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Predation of Juvenile Ringed Salamanders (*Ambystoma annulatum*) During Initial Movement Out of Ponds

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Abstract.—**Natal dispersal is often accompanied by substantial risks to survival, which may dictate the movement behavior of individuals. For pond-breeding salamanders, initial natal dispersal is accompanied by an ontogenetic habitat shift, and individuals are naïve to terrestrial surroundings and accompanying movement risks. Although there have been numerous studies on the effects of habitat type on amphibian movement and survival, few studies have directly documented predation risk to free-ranging, newly-metamorphosed salamanders. We tracked the movements of 124 Ringed Salamanders (*Ambystoma annulatum*) at four ponds and found that 23% were consumed by anuran predators during the first night in terrestrial habitat. These results document that predation may constitute a substantial risk to pond-breeding salamanders after metamorphosis and should be considered in studies analyzing the survival consequences of movement behavior.**

Key Words.—Ambystoma annulatum; amphibian; dispersal; movement; predation; Ringed Salamander

Introduction

Dispersal behavior is driven by tradeoffs between risks and benefits associated with movement (Clobert et al. 2001; Zollner and Lima 2005; Delgado et al. 2010). Understanding the risks animals face during dispersal is critical to explaining and analyzing observed movement patterns (Clobert et al. 2001; Nathan et al. 2008; Pe'er and Kramer-Schadt 2008). For many species, initial movement away from natal locations is accompanied by substantial risks to survival as a result of individuals' lack of experience in the new environment, small body size relative to conspecifics, and novel antagonistic interactions with heterospecifics (e.g., Barbraud et al. 2003; Yoder et al. 2004; Chaput-Bardy et al. 2010). The ways that individuals mitigate the risks associated with natal dispersal may have important implications for the spatial dynamics of the species (Barbraud et al. 2003; Zollner and Lima 2005). Numerous studies have concluded that movement behavior may predict the importance of corridors or other wildlife management regimes to the functional connectivity of populations (Haddad 1999; Knowlton et al. 2010), and risk-taking strategies influence the movement of individuals in relation to resource distribution (Sih et al. 2004). The risks encountered by juvenile pond-breeding amphibians, and their behavioral reactions to them, may therefore profoundly influence population persistence and connectivity.

Relatively little is known concerning the initial movements of juvenile pond-breeding amphibians out of ponds, even though this life stage is widely acknowledged to be critical to population regulation (Harper et al. 2008). Dispersing juvenile amphibians undergo an ontogenetic habitat shift (aquatic to terrestrial habitat) and are subject to high mortality during the first year post metamorphosis (Rothermel and Semlitsch 2002). Documented causes of mortality include energy depletion (Scott et al. 2007), desiccation (Rothermel and Luhring 2005), density effects (Harper and Semlitsch 2007; Rittenhouse and Semlitsch 2007; Berven 2009), and predation (Rittenhouse et al. 2009). Numerous studies have found that habitat quality surrounding ponds influences juvenile survival and the duration and directionality of juvenile movements (e.g., deMaynadier and Hunter 1999; Rittenhouse and Semlitsch 2006; Popescu and Hunter 2011). However, few studies have directly documented predation of juveniles during initial movement in terrestrial habitat, and there is currently little evidence to address the question of whether predation represents a significant risk factor to dispersing pond-breeding amphibians.

Pond-breeding Spotted Salamanders (*Ambystoma maculatum*) and Ringed Salamanders (*A. annulatum*) make initial movements away from ponds on the scale of 20−50 m, and the choices that individuals make during this initial phase of dispersal have profound implications for future survival (Osbourn 2012). For example, recently-metamorphosed salamanders are susceptible to predation by larger anurans (e.g., Chivers et al. 2001; Murray et al. 2004). Search strategies of pond-breeding amphibians during initial movement out of natal ponds are often considered in relation to their effectiveness in locating quality habitat (e.g., Rothermel 2004; Walston and Mullin 2008); few studies acknowledge the potential of predation pressure to dictate optimal movement strategies, potentially because relevant data on predation risk are scarce. Because terrestrial amphibian density is negatively correlated with distance from ponds (Rittenhouse and Semlitsch 2007), predation pressure by anurans is likely highest closest to the pond. Therefore, we hypothesize that juvenile amphibians face high predator densities immediately upon exiting ponds after metamorphosis (Madison 1997).

In this study, we used fluorescent powder tracking to follow the movements of recently-metamorphosed Ringed Salamanders away from natal ponds in order to document the occurrence of predation, the identity of predators, and the locality of predation events in relation to the pond.

Materials and Methods

This study was conducted at Daniel Boone Conservation Area (DBCA, 1,424 ha) in Warren County, Missouri, USA (Latitude: 38°46′54″; Longitude: -91°23′0″). The DBCA is characterized by mature second-growth forest dominated by oak and hickory tree species in the canopy and Sugar Maple in the understory. The study took place at four small permanent ponds within DBCA. Each of the four ponds was surrounded by a closed-canopy forest with similar amphibian communities (Hocking et al. 2008). All four ponds contained Ringed Salamanders, Spotted Salamanders, Eastern Newts (*Notophthalmus viridescens*), Green Frogs (*Lithobates clamitans*), American Bullfrogs (*Lithobates catesbeianus*), Wood Frogs (*Lithobates sylvaticus*), Spring Peepers (*Pseudacris crucifer*), and Southern Leopard Frogs (*Lithobates sphenocephalus*). One of the four ponds additionally contained Marbled Salamanders (*Ambystoma opacum*).

We captured late-stage Ringed Salamander larvae from the ponds and raised the larvae in cattle tanks within 500 m from the natal ponds. We collected metamorphosed salamanders from the cattle tanks and held them in containers with damp moss until conditions were ideal for release and tracking, which were defined as: (1) within 24 h of, but not concurrent with, a rain event; (2) when minimum nightly temperatures were above 10° C; and (3) within two weeks of the individual's metamorphosis. Salamanders were released at the pond from which they were collected as larvae between June and July 2011 on 12 separate nights. We released up to 10 salamanders in a night between 2030 and 2200, soon after a rain event when the ground was wet and relative humidity was high. Previous studies have found that salamanders readily disperse from ponds under these conditions (e.g., Rothermel 2004) and make dispersal movements up to 9 d after a rain event (Shannon Pittman, unpubl. data). We therefore believe that the behavior of individuals in this study approximated that of individuals initially moving from their natal ponds.

During salamander releases, we placed salamanders approximately 20 cm from the edge of the pond, under upside-down clay flowerpots spaced a minimum of 5 m apart. The clay pots served as release enclosures and allowed animals to acclimate to the environment for approximately 20 min. prior to release. To minimize the influence of observer orientation in salamander movement decisions, we lifted the release chambers from a distance of at least 3 m. Although the overall bearing of juvenile emigration from natal ponds is often found to be significantly non-random (Rothermel 2004; Watson and Mullins 2008), previous studies have also concluded that the mean direction of exit varies among ponds and years (Jenkins et al. 2006). Therefore, we were unable to predict the mean emigration direction for this study and spaced animals haphazardly (but non-overlapping and a minimum of 5 m apart) around the edges of the ponds.

Prior to placing the salamander in the release chamber, we covered the posterior half of salamanders with pink, orange, or green fluorescent powder (DayGlo Color Corp, Cleveland, Ohio, USA) to enable us to track continuous movement of salamanders after release. By alternating pigment color, we reduced the likelihood of two identically-colored paths intersecting. Fluorescent powder has been used successfully in previous studies to track short-term movements of small amphibians (Eggert 2002; Graeter et al. 2008; Roberts and

Liebgold 2008; Roe and Grayson 2008, 2009; Orlofske et al. 2009). Previous work has shown that the pigment does not affect survival or level of cutaneous respiration in newts and ambystomatid salamanders (Rittenhouse and Semlitsch 2006; Orlofske et al. 2009). Therefore, we do not think it likely that powder affected the movement behavior of animals in this study.

Two hours after release we returned and used ultraviolet lights (Arachnid A14, Blacklight.com, Volo, Illinois, USA) to locate and follow powder trails deposited by salamanders. We followed trails until we located the salamander, the trail was lost, or the trail ended at a predator with traces of fluorescent powder on its mouth or evidence of an obvious predation event (Fig. 1). We identified the species of the predator and measured the distance between the predation event and the edge of the pond. Predators were identified as 'unknown anuran' if the powder trail post-predation exhibited a pattern indicative of anuran movement (such as hopping prints).

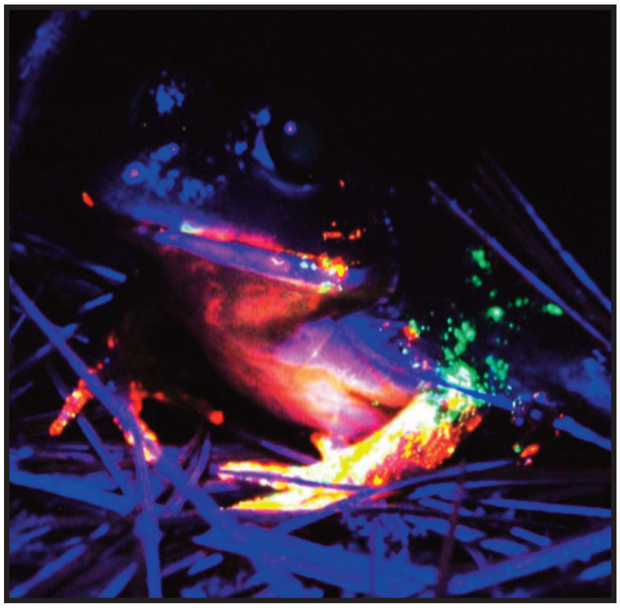

Figure 1. Green Frog (*Lithobates clamitans*) after predation event. This individual consumed two salamanders at minimum during this tracking night, and was found at the end of one salamander's powder trail. (Photographed by Dana Drake).

Results

Of the 124 salamanders tracked for this study, 29 (27%) were consumed by predators (23%), 33 were relocated alive, and 62 (50%) were not found on the surface at the end of their trails. Predation rates among the four ponds ranged from 17−25%. Salamanders were preyed upon by Green Frogs (52%; n = 15), American Bullfrogs (17%; n = 5), and unknown anurans (31%; n = 9). The majority of predation events occurred within 5 m of the pond edge (Table 1; Fig. 2). The mean percentage predation per

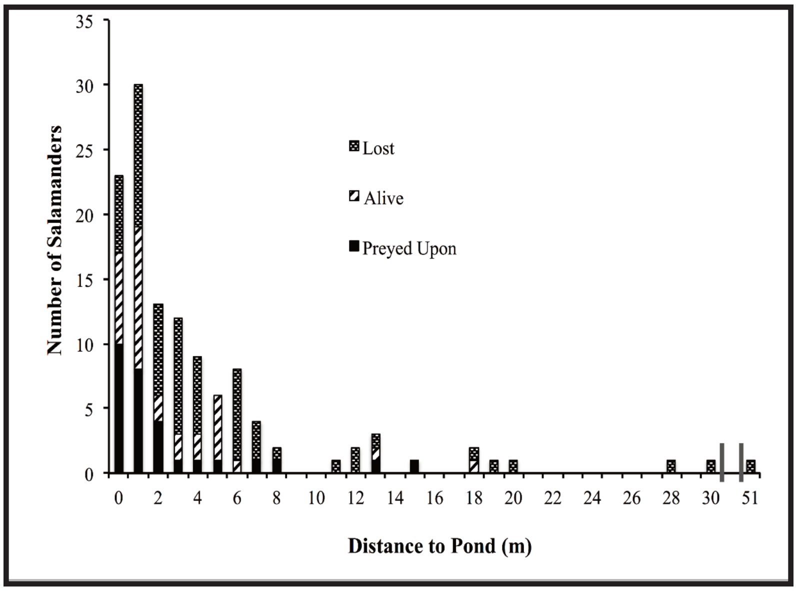

Figure 2. Fate of salamanders according to distance from pond. "Lost" represents salamanders which were not located at the end of the trail; "Alive" represents salamanders that were located alive on the surface; and "Preyed Upon" represents salamanders which were consumed. Gray vertical lines on x-axis indicate axis truncation.

Table 1. Predation events based on distance from the pond. "# Present" refers to the number of salamanders that traveled at least the minimum distance from the pond. "# Preyed Upon" refers to the number of salamanders that were consumed by anurans within the distance from pond range. The "% Preyed Upon/m" indicates the mean percentage of animals that were consumed at each meter within the distance range indicated. We did not include data from distances greater than 15 m because we did not detect any predation events farther than 15 m from the pond.

Distance from Pond (m)	# Present	# Preyed Upon	% Preyed Upon/m
0 to 5	124	25	4.9
6 to 10	27	2	2.4
11 to 15	13	2	3.2

meter did not decrease with distance from pond between 6–15 m (Table 1).

Discussion

This study found that anuran predators present a substantial risk to Ringed Salamanders during initial movement away from natal ponds. Overall, we estimated that approximately 23% of salamanders were consumed by predators in this study, and predation events occurred up to 15 m from the pond edge. The predation documented also likely represents an underestimation of actual number of predation events, as a considerable proportion of salamanders were not relocated and their fates were unknown.

Studies documenting the terrestrial movement of amphibians after metamorphosis often analyze movement in relation to habitat type and structure (e.g., deMaynadier and Hunter 1999; Jenkins et al. 2006; Popescu et al. 2012). While habitat plays a profound role in amphibian movement decisions, predation risk may also influence movement behavior and search strategies. Both theoretical and empirical studies have found that predation risk has potentially large impacts on the consequences of prey movement decisions (Zollner and Lima 2005; Rittenhouse et al. 2009; Fraker and Luttbeg 2012). For example, Rittenhouse et al. (2009) found that Wood Frog survival was highly influenced by movement strategy; Wood Frogs that remained close to the pond were more likely to die as a result of predation.

Juvenile salamanders likely behave in response to both habitat quality and predation risk under the limitations of movement and sensory capacity. Rittenhouse and Semlitsch (2007) found that terrestrial amphibian density is highest closest to breeding ponds and decreases substantially 30 m from the pond edge. We found that the highest proportion of predation events occurred close to the natal pond (0−5 m). We did not detect a decline in predation rates between 6−10 m and 11−15 m from the pond, but sample sizes at these distances were small. Linear movement perpendicularly away from the pond edge should minimize the time that salamanders spend in areas with the highest predator densities. It is possible that during initial movement bouts into terrestrial habitat, juveniles have an evolved propensity to move linearly away from the pond regardless of acquired information in order to reduce predation risk (Jenkins et al. 2006; Patrick et al. 2007). Additionally, the spacing of emigrating juveniles out of natal ponds may impact predation rates. We spaced salamanders haphazardly around the pond edges, while most studies have found that juvenile distribution around the pond during emigration is nonrandom (e.g., Jenkins et al. 2006). More information is needed on the effect of salamander emigration distribution on predation rates.

Studying the movement decisions of juvenile amphibians based on an incomplete accounting of risk may yield incorrect or misleading conclusions about the survival costs of movement behavior. Movement in response to predation risk may not be the best search strategy for locating ideal habitat for settlement, especially in fragmented areas or areas with highly clumped habitat. Movement behavior that is optimal for reducing predation risk may therefore appear maladaptive when considered in the context of locating settlement habitat. Future studies of juvenile salamander movement should seriously consider the impact of predation pressure on movement decisions during initial movement out of ponds in order to garner a more comprehensive understanding of the basis of amphibian dispersal behavior.

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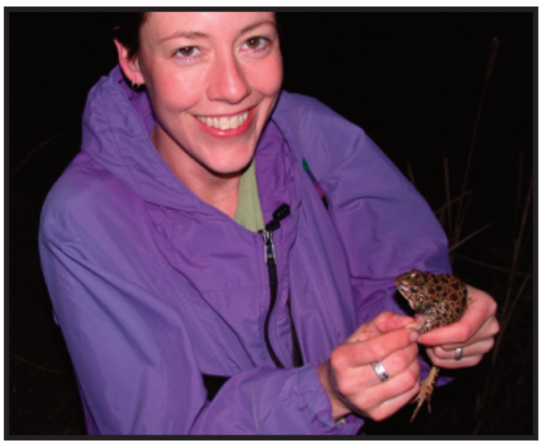

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