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Perspective

Movement ecology of amphibians: A missing component for understanding population declines

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ABSTRACT

Movement is a fundamental process of all organisms that has strong consequences for individual fitness, gene flow, natural selection, adaptation, population persistence, metapopulation dynamics, and species distributions. Yet, a lack of understanding about how different organisms move in relation to landscape structure and resource availability may prevent full understanding of species declines and extinctions. In this perspective, we introduce the concept of movement ecology for aquatic-breeding amphibians, summarize our knowledge on amphibian movement, identify critical gaps, and provide a context for how understanding movement will help develop solutions for more effective amphibian conservation. Juvenile amphibian movement is a multi-phase process during which individuals adjust movement speed, responsiveness to habitat features, and propensity of settling based on internal state and the external environment. Our review enables future studies to place amphibian movement data into a larger explanatory context and could help guide new avenues of research. Understanding juvenile responses to habitat features during dispersal will aid in developing realistic, predictive models of amphibian movement that could be used to further conservation and management efforts such as mitigation and restoration, and will also add to theory about how movement mechanisms during dispersal impact population persistence in altered landscapes.

Contents

1. Introduction

Movement is a fundamental aspect of an organisms' ecology (Nathan et al., 2008), defining the spatial and temporal scale of an organism's interactions with other organisms, resources, and the environment (Clobert et al., 2001, 2009). Movement mechanisms employed by individuals coupled with the structure of the landscape and the availability and predictability of resources can influence the spatio-temporal dynamics of populations (Mueller et al., 2011). The movement process used by individuals either to disperse to new sites or settle near natal sites has strong consequences for individual fitness, gene flow, natural selection, adaptation, population persistence, metapopulation dynamics, and species distributions (e.g., Clobert et al., 2001; Knowlton and

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Graham, 2010). Despite the importance of movement to the persistence of species, there are significant gaps in our understanding of movement processes (e.g., Bonte et al., 2012; Clobert et al., 2009; Ronce, 2007). Molecular genetic tools have allowed us to describe patterns of movement based on gene flow and the distribution of genotypes across the landscape. However, those results merely present the outcomes of movement and fail to inform an understanding of the underlying mechanisms of movement nor their fitness consequences. This lack of understanding is increasingly problematic as more species and populations face threats of decline and extinction due to global climate change, habitat fragmentation, and increasing human land use (Clobert et al., 2009). This is especially true among amphibians, where it has been reported that at least 2468 species or 43.2% of species worldwide are experiencing some form of population decrease (Stuart et al., 2004; Wake and Vredenburg, 2008).

Historically, amphibian research has been focused on the aquatic larval stage, while the terrestrial juvenile and adult stages have received less attention until recently. Many amphibians, in all regions of the world, depend on aquatic breeding habitats (e.g., seeps, springs, bogs, ponds, streams, lakes) that are clumped in space (Gill, 1978; Sjogren-Gulve, 1994; Jehle et al., 2005; Griffiths et al., 2010; Heard et al., 2012). Adult populations reside in the terrestrial habitat often within 300 m but up to 1000 m of aquatic breeding sites (varies by taxa; e.g., Semlitsch and Bodie, 2003; Schabetsberger et al., 2004; Crawford and Semlitsch, 2007; Sinsch et al., 2012). These breeding resources are strongly affected by both deterministic processes of succession and stochastic processes of weather or fish colonization that cause them to vary in suitability over time, and occasionally, amphibians using them may be subject to catastrophic reproductive failure and local extinction (e.g., Semlitsch et al., 1996; Taylor et al., 2005). As a result of a relatively high rate of local population extinction that occurs naturally across the landscape, dispersal ability has a profound impact on aquatic-breeding amphibian persistence (Sjogren-Gulve, 1994; Trenham et al., 2001; Werner et al., 2009; Grant et al., 2010). Population dynamics are therefore highly susceptible to the effects of habitat loss and fragmentation that impede or limit dispersal movement (Cushman, 2006; Laan and Verboom, 1990; McDonough and Paton, 2007). Juveniles are widely regarded as the primary long-distance dispersers in pond-breeding amphibian populations (Berven and Grudzien, 1990; Gamble et al., 2007; Gill, 1978; Griffiths et al., 2010), and population persistence is disproportionately sensitive to survival at this terrestrial life stage (Harper et al., 2008; Taylor et al., 2005). Despite the importance of juvenile dispersal, we know relatively little about the movement and search strategies of juvenile amphibians as they make initial movements into terrestrial habitat or disperse among populations.

The overall goal of this paper is to introduce the concept of movement ecology and its application to amphibian conservation. We summarize the state of knowledge on amphibian movement, identify critical gaps in our knowledge, illustrate how amphibian movement data can be used to parameterize predictive models, and provide a context for how understanding movement will help understand species declines and susceptibility to extinction. This paper generally focuses on temperate pond-breeding amphibian species, and where possible, addresses application to other aquatic breeding species (e.g., stream breeders), terrestrial species, and species from tropical regions.

2. Movement paradigm

Nathan et al. (2008) proposed a unifying paradigm of organismal movement that emphasized linking observed movement patterns to specific movement phases, which may be comprised of multiple behavioral states (i.e. movement modes; Fig. 1). This movement paradigm is highly applicable to aquatic-breeding amphibians, which exhibit well-defined life stages associated with distinct movement patterns and movement goals over their lifetime (Fig. 1). For example, an amphibian undergoing a breeding migration may maximize net displacement during movement to expend energy the most efficiently, and as a result of a cognitive capacity to locate the breeding pond. Alternatively, an amphibian that is foraging within a home range may exhibit highly tortuous movement to exhaustively search an area while minimizing net displacement. The movement patterns of these two examples are therefore fundamentally different, and analysis and interpretation of movement paths should thus be sensitive to the spatio-temporal scale of movement goals and the sensory and motion capacity of the animal (Fig. 1).

We hypothesize that movement phases are comprised of multiple movement modes of aquatic-breeding amphibians based on Nathan et al., 2008 (Table 1). In the following, we review the ways in which internal and external factors may interact to affect observed amphibian movement patterns and how those movement patterns may be described in a mechanistic movement-modeling framework. Specifically, we posit and define behavioral modes within each movement phase that can be characterized by a pattern of movement (Table 1), and associated features of the organism and landscape that impact the pattern. These phases are presented with the goal of providing amphibian researchers with a structure in which to view, collect, and analyze movement data (Table 1).

The influence of movement goals on the movement patterns of aquatic-breeding amphibians during natal dispersal is currently poorly understood (Semlitsch, 2008). For example, juvenile pond-breeding amphibians emerge from the aquatic environment naïve to the distribution, abundance, and quality of habitat in the terrestrial environment and are greatly affected by external conditions as a result of their susceptibility to predation and desiccation (Rohr and Madison, 2003; Rothermel and Luhring, 2005; Shoop, 1974). Initial movement into terrestrial habitat may constitute a substantial ecological bottleneck for amphibian populations. For example, as few as 17% of juvenile spotted salamanders (*Ambystoma maculatum*) survive one year after metamorphosis even in high-quality forest habitat (Rothermel and Semlitsch, 2002, 2006). Therefore, the behavioral decisions of juveniles in the dispersal life stage have profound implications for survival and population persistence, especially in highly altered and fragmented landscapes. Explicit investigation of the movement patterns of juveniles will aid in developing mechanistic movement models that can predict the ability of amphibians to behaviorally mitigate the effects of environmental perturbations.

2.1. Pre-departure phase

The pre-departure phase primarily describes the timing and initial orientation of juvenile departure from a natal site (Table 1). Because entire cohorts of juveniles emerge from what is ostensibly a single location within the landscape (e.g. an ephemeral puddle or a headwater stream), juvenile behavioral responses to external factors such as habitat arrangement in close proximity to the natal site can affect the survival of large numbers of individuals. However, we know relatively little about what information is used by juveniles to make initial departure decisions. There is not currently a strong consensus on the degree to which juveniles acquire and respond to information about terrestrial habitat while in the predeparture phase, or the role of temporal variation in weather conditions, making this a critical area for future research. We identify two distinct movement modes within the pre-departure phase: pre-emergence mode and wait mode (Table 1).