BIOLOGICAL CONSERVATION 139 (2007) 247–257

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation

Lloyd R. Gamble, Kevin McGarigal, Bradley W. Compton*

Department of Natural Resources Conservation, 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003, USA

ARTICLE INFO

Article history:
Received 25 July 2006
Received in revised form
15 March 2007
Available online 28 August 2007

Keywords:
Metapopulation
Wetland
Seasonal pond
Marbled salamander
Movement ecology

ABSTRACT

The spatio-temporal dynamics of amphibian populations and the models that describe them are largely influenced by the frequency of dispersal among breeding sites; however, dispersal has rarely been addressed rigorously in empirical studies. In a 7-year landscape-level investigation, we monitored breeding populations of marbled salamanders (*Ambystoma opacum*) among 14 seasonal ponds in western Massachusetts, USA, to quantify dispersal probabilities and distances. Emerging juveniles (n = 11,168) received cohort marks and adults (n = 5560 capture events) were photographed for individual identification using computer-aided dorsal pattern analysis. We found that 91.0% of first-time breeders returned to natal ponds to breed and 96.4% of experienced breeders maintained breeding site fidelity through multiple seasons. These findings confirm a high level of philopatry in this species and the prominence of local factors in determining local population trends. However, the remaining survivors dispersed to other ponds, with several individuals exceeding distances of 1000 m. Though breeding populations were clearly subdivided, dispersal at these rates may offset effects of genetic drift and inbreeding depression by increasing effective population size (through the aggregation of breeding populations). Outward dispersal probabilities were higher at ponds with small breeding populations and inward dispersal was biased toward larger populations, suggesting that salamanders were cueing to the presence of other individuals and/or to unmeasured habitat characteristics. Our findings suggest that small and dynamic local populations may operate inter dependently in a metapopulation context. Effective conservation strategies targeting these and similarly structured amphibian populations must address landscape-level processes (e.g., dispersal) as well as local demographic factors.

1. Introduction

Much debate has centered on whether the metapopulation paradigm accurately describes many amphibian populations (Semlitsch, 2000; Marsh and Trenham, 2001; Smith and Green, 2005). Though the terminology has been applied broadly, metapopulations are generally defined as groups of populations that experience routine local extinctions but may persist regionally as a result of dispersal and recolonization (Levins, 1969, 1970; Hanski and Gilpin, 1997). Broader interpretations include source-sink populations (Brown and Kodric-Brown, 1977), rescue-effect populations (Stacey et al., 1997),

* *Corresponding author:* Tel.: +1 413 887 8557.
E-mail addresses: lloydgamble2@gmail.com (L.R. Gamble), mcgarigalk@nrc.umass.edu (K. McGarigal), bcompton@nrc.umass.edu (B.W. Compton).
0006-3207/$ - see front matter
doi:10.1016/j.biocon.2007.07.001

or virtually any spatially subdivided populations connected by occasional dispersal. Where the paradigm applies, it carries clear conservation implications, such as the need to focus on landscape-level connectivity (e.g., see Cushman, 2006) and to maintain both occupied and potential habitat patches. However, misapplication of the paradigm can be risky, as in cases where a fragmented population in decline may be viewed as a metapopulation at equilibrium or where deterministic local factors may be more important to population persistence than regional connectivity (Marsh and Trenham, 2001).

At face value, the metapopulation paradigm appears well suited to many amphibians. For example, pond-breeding amphibians: (1) are associated with discrete aquatic breeding sites, (2) often experience wide population fluctuations (Semlitsch et al., 1996; Green, 2003) that may vary temporally among proximate sites (Trenham et al., 2003) and (3) often appear to have high fidelity to natal ponds (i.e., philopatry) (Pechmann et al., 1991). The degree to which populations exhibit philopatry is critical in determining the scales at which populations operate; however, this is often the condition we know least about in real populations. For example, how often do individuals successfully disperse in a true ecological sense – that is, to leave a natal site and breed at a new location – and what factors regulate this behavior? Is dispersal a density-dependent response to local conditions or does it occur at more constant, predictable rates? How is dispersal success mediated by distance, landscape permeability, and/or active habitat selection? Addressing these types of questions is necessary to assess the applicability of the metapopulation paradigm and its conservation implications for pond-breeding amphibians (Semlitsch, 2002).

Though a number of studies have concluded that pond-breeding amphibians exhibit philopatry, most of these studies have been limited primarily to observations of returning individuals at a single breeding site. For example, both Husting (1965) and Whitford and Vinegar (1966) conducted multi-year studies on spotted salamanders (*Ambystoma maculatum*) that were focused on single breeding sites with limited sampling at nearby ponds. In both cases, no marked animals from the primary sites were observed elsewhere and it was concluded that little or no dispersal occurred. Findings have differed in studies that have incorporated numerous breeding sites. For example, in a study of the California tiger salamander (*Ambystoma californiense*), Trenham et al. (2001) directly observed interpond dispersal at probabilities exceeding 20% in both first-time and experienced breeders. Gill (1978) documented perfect breeding site fidelity among adult red-spotted newts (*Notophthalmus viridescens*) but inferred dispersal by juveniles based on the persistence of several apparent sink populations. Multi-site studies of anurans have documented abundant dispersal in some cases (Breden, 1987) and infrequent, age-specific dispersal in others (Berven and Grudzien, 1990). To our knowledge, no published studies have directly measured dispersal in any Ambystomatids in eastern North America.

Here we present results from a 7-year field study in which we continuously monitored breeding populations of the marbled salamander (*Ambystoma opacum*) at 14 seasonal ponds in a western Massachusetts landscape. Our primary objectives in this paper are to:

(1) address pond fidelity in marbled salamanders by measuring successful return and dispersal probabilities among first-time and experienced breeders,
(2) use these empirical data to fit a distance-dispersal function that can (a) help to generalize our findings to different landscapes (with several important limitations) and (b) be used to set parameters for spatial population and connectivity models,
(3) describe several observations that reveal elements of dispersal behavior and may be used to frame future experimental work,
(4) discuss the implications of our findings for spatio-temporal population dynamics in this species and for conservation approaches to pond-breeding amphibians in general.

2. Methods

2.1. *Study organism*

The marbled salamander is a terrestrial salamander whose natural range extends across the eastern United States from Florida to southern New England (Petranka, 1998). The marbled salamander is one of several species in its genus that breed primarily in seasonal ponds and spend the majority of their lives in upland forests surrounding these ponds. In contrast to most of their eastern congeners, however, adult marbled salamanders court in the late summer and early fall and subsequently lay eggs terrestrially in receded or dry pond basins (Noble and Brady, 1933; Bishop, 1941). Eggs are typically inundated by rising waters in the fall or winter months and then hatch almost immediately into aquatic larvae. These larvae overwinter in the ponds and surviving individuals metamorphose into terrestrial salamanders in the late spring and early summer. In Massachusetts, breeding populations of marbled salamanders are fairly small (likely due to proximity to northern range limits) and the species is listed as "Threatened" under the state Endangered Species Act (M.G.L c.131A and regulations 321 CMR 10.00). High pond fidelity in this species is suspected (Pechmann et al., 1991), in which case local "pond-populations" even in close proximity may be effectively discrete, related only by occasional dispersal of juvenile animals (but see Petranka et al., 2004).

2.2. *Study area*

The study area encompasses approximately 300 ha of mixed-deciduous hardwood forests on the Holyoke Range in western Massachusetts, USA. The site is mostly undeveloped, but is bisected by a 30-m wide power line corridor and contains numerous carriage roads and trails. Estimated modal stand age is 70 years. Ten seasonal ponds are clustered tightly in the western section of the study area and four are distributed more widely to the east, with interpond distances ranging from 50 to 1500 m. The ponds range in surface area at high water from 0.03 to 0.35 ha, and vary considerably in structure – including shrub-dominated, open-deep water, and shallow (open and/or vegetated) ponds. Hydroperiods and water level