability to home to differ from upstream or downstream displacement as the mechanism used to home, which involves olfactory cues, is the same (Barthalmus and Bellis 1972). The overall recapture rate (33.3%) of salamanders in our study was consistent with previous mark-recapture studies of aquatic stream salamanders, in which recapture rates have tended to fall within 10–50% (Barthalmus and Bellis 1969; Barthalmus and Bellis 1972; Lowe 2003; Johnson et al. 2006; Cecala et al. 2009), with few reporting recaptures of more than 60% of marked individuals (Holomuzki 1982).

Salamander homing behavior studies conducted for a longer period of time and with greater displacement distances to determine the upper limits of homing ability in *G. porphyriticus* would be a logical next step from our study. In our study, the act of homing did not have an effect on body condition of recaptured individuals; however, the lack of a cost to homing could be attributed to the short duration of our study. Other homing studies on aquatic salamanders have extended over several months (Barthalmus and Bellis 1972; Holomuzki 1982), but most have individuals displaced approximately 30 m and few have actually determined the maximum distance from which individuals will home. Though the majority of Spring Salamanders remain within approximately 3 m² of habitat throughout their lifetime (Lowe 2003), a few have been found to disperse 500 m (Lowe and McPeck 2012), suggesting that their homing movements could also be greater. However, homing may require greater goal-oriented navigational abilities than dispersal, and thus could be more limited.

In addition to our low recapture rates, the lack of homing by *G. porphyriticus* larvae could be attributed to the inability of larvae to establish and defend territories (or home areas) against adults or to navigate home if

displaced. Plethodontid salamanders are known to be territorial and aggressive towards conspecifics and congeners (Jaeger et al. 1995; Petranka 1998), and larger species tend to be more aggressive and superior competitors when defending territories (Thurow 1975). Although the extent of territorial behavior of *G. porphyriticus* is unknown, *G. porphyriticus* does engage in agonistic behavior with conspecifics (Bernardo and Arnold 2002). The ability to navigate and recognize odors has largely been attributed to the use of olfactory cues (Madison 1969; Barthalmus and Bellis 1972; Forester 1979). Although adult salamanders recognize and are attracted to their own odors (Vignoli et al. 2012), this ability and behavior has not been well documented in larval salamanders. In a study similar to ours, Ellis-Quinn and Simon (1989) found that although adult *Sceloporus* lizards homed up to 200 m, juveniles displaced over 50 m homed poorly. One-year-old adult lizards were also relatively poor at homing compared to older adults, suggesting that bonds to home ranges may strengthen with age (Ellis-Quinn and Simon 1989).

Lowe et al. (2008) found that *G. porphyriticus* populations in the upper reaches of some northeastern streams, including the stream in which this study was conducted, have genetically diverged from populations in lower reaches. Strong homing behavior of individuals in the stream could be acting as a barrier to gene flow between upstream and downstream populations. Several studies have reported homing behavior as an important mechanism of genetic isolation, but these have mostly examined fish populations that home to natal sites to breed (Ferguson and Taggart 1991; Svedang et al. 2007). This possibility could be further investigated in *G. porphyriticus* through comparative homing studies between streams with genetically divergent and non-divergent populations.

The homing abilities and tendencies of aquatic species may become increasingly relevant as the climate changes. Climate models predict changes in not only higher annual temperatures of the northeastern United States (Hayhoe et al. 2007), but also increases in precipitation and weather variability (Karl and Knight 1998; Hayhoe et al. 2007; Collins 2009), which could have particularly strong effects on aquatic habitats (Meyer et al. 1999; Brooks 2009). An increase in precipitation of up to 15% over the next century has been predicted, and will result in higher average stream flows as well as larger and more frequent flooding events (Groisman et al. 2001; Hayhoe et al. 2007; Collins 2009). These events could increase the frequency of involuntary displacement of aquatic organisms, including stream salamanders, from their established home ranges. Conversely, drought events also have the potential to cause displacement, if organisms must leave home in search of temporary, more suitable conditions (Kleeberger and Werner 1982).

The ability (or inability) of individuals to return home after displacement by such severe weather events could potentially influence population dynamics and gene flow. Although our study did not focus on downstream displacement as could happen after flooding events, this research does suggest that adult *G. porphyriticus* have the ability to return home after short displacements. However, the stage-specific nature of homing in *G. porphyriticus* needs further investigation because larvae were infrequently detected after displacement. The potential long displacement of adults coupled with reduced homing ability in larvae could increase extinction risk and threaten population stability.

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WINSOR LOWE grew up in rural New Hampshire, received a B.A. from Middlebury College in 1994, and then spent several years bouncing back and forth between Montana and New England as a research assistant on studies of wolves, salamanders, and stream insects. He received a M.S. from The University of Montana in 1997, where he worked on the thermal ecology of stream insects. Winsor's dissertation at Dartmouth College and postdoc at The Cary Institute of Ecosystem Studies focused on the spatial ecology of salamanders in headwater stream networks. Winsor has been at The University of Montana since 2005, where he is a member of the programs in Organismal Biology and Ecology and Wildlife Biology. Along with an amazing group of students and collaborators, Winsor studies how dispersal affects the evolution, population biology, and community ecology of stream animals. He is especially interested in the ecological and evolutionary drivers of individual dispersal patterns (e.g., stay vs. leave, go short vs. go long) and how these proximal drivers influence emergent population and community dynamics. Winsor tries to make his research relevant to large-scale management and conservation challenges facing stream ecosystems, such as climate change, timber harvest, and headwater fragmentation. He also just really enjoys walking along small streams and seeing what is under rocks. (Photographed by Jenny Tollefson).