ABSTRACT

Title of Document: HOW DENDRITIC ECOLOGICAL NETWORKS

STRUCTURE THE DISTRIBUTION AND

MOVEMENT OF STREAM SALAMANDERS

Evan H. Campbell Grant, Doctor of Philosophy,

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Directed By: Professor Margaret A. Palmer, Department of

Entomology and Chesapeake Biological

Laboratory

Research in population biology is concerned with factors affecting the change in a population over time, including births, deaths, immigration and emigration. Despite the potential importance of dispersal, empirical data on movement are lacking in many systems. Hence, there is a large body of theory on dispersal that remains to be tested in real biological systems.   In particular, many organisms exist in ecological networks with the complex geometry common to caves, plants and streams. This alternative network topology might influence population and community-level patterns and processes.

Chapter 1 introduces the concept of the "dendritic ecological network," highlighting special properties and characteristics useful for understanding

community and population-level processes. Of most interest for this dissertation is how the rigid spatial structure and branching topology may have implications for patterns of population distribution and the evolution of movement behaviour in stream organisms.

In chapters 2 and 3, I investigate patterns of stream salamander distribution, which may be related to the spatial configuration of stream habitat branches. First, I determined the sampling methods suitable for estimating the probability a site is occupied by one of three stream salamander species. I then applied these methods to investigate occupancy patterns, in relation to stream spatial layout across two mid-Atlantic regions. I found that all three species have higher occupancy in streams with a confluent, firs-order stream, though the strength of this association seems to be related to life history characteristics.

Finally, in chapters 4 and 5, I sought to identify movement pathways for larval, juvenile and adult *Desmognathus* stream salamanders. First, I tested my marking method on larval individuals, and found that the visual implant elastomer marks can be retained through metamorphosis. Then, using individual mark-recapture and multistate modeling, I found that stream salamanders move during the juvenile stage, with both an upstream-biased movement, and a proportionally large probability of moving overland to an adjacent stream reach.

The chapters in this dissertation combine empirical investigations of the patterns and pathways of stream salamander movement. Taken together, they elucidate the underlying importance of dendritic ecological networks, and provide direct evidence of dispersal in stream salamanders.

HOW DENDRITIC ECOLOGICAL NETWORKS STRUCTURE THE DISTRIBUTION
AND MOVEMENT OF STREAM SALAMANDERS

By

Evan H. Campbell Grant

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Advisory Committee:
Professor Dr. Margaret A. Palmer, Chair
Dr. James D. Nichols
Dr. William F. Fagan
Dr. Winsor H. Lowe
Dr. David Secor

Preface

This dissertation contains a single introduction section, five research chapters and an appendix. The chapters (I-V) in the dissertation represent primary work; an appendix provides a supporting chapter which is referenced in chapter V. All chapters are presented in manuscript form, and formatted depending on the journal in which they were published (chapters I-IV) or for which they are intended (chapter V). The appendix comprises a book chapter, which was coauthored during the dissertation, but separate from the main work of the dissertation. A single reference section occurs at the end for literature cited throughout the dissertation.

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Introduction

Spatial structure has long been recognized to be a key component in structuring ecological patterns and processes. Amphibians are often cited as key components of many ecosystems, with their physiological tolerances and complex life cycles making them potentially good indicators of environmental changes. Despite the attention paid to amphibians since the 1990's, scientists have relatively little understanding of the controls on stream salamander populations, especially with respect to their movement ecology. Because these animals live in complex stream networks, their patterns of distribution may be constrained both by their individual propensity to move among the stream branches, and by the spatial layout of the stream network.

Chapter one introduces the concept of the Dendritic Ecological Network (DEN), which provides the foundation for the questions investigated in this dissertation. Despite the importance and historical attention to complex spatial networks of discrete habitat patches, there has been relatively little theory and research on networks with alternative geometries, such as that common to river networks. By outlining the special properties of DENs, and summarizing existing theory and empirical research in these networks, we can make predictions as to the role of the network in structuring patterns of distribution and movement probabilities in stream salamanders.

In chapters two and three, we ask whether the distribution of three stream salamander species with different life histories is related to the larger network structure. We use patch occupancy models and information-theoretic approach to determine the support for the hypothesis that stream branches with a confluent, first-order stream branch have a higher probability of occupancy than those without such a connection. We interpret differences in the relative strength of each species'

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relationship with the stream spatial layout to result partly from differences in life history.

Knowing how the spatial layout of a DEN may influence patterns of distribution is an indirect measure of the relationship between animals and the network. A mechanistic understanding of movement paths, and life history stages responsible for dispersal is essential to elucidating the underlying cause of any relationship between network structure and stream salamander distribution. Further, information on movement paths is essential to conservation planning and resource management problems. Chapters four and five ask whether the movement decisions of stream salamanders is related to life history stage and stream network configuration in one species of stream salamander. I use mark-recapture and multistate modeling to estimate the probabilities of movement among and within stream networks of differing complexity. The combinations of movement probabilities suggests a distinct dispersal stage for stream salamanders, and has implications for understanding extinction risk in complex dendritic networks.

Chapter I: Living in the branches: population dynamics and ecological processes in dendritic networks.

Coauthored with: Winsor H. Lowe, William F. Fagan

Abstract

Spatial structure regulates and modifies processes at several levels of ecological organization (e.g. individual/genetic, population, community) and is thus a key component of complex systems, where knowledge at a small scale can be insufficient for understanding system behaviour at a larger scale. Recent syntheses outline potential applications of network theory to ecological systems, but do not address the implications of physical structure for network dynamics. There is a specific need to examine how dendritic habitat structure, such as that found in stream, hedgerow and cave networks, influences ecological processes. Although dendritic networks are one type of ecological network, they are distinguished by two fundamental characteristics: (1) both the branches and the nodes serve as habitat, and (2) the specific spatial arrangement and hierarchical organization of these elements interacts with a species' movement behavior to alter patterns of population distribution and abundance, and community interactions. Here, we summarize existing theory relating to ecological dynamics in dendritic networks, review empirical studies examining the population- and community-level consequences of these networks, and suggest future research integrating spatial pattern and processes in dendritic systems.

Introduction

Ecologists' interest in spatial processes has grown tremendously over the last few decades (MacArthur & Wilson 1967, Fretwell 1972, Forman & Godron 1986,

Hanski & Gilpin 1997, Clobert *et al*. 2001). Attention has focused especially strongly on issues relating to habitat geometry, such as patch size (Skellam 1951, Hanski & Ovaskainen 2000, Speirs & Gurney 2001), patch edges (Fagan *et al.* 1999, Ries *et al*. 2004), and corridors (Haddad *et al.* 2003). In metapopulations, mainland-island networks, and other multi-patch systems, substantial effort has centered on characterizing and quantifying aspects of ecological connectivity that influence the flow of genes and individuals, and that regulate ecosystem services. Empirical and theoretical investigations of the interaction between habitat configuration and ecological processes, such as population growth and spread, are becoming more prevalent in ecology and conservation biology (e.g., Hanski 1998, With 2002). Here, we (1) review current paradigms and tools for studying complex systems, (2) describe a specific, important class of networks where hierarchical, branching geometry imposes special structural and dynamic properties, (3) summarize existing theory relating to ecological dynamics in these dendritic networks, (4) review empirical studies examining the population- and community-level consequences of dendritic ecological networks, and (5) suggest future research integrating spatial pattern and processes in these networks.

Recent syntheses have applied network theoretic analyses to understand the functioning of a diverse set of complex systems (Newman 2003, Stewart 2004, Proulx *et al.* 2005, May 2006, Montoya *et al.* 2006), suggesting that emergent characteristics, such as system-level responses to disturbance, can be predicted from the structure of a network and the strength of interactions among network elements. These reviews constitute a coherent treatment of "lattice" networks, which are node-focused systems in which the role of network links is to connect processes that occur within the system of nodes (Fig. 1.1a). Lattice networks include rasterized networks, in which each cell in a regular spatial grid is connected to a fixed number

of neighbors, as well as patchy networks, in which each patch is (potentially) directly connected to all other patches in the network. Thus, our use of the term 'lattice' includes those systems that lie between a random graph and a regular spatial lattice (e.g., a 'small world' network, Watts & Strogatz 2001).

Ecologists have utilized theory developed for complex networks in other systems to understand dynamics in spatially structured ecological networks. One such framework involves the application of a field of mathematics known as graph theory (Urban & Keitt 2001, also referred to as network theory: Newman 2003 and references therein), a set of tools that offer substantial advantages in studies of ecological connectivity (Calabrese & Fagan 2004). In graph theory, spatially structured systems can be idealized as a system of 'nodes' and 'links' (also called 'edges'; not to be confused with habitat edges, as in landscape ecology), and spatial ecologists working with graph theory have generally viewed nodes as discrete habitat patches and the links as the connections along which individuals or resources flow. This conceptual framework has been applied to spatially structured networks with lattice-like topology to identify important habitats for metapopulation conservation (Urban & Keitt 2001), to investigate the response of migration corridors to the positioning of stopover sites (e.g., bird migration routes, Shimazaki *et al.* 2004), or to forecast the response of a population to landscape change (e.g., amphibian population response to drought, Fortuna *et al.* 2006).

In contrast to the wide theoretic interest in spatially structured networks with lattice-like architecture, there has been little discussion of systems with alternative network geometries, such as the dendritic (branching) geometry common to plants, river systems, and caves. This lack of attention may arise because, from a theoretical standpoint, dendritic geometries are merely a special case of network topology. However, dendritic geometries are widespread in ecological systems and

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feature particular structural and dynamic characteristics that deserve special attention. Dendritic ecological networks (DENs) are a unique type of spatially structured network, which differ from lattice networks in several important ways (Table 1.1).

Recent theoretical advances in spatially structured networks focus primarily on the development of statistical indices of network properties (Newman 2003) that contribute to large-scale connectivity and, therefore, to network-level persistence of populations (e.g., Jordán *et al*. 2003, Pascual-Hortal & Saura 2006). However, ecological processes in DENs are sensitive to specific structural features of the network that are obscured by these statistical indices. This sensitivity results, in part, because in DENs there is a closer match between the physical scale at which the network is considered and the scales at which ecological processes are acting. This sensitivity also underscores the importance of developing alternative tools for exploring and understanding ecological dynamics in DENs.

What are dendritic ecological networks?

'Dendritic' describes the geometric pattern of arborescent bifurcation, consisting of a 'mainstem' and 'branches' which decrease in size and increase in number hierarchically as one proceeds upwards through the network (Fig. 1.1c). Many DENs are fractal-like, with elements of self-similarity across scales. The classic example of dendritic geometry in nature is the branching architecture of individual plants (Thompson 1917). However, the hierarchical branching geometry of stream systems has received considerable attention regarding the relationship between network geometry and dynamics (Fisher 1997, Fisher *et al.* 2004, Rodriguez-Iturbe & Rinaldo 1997).

From this background, the DEN concept can be generalized to describe any system where critical resources are concentrated in a linear arrangement and where those linear subunits intersect to create a branching architecture. This structure may result from landscape alteration that maintains linear units of distinct habitat, for example, hedgerows and fence lines (Hilty & Merenlender 2004, Deckers *et al.* 2005), the formation of caves by dissolution in karst landscapes (Christman *et al.* 2005), or the construction of transportation corridors (Christen & Matlack 2006). Though not dendritic in the strict sense, hedgerow and transportation corridors exhibit key structural features of other natural dendritic networks, such as streams or caves.

In systems structured as DENs, ecological processes (e.g., dispersal, population growth, community interactions) are carried out within the branches themselves, while the nodes serve as "transfer" points where branch dynamics may be modified as one proceeds along the network. These processes may change depending on branch size, the juxtaposition of different branch types at nodes, and the interplay between species (or individuals) and network geometry. This conceptualization means that DENs are structurally and functionally different from other types of ecological networks, such as metapopulations and foodwebs, where the focus is largely on the nodes of the network, with links that define connections between nodes (Table 1.1; Hanski 1998, Ricketts 2001, Polis & Winemiller 1996). For example, within DENs such as river or cave networks, branches serve as primary habitats for resident species, whereas in lattice-type spatial networks, the links are typically routes for connections between habitats. Furthermore, when links exist as discrete features in lattice networks, they are typically of lower quality (e.g., movement corridors between patches). As we discuss below, the branching, hierarchical geometry of DENs drives key patterns and functional properties.

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Because these structural differences are difficult to incorporate explicitly in lattice models, conclusions drawn from these models may not be applicable to DENs. Graph theoretic approaches have great potential in studies of spatially structured lattice networks (e.g., metapopulations; Urban & Keitt 2001), but such approaches are of limited utility in studies of DENs, where spatially constrained network topology and hierarchical geometry interact. In some cases, representation of a DEN as habitat branches linked at the branch intersections (Fig 1.1b, upper) may be appropriate when interest is focused on dynamics within the linear habitat units alone. Likewise, when interest is focused on dynamics and processes occurring at habitat intersections, a DEN can be conceptualized as nodes linked by habitat branches (Fig. 1.1b, lower). However, such graph theoretic perspectives will obscure processes that are functions of both nodes and branches. Accounting for the interaction of these two fundamental network components is critical to understanding ecological dynamics in DENs.

Dynamics in dendritic ecological networks

Identification of general patterns resulting from network architecture provides a way to move beyond a case-by-case analysis of the consequences of spatial patterning in ecological systems. Just as consideration of network topology has improved understanding of food webs (Dunne *et al.* 2002, Power & Dietrich 2002) and metapopulations (e.g., Fortuna *et al.* 2006), we argue that further study of DENs as a class of spatial structures will improve our understanding of ecological systems that involve branching, hierarchical geometries. Most empirical studies of dendritic geometry have dealt with stream systems, though other types of systems also fit the general topological form of a DEN. We believe that developing a conceptual framework for these types of networks will (1) guide development of theory suitable

for DENs, and (2) provide direction for studies in a diverse set of systems where branching, hierarchical geometries are important. Because the architecture of a DEN is usually rigid and ecological processes occur in the network branches, the network imposes constraints on population processes such as spread, growth, and survival (Fig. 1.2). By influencing the population dynamics of individual species and by differentially mediating the movement of species among branches, the network architecture of DENs may also affect community dynamics (Fig. 1.2).

Population-level implications of dendritic network structure

In a DEN, connectivity is a function of network topology, which interacts with species- and individual-level behaviours. Individual movements can follow two pathways in dendritic networks: along the network geometry (within-network movement), or between branches of the network (out-of-network movement). For example, while larval stream insects are restricted to within-network movements (e.g., Waters 1972), many adult stream insects are capable of out-of-network movement by flying overland among branches (Miller *et al*. 2002, MacNeale *et al*. 2005). For some species, such as stream amphibians, certain life stages are capable of both in- and out-of-network movement. A variety of taxa exhibit preferential movement paths along the branches of habitat networks (e.g., butterflies in open, non-forest habitat, Haddad 1999; organisms moving across migration networks, Alerstam 2006; migrating fish, Keefer *et al.* 2006), suggesting that organisms respond to structural cues within the habitat network. For example, Keefer *et al.* (2006) found that migrating, radio-tagged Chinook salmon (*Oncorhychus tshawytscha*) selectively used those portions of the rivers that exhibited cues of their natal tributaries. Where in the river network individuals began to use chemical cues to navigate towards their natal tributary depended on the size

(and discharge) of their natal tributary and the proximity of dams in the mainstem that could alter directional cues via mixing and turbulent flow. Additionally, in a habitat with stark boundaries between habitat and non-habitat, Haddad (1999) found that butterflies movement behaviour at habitat patch boundaries was a good predictor of the use of habitat corridors through non-habitat matrix. He observed that species whose movement behaviour suggested reflection off the patch boundary were likely to move through habitat corridors. These examples illustrate the types of spatially referenced cues that organisms may use to facilitate movement through the linear habitat features in a DEN.

For species that preferentially travel along the network branches, patterns of genetic relatedness can reflect the constraints imposed by the network architecture (Rissler *et al*. 2004, Lowe *et al.* 2006). When species are obliged to move within the network, strong demographic and genetic isolation may occur among locations that are nearby in Euclidean space, but distant along network branches (Fagan 2002, Rissler *et al*. 2004). In cave networks, populations of obligate cave-dwelling organisms may be isolated if networks of underground passages are extensive, even when cave entrances are separated by short above-ground distances. As cave animals are restricted to subterranean pathways, the branching architecture of cave networks imposes a structural constraint on dispersal which may explain the high levels of endemism in this group of organisms (Christman *et al.* 2005). For example, Fong & Culver (1994) described the distribution of several cave-dwelling aquatic crustaceans and ascertained the history of species' invasion of the network by mapping the occurrence of each species in relation to the network's branching geometry. The distribution of one species (*Gammarus minus*) was best explained by movement upstream through the branching cave network. This pattern of movement resulted in occupancy of only a portion of the network of cave passages, even when

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surface connections with the adjacent cave passages were nearby in Euclidean

space. Another species (*Caecidotea holsingeri*) was postulated to have invaded the

cave network from the tips of the network branches, as suggested by its

contemporary distribution throughout the cave network.

The linear habitat arrays of a DEN can also enhance population connectivity by

acting as movement corridors, which channel dispersal along pathways of suitable

habitat (Fig. 1.2b; Beier & Noss 1998, Joyce *et al*. 1999). The enhanced connectivity

of a DEN can increase the likelihood of metapopulation persistence, provided

dispersal is sufficient to recolonize extirpated patches (Fagan 2002). Similarly, the

topology of a network of habitat patches may interact with dispersal vectors and

species' life history traits to influence the rate and extent of population expansion

(Cuddington & Yodzis 2002). Empirical evidence of high population connectivity in

DENs includes rates of seed spread via the edge-following behavior of birds (Levey

et al. 2005), the distribution of plant communities along riverbanks and within

hedgerows (Honnay *et al.* 2001, Deckers *et al.* 2005), the preferential flight

orientation of emerging stream invertebrates (Macneale *et al*. 2004, 2005), and the

recovery of salamander populations following logging in headwater drainages (Lowe

and Bolger 2002). In European hedgerows, the probability of pin cherry (*Prunus

pensylvanica*) occurrence increased near nodes where hedgerows intersected. This

pattern was attributed to the edge-following behavior of birds that serve as the tree's

primary seed dispersal vector (Deckers *et al.* 2005). Likewise, the presence of

confluent or intersecting branches may enhance the size and demographic resilience

of a population (Fig. 1.2b) by providing a ready source of colonists (the rescue effect

of Brown & Kodric-Brown 1977) or through transient source-sink dynamics (Pulliam

1988). For example, Lowe & Bolger (2002) found that networks with greater

complexity (e.g., networks having confluent branches versus linear, unbranched

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networks) harbored larger populations of a stream salamander species (*Gyrinophilus porphyriticus*) that is primarily limited to movement along the network branches.

Organisms searching for high quality habitat may take advantage of spatially referenced clues. In DENs, node habitats often feature distinct physical and chemical conditions that may create high quality habitat at nodes, or provide information on habitat quality in the intersecting branches (Fig. 1.2d,e; e.g., Joyce *et al*. 1999, Liu *et al.* 2003, Benda *et al.* 2004, Keefer *et al*. 2006). For example, Riffell & Gutweiller (1996) found that the shape of hedgerow intersections influenced plant species richness, with more intersecting branches correlating with higher richness. In these hedgerow systems, such 'intersection effects' were a result of both the unique abiotic conditions at the nodes and the increased chance of seed deposition by bird and mammal dispersal vectors at those nodes with many branch intersections. Such intersection effects in hedgerows are particularly strong in carabid beetles, which were more abundant at those habitat nodes with many branch intersections than in the confluent branches (Joyce *et al*. 1999). Likewise, in stream networks, two-lined salamander larvae (*Eurycea bislineata*) and all life stages of the northern spring salamander (*Gyrinophilus porphyriticus*) prefer microhabitats in headwater streams with low proportions of fine particles, which can limit the suitability of the stream bed as a refuge from predatory fish (Barr & Babbitt 2002, Lowe & Bolger 2002). Disturbance in upstream tributaries can result in greater deposition of fine sediments at nodes (Benda *et al*. 2004), which may prevent salamanders from moving through those nodes and into upstream tributaries.

The spatial pattern of disturbance is also likely to have a strong affect on population connectivity in DENs. For example, in stream networks, Euclidean (i.e., overland) distances between adjacent, low-order streams (e.g., headwaters) are typically shorter than distances to the same point if traveling along the network

branches. Therefore, in species that are restricted to within-network movements (e.g., most fish), the likelihood of recolonization following disturbance will increase as the size of the impacted stream decreases (Fagan 2002, Fagan *et al.* 2002). Likewise, in cave systems, populations may be sensitive to disturbances that are correlated in space, when surface entrances to branches of the cave network are nearby in Euclidean distance. In this way, the architecture of the DEN impedes recolonization of the branch tips by inducing a mismatch between the dispersal ecology of a species (which is restricted to movements along the network branches) and the spatial pattern of disturbance in the network (Fagan 2002). Further, due to the hierarchical geometry of DENs, a disturbance in one branch segment may be more easily translated through the network (Jones *et al.* 2000). Such connectivity results in correlated extinction risks for branches along the network, and will likely be most severe in directed systems (e.g., streams).

The dynamics of an invasion can also be sensitive to the underlying geometry of a DEN. In a complex network, a population undergoing diffusion will be partitioned between (1) movements along the main stem of the network and (2) spread to the branches (Fig. 1.2; Johnson *et al.* 1995). In this way, the branches may act as population 'sinks' (Pulliam 1988), preventing rapid spread through the network. This feature may be especially important in understanding the spread and dynamics of diseases in DENs. Further, network geometry and complexity allow for increased equilibrium densities of prey populations, especially when predator movement is limited (Cuddington & Yodzis 2002). Out-of-network connectivity may remove the restrictions imposed by network architecture (Cuddington & Yodzis 2000), and this increased topological connectedness may enhance dynamic stability of the network (Csermely 2004). Such results would be qualitatively similar to theoretical models of metapopulation dynamics occurring in dendritic networks (e.g., Fagan 2002, Lowe

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2002). In a theoretical investigation of the effect of dendritic network geometry on

population persistence, Fagan (2002) studied the influence of network topology on

extinction risk in dendritic and linear (unbranched) networks, simulating the response

of species that only move along the network branches. He found that when

colonization probability was small relative to extinction, the shape of the network did

not change the metapopulation extinction risk. However, when colonization

probability was high and not directed (i.e., individuals could move both up- and

downstream through the network), population persistence times were enhanced in

the dendritic system, highlighting the importance of network geometry. Additionally,

Lowe (2002) included a small probability of out-of-network movement (i.e.,

movements that did not follow the network branches) in his model of metapopulation

dynamics in DENs. He found that when a population was concentrated in the

uppermost branches of the network (as may be common in stream salamanders),

this out-of-network dispersal was important in promoting stability of the population in

the network. These results highlight the importance of network architecture on

regulating ecological processes such as movement and colonization. Further, in

species or life stages capable of out-of-network movements, the interaction between

population distribution and the bifurcation angles of habitat branches in a DEN may

play a key role in regulating spread to adjacent branches. More theoretical work is

needed to understand the range of conditions under which dendritic geometry

enhances dynamic stability of ecological systems.

Community-level implications of dendritic network structure

Because dendritic geometry constrains local patterns of movement, and may do

so differentially among species, the physical structure of a DEN may strongly

influence interspecific interactions. In dendritic networks, the complexity of the

network architecture can impede the movement of individuals (Johnson *et al*. 1995),

which can reduce predator-prey interaction rates (Cuddington & Yodzis 2002). This

results from the interaction of environmental attributes (i.e., the geometric complexity

of the network) with the movement behaviour of individuals, which only have local

spatial knowledge and cannot perceive the overall structure of the network. Within a

geometrically complex network, predators may be unable to respond to spatial

variation in prey population density, increasing the variation in local reproductive

rates, persistence, and equilibrium densities of prey populations (Cuddington &

Yodzis 2002). The link between dendritic geometry and species interactions is

especially well developed in insect-plant systems (e.g., Grevstad & Klepetka 1992,

Kareiva & Sahakian 1990). Many attributes of plant architecture may affect species

interactions, including size and gross morphology, number and variety of plant parts,

and number of physically touching ('connected') parts (Grevstad & Klepetka 1992,

Gingras *et al*. 2002, Marquis *et al*. 2002, Legrand & Barbosa 2003). In an

experimental test of the influence of network architecture on parasitoid-host

interactions, Gingras *et al.* (2002) constructed artificial plants of varying geometric

complexity, and evaluated the influence of plant architectural complexity on

parasitism rate. They found that increasing connectedness (defined as the number

of nodes present in the plant's architecture) reduced the rate of parasitism by

decreasing the efficiency of locating a host. The parasitoid found hosts by walking

along the branches of the plant, and therefore, increasing the number of connections

decreased the encounter rate and the probability of finding a host in a given unit of

time (Fig. 1.2f). Legrand & Barbosa (2003) reported similar results in an aphid-

predator system, and attributed the persistence of aphid populations on structurally

complex plants (those with a larger number of nodes) to a decrease in predator

search area efficiency.

The geometry of intersecting habitat branches influences the distribution of species within the network, and the branching architecture can therefore determine patterns of species diversity. For example, the species richness of electric fish communities of the Amazon River is enhanced at tributary confluences (i.e., nodes; Fig. 1.2d; Fernandes *et al.* 2004). In general, this enhancement of diversity may depend on the branching patterns of the network (Grenouillet *et al.* 2004), and on the specific dispersal ecology of the species involved (Skalski & Gilliam 2000, Cuddington & Yodzis 2002). In stream networks, the presence of confluent branches at nodes may enhance diversity by (1) providing refugia for sensitive life stages or species, (2) enhancing local habitat heterogeneity, and (3) providing access to the mainstem for migratory individuals. The side branching architecture of stream networks (i.e., lower order branches that link directly to a mainstem; Turcotte *et al.* 1998) affects distributional patterns of fish (Smith & Kraft 2005, Grenouillet *et al.* 2004) and invertebrates (Rice *et al*. 2001). In these studies, increased local diversity was related to the large-scale branching geometry and spatial arrangement of the stream network, rather than tributary presence *per se*. One reason for this relationship may be that the hierarchical branching of stream tributaries affects aspects of habitat structure and water quality both at the tributary confluences and in the mainstem downstream of the confluences (Rice *et al.* 2001, Liu *et al.* 2003, Benda *et al.* 2004). More generally, the nodes of DENs are likely to support high level of species diversity because they represent intersections of distinct habitat types where, consequently, localized habitat diversity is high relative to areas of similar size within network branches.

Network architecture can also influence food web structure (Power & Dietrich 2002, Fisher *et al.* 2004), and three characteristics of DENs seem especially important in regulating food web structure. First, nodes serve as unique habitats,

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where resources are concentrated before they are dispersed through the network. Concentration of resources can occur via advective transport or active individual choice for specific habitat conditions at nodes (Fig. 1.2e), and accumulation of resources at branch junctions may regulate the flux of resources through the network. For example, the effect of persistent downstream movement of material and individuals from tributaries may override competitive interactions further down in the network, resulting in a type of mass-effect (Kunin 1998). Second, the juxtaposition of independent branch habitats provides diverse habitat types and resource flows at nodes, especially where smaller tributaries intersect larger branches (Fig. 1.2d). Via advection and concentration, smaller branches may provide resource subsidies to organisms that are restricted to larger branches by size or other abiotic habitat requirements ('landscape complementation'; Dunning *et al*. 1992). This effect would likely be highly dependent on the size and configuration of the network branches. Finally, the presence of spatially repeating, but indirectly linked branches introduces a source of spatial heterogeneity in predation pressure and resource availability. Theoretical studies by Cuddington & Yodzis (2002) demonstrated that the topological complexity of DENs alters stopping rules of predators, which can get caught in network branches with depleted resources (Fig. 1.2b). The architecture of a DEN thus induces a mismatch between scale at which a consumer can respond to the spatial structure of the network and the scale over which resources are distributed within the network.

Moving beyond branches and nodes: Integrating pattern and process in dendritic networks

Compared to lattice networks, networks with dendritic architecture lack a general theory relating to ecological patterns and processes. Stream ecologists have long

recognized that the spatial layout of tributary branches can affect processes in the mainstem (e.g. Vannote *et al.* 1980, Bruns *et al.* 1984, Fisher 1997). However, despite a focus on large-scale spatial structure in riverine systems (Fisher 1997), empirical studies of how dendritic network geometry affects ecological patterns and processes in these systems are rare. Empirical examinations of the role of spatial structure in other types of DENs are similarly sparse. Indeed, our review revealed only a handful of studies dealing with the influences of plant architecture, cave, or hedgerow networks on population or community level dynamics.

Much of the work on lattice networks falls into a few broad categories: (1) mechanisms for the formation of complex networks (e.g., preferential addition of links to highly connected nodes), (2) assembly characteristics for attachment of links to nodes, (3) properties of the network (e.g., robustness to node removal), and (4) the form and function of links (Newman 2003, Proulx *et al.* 2005). Thus, in spatial networks with lattice-type geometry (e.g., Fig. 1.1a), much of the interest is on features of the landscape that promote or inhibit network connectivity. In contrast, the exciting future for DENs lies in the identification of patterns and processes specific to and resulting from the rigid, branching geometry and the interaction of branches and nodes. Characteristics important to DENs include: (1) number of branch intersections, (2) size and shape of branches, and (3) the hierarchical geometry of branching. In particular, more theoretical and empirical efforts are needed to characterize the relationship between dendritic network structure and (1) population dynamics, limitation, and regulation, (2) speciation and evolutionary dynamics and limitations, (3) species extinction risks and conservation, (4) land management and response to disturbance, and (5) species interactions.

Empirical case studies discussed above suggest that the topology of dendritic networks results in special properties and patterns that may be generalized to other

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systems sharing important features of this network structure (e.g., caves, transportation networks, and potentially, migration routes and corridors). Concern about habitat fragmentation has inspired research into habitat features controlling population connectivity and ecosystem fluxes, such as habitat edges (e.g., Fagan *et al*. 1999) and corridors (e.g., Haddad *et al.* 2003), that can also be addressed within a conceptual framework for DENs. Linking DENs to work in lattice networks would benefit our general understanding of ecological networks, but the rigid geometry of DENs and importance of branches rather than node habitats does not fit well into existing network models for node-focused lattice systems. Regardless, we need a better way to generalize patterns and processes resulting from the geometry of dendritic systems. Looking forward, several topics deserve special attention:

Within-network versus out-of-network movements. The fraction of movements taking place within the restrictive geometry of a DEN relative to out-of-network movements (e.g., from one branch to another) is undoubtedly critical to population demography and genetics. For organisms that have evolved within spatially structured systems, within-network movements can reasonably be considered as primary movement pathways, and out-of-network movements as secondary pathways (or 'weak' links; Csermely 2004). However, out-of-network movements may be particularly important for maintaining genetic diversity within populations in DENs (Lowe 2002, Rissler *et al*. 2004), and may be crucial for population persistence, should a dendritic network become fragmented (Fagan 2002). In addition, when species' movements are not constrained by the branching geometry of a DEN (e.g., a greater proportion of out-of-network as compared to within-network movements), measures of community stability will likely increase, as is found in lattice networks with increasing connectance (e.g., Dunne *et al*. 2002).

Natural versus human-generated DENs and species adaptation to network geometry. Examples exist of both natural (e.g., streams, desert riparian vegetation) and human-created DENs (e.g., hedgerows). Likewise, we have sets of species that have existed for many generations in DENs and others for which dendritic geometries are a relatively new feature of their landscapes. Consequently, it would be informative to compare the response to disturbance of species that are adapted to dendritic systems with the response of species that have not evolved in spatially structured systems. Large scale, manipulative experiments of network configuration and population abundance or distribution, combined with observational studies on the distribution of organisms in existing natural and manipulated systems, can provide strong inference on the effect of network structure and evolutionary history of species responses.

Expanding the scope of DEN models. Most DEN modeling thus far has focused on the dynamics of one or a few species, and almost none of it has been firmly tied to particular systems. One logical area for further modeling efforts is the dynamics of biological invasions, where dendritic geometry can have overriding influences (Johnson *et al.* 1995). Interestingly, dendritic geometry may both facilitate invasions (via corridor-following behaviour) and inhibit invasions (by the presence of side branches). Theoretical studies of the consequences of dendritic geometry are also needed in evolutionary biology. For example, n the context of DENs, models of speciation, the development of patterns of endemism, and related topics are effectively absent. Because limitations on movement can have such important consequences in evolutionary biology and population genetics in particular, future work should investigate how the specific types of limited movement that arise because of dendritic geometry may affect aspects of species evolution.

Investigating when geometric details matter. Distributional patterns of a population in a DEN is likely a function of the area and arrangement of intersecting branches, but the nature of these relationships has not been adequately investigated. Decomposing patterns of species distribution in hierarchically structured branches may be aided with a general understanding of the effects of branch area, intersection effects (i.e., number and angles of intersecting branches), and the sequence of branch additions to a network. Better understanding of how an individual or population responds to the network geometry will, for example, elucidate those combinations of life history characteristics, movement preferences and rates, and interactions with the dendritic network architecture that maximize population spread or invasion dynamics in networks of varying complexity (e.g., Cuddington & Yodzis 2002).

Understanding mechanisms for formation of dendritic networks. Models of dendritic network formation are likely different than in lattice network assembly models (reviewed in Newman 2003), and may provide greater understanding of, for example, biogeographic patterns in species distributions, or species responses to habitat fragmentation or the addition of habitat corridors. Network formation in a DEN (e.g., dissolution of karst geology, stream capture) may interact with species evolution by reworking network connections in hierarchical dendritic landscapes on timescales comparable to those of speciation processes. Additionally, understanding how natural dendritic systems form may aid efforts to promote landscape level conservation of species over long timescales by identifying movement corridors preemptively, even when faced with rapid fragmentation of natural habitats. Combined with an understanding of species' adaptations to DENs, and how species are likely to respond to this network architecture, such perspectives may be a

powerful tool in assessing and forecasting the effect of landscape change on natural communities.

Conclusions

Recognizing that network geometry may shape ecological patterns and processes will lead to understanding of system properties that would not be possible by examining the individual parts alone (Proulx *et al.* 2005). Key to this argument is the expectation that specific characteristics of network architecture can be linked to system-wide properties (e.g., small world networks, Watts & Strogatz 1998). In this review, we have highlighted how the definitions and functions of nodes and branches in dendritic networks are distinctly different from those in lattice networks, and illustrated the impacts of this alternative geometry on population- and community-level processes. Overall, a close correspondence exists in DENs between the spatial scale over which the network branches and the scale over which ecosystem processes act. Consequently, the arrangement and dimensions of the network components (habitat branches or patches) should play a large part in regulating the emergent properties of the network as a whole.

A reasonable target for theoretical studies of population dynamics and community processes in spatially structured systems would be the development of a general conceptual framework that encompasses both dendritic and lattice networks. This framework would allow dynamic modeling between network states, where key regulators of ecological processes (such as dispersal) and emergent properties imposed by the dendritic architecture change with the relative contributions of within- and out-of-network connectivity. With this approach, a DEN might function like a lattice network, but this outcome would depend on spatio-temporal dynamics of population, community, and evolutionary processes in the focal system, and would

not be predetermined by network geometry alone. In such an integrative framework, tools from existing network theory would be useful in describing the general characteristics and statistical properties of the network, while understanding of the effect of the specific geometry of the network would come from a dendritic network theory. Borrowing (and modifying) components of lattice network theory may prove a fruitful starting point. Improved understanding of the contribution of network geometry should lead to better understanding of community- and population-level dynamics in systems inherently assembled in dendritic ecological networks, and in those systems that are artificially constrained to this architecture by human activities.

Table 1.1. Conceptual contrasts between spatially structured lattice networks and

dendritic ecological networks.

Lattice networks	Dendritic networks
Nodes (patches) and edges (links) are discrete features, with nodes as habitat and edges as functional links between habitat patches	Both nodes and edges (branches) are habitat, with branches as primary habitat patches
Primary movement between habitat patches (edges or links)	Primary movement along network branches
All connections possible, provided they satisfy constraints specific to the species or individual (e.g., dispersal distance, matrix permeability)	Movement generally restricted to occurring along the network branches. Out-of-network connections sometimes possible (depending on species, life stage, branching geometry of the network)
Geometry of habitat patch layout affects processes and patterns in the network	Geometry of branching affects processes and patterns in the network
Movement through the network constrained by inter-patch distance and conditions in the non-habitat matrix between patches	Movement through the network primarily a function of distance following the network branches and branching geometry
Patches of varying shapes	Elements of habitat largely linear
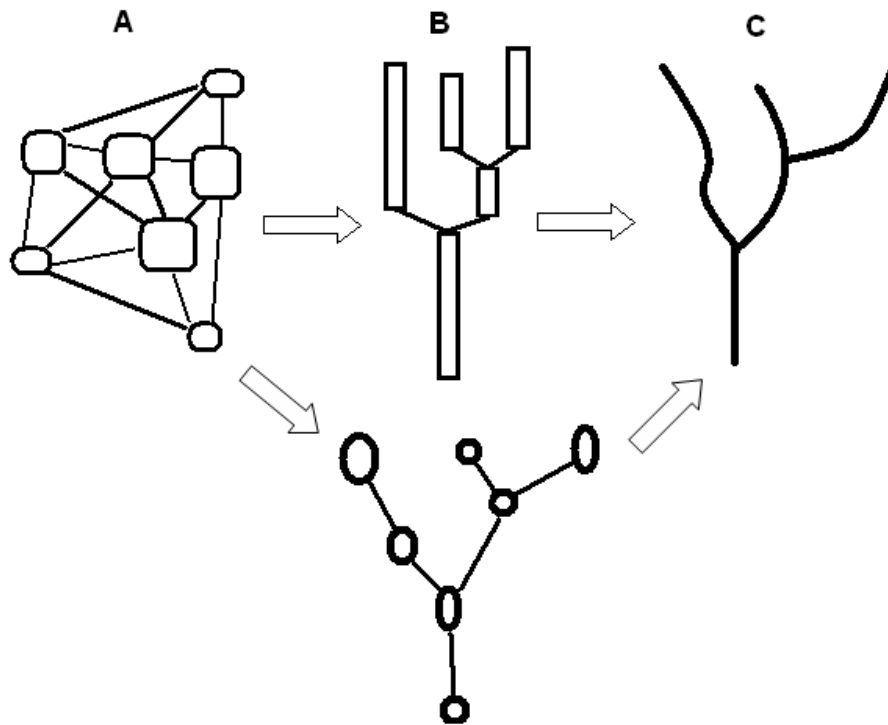
Figure 1.1. Types of spatial networks considered in this review. Lattice networks (a) are often represented as a system of patches and links. In this conceptual model, patches represent populations or other subunits of a system, and links function as pathways of dispersal or interaction. Dendritic networks (c) are distinctly different from lattice networks in that the links (or 'branches') are no longer mere representations of functional interaction, but are instead primary habitat.. Likewise, the nodes of dendritic networks are transfer points between branches, and often constitute distinct types of habitat themselves. Representation of dendritic networks using existing conceptual models (e.g., with stream reaches as habitats [b, upper] or confluences as nodes [b, lower]) may be insufficient to capture the key features inherent to ecological networks with dendritic geometry (c).

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Figure 1.2. Conceptual diagram of population and community processes in dendritic ecological networks. Dendritic networks are unique in that both 'nodes' and 'branches' serve as habitat (a). A principal consequence of dendritic architecture is to alter patterns of dispersal. For example, dendritic geometry may facilitate rescue of declining populations (b), alter vector stopping rules (c), and enhance diversity at 'nodes' (confluence points) by providing heterogeneity in resource distribution (d), or as a function of advective displacement (e). The spatial isolation imposed by the branching geometry of the network may also interact with individual mobility to slow spatial spread along the network (f).
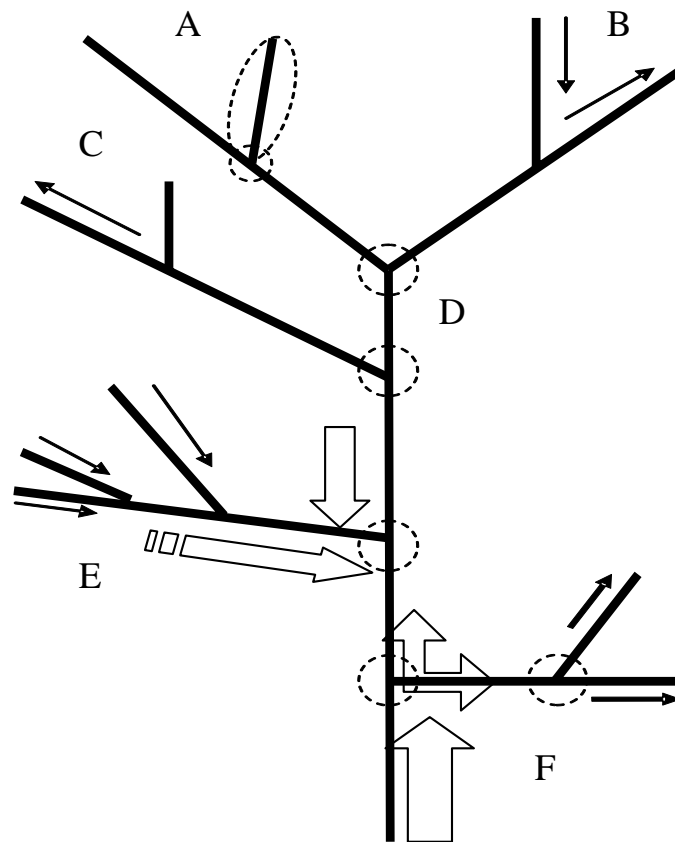
Chapter II: Are two methods better than one?: Area constrained transects and leaf

litterbags for sampling stream salamanders

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Coauthored with: Sandra D. Mattfeldt

Introduction

Concern over large-scale amphibian and reptile declines and general

acknowledgement of sparse baseline information for most herpetological species has

prompted the initiation of several monitoring programs. These programs, as well as

ecological studies focused on metapopulation dynamics and habitat associations,

often use presence-absence (or probability of occupancy) as the parameter of

interest. For example, the long-term monitoring design of the US Geological Survey's

Amphibian Research and Monitoring Initiative (ARMI) uses multi-season models

developed by MacKenzie et al. (2003) to estimate the changes in the proportion of

sites occupied by a species. As a national program, ARMI has chosen occupancy as

the state variable of interest (rather than abundance), because of the ease and

relative cost efficiency of collecting survey data (i.e., detection or non-detection of

each target species), and the ability to incorporate the probability of detecting a

species to obtain unbiased estimates of occupancy (MacKenzie et al. 2002).

Sampling methods may differ in their effectiveness in detecting a species at an

occupied site (Bailey et al. 2004). Because a higher probability of detection means

fewer surveys are needed to obtain good precision for the occupancy estimator

(MacKenzie and Royle 2005), efficient survey designs should consider detection

probabilities in the cost/benefit analysis of sampling methods. The goal of this study

was to determine the most efficient method for estimating stream salamander habitat

occupancy at a regional scale, as part of the Northeast region of the ARMI program (NE ARMI).

Several methods exist for sampling stream salamanders including area-constrained transects (Grant et al. 2005; Heyer et al. 1994), cover-controlled active searches (Heyer et al. 1994; Lowe and Bolger 2002), time-constrained searches (Barr and Babbitt 2002) and leaf litter refugia bags ('leaf litterbags'; Pauley and Little 1998). Area-constrained transect surveys may give a reliable index of the relative abundance of stream salamanders, and multiple passes can be used to estimate population sizes using removal models (Bruce 1995; Jung et al. 2000). Leaf litterbags are a uniform way to sample the leaf litter habitat and are an effective method for determining species presence, but not abundance (Chalmers and Droege 2002; Waldron et al. 2003). Leaf litterbags have been proposed as an appropriate method for determining site occupancy (Pauley and Little 1998; Waldron et al. 2003), and they may increase detection probabilities of some species or life stages.

During a survey, a species can be present but not detected (i.e., a false absence), causing the site to appear unoccupied. To estimate the true occupancy state of a species, multiple 'surveys' are required, which can be in the form of repeat site visits, multiple observers, replicate surveys, or multiple methods conducted simultaneously. Methods that increase detection probabilities of a species can reduce the optimal number of surveys of a site needed to obtain a precise estimate of occupancy (MacKenzie and Royle 2005). To determine the most efficient survey design, we compared the probabilities of detecting *Desmognathus fuscus, Eurycea bislineata*, and *Pseudotriton ruber* using area-constrained transects (hereafter 'transects') and leaf litterbags in twenty-five 30 m stream reaches within 12 first- and second-order streams in the Chesapeake & Ohio Canal National Historical Park, Maryland (38° 59'N, 77° 14'W) and Rock Creek National Park, District of Columbia

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(38° 57'N, 77° 02'W). We surveyed each site twice from 16 June - 29 July 2005. During the sample period, all age classes of *E. bislineata* and *P. ruber* were available for capture, while only adult and juvenile *D. fuscus* were available (as the previous year's larvae had metamorphosed by this time). By sampling with both methods within the same stream reach, we were able to estimate detection probabilities for each species-method combination, and determine the possible bias associated with each sampling method.

Methods

The transects consisted of two 15 x 3 meter areas (1 meter in the water and 2 meters on the bank), located on opposite banks and separated by 15 meters. To survey each transect, one observer proceeded upstream, turning all cover objects greater than 6 cm in diameter. An aquarium net was used to facilitate the capture of salamanders. Three leaf litterbags were placed within each 15 meter transect at 0, 7.5 and 15 m. The bags were placed one week prior to sampling to allow colonization by salamanders. Our leaf litterbags were constructed of two layers of 50 x 50 cm Deer Block brand plastic netting, with a mesh size of 15 x 15 mm, and filled with 50-60 grams (dry weight) of leaf litter (Chalmers and Droege 2002; Waldron et al. 2003). To maximize the likelihood of capturing larval salamanders, leaf litterbags were partially submerged (Waldron et al. 2003), using a rock to hold each bag in place. The leaf litterbags were checked after a week and again 3-4 weeks later by placing a net under the bag, and immediately placing the bag into a wash basin with water. We shook the bag in water for 15-20 seconds to loosen salamanders, then drained the contents of the basin into a net, and searched for salamanders.

We defined a site as a 30 m stream reach and used the program PRESENCE (MacKenzie et al. 2002) to estimate the proportion of sites that were occupied. For

each of the following analyses we used the detection/non-detection data for each

species separately, and estimated the species-specific detection probability (p;

defined as the probability of detecting the species at an occupied site) and the

proportion of sites occupied (Ψ), while accounting for a species not always being

detected when present (i.e., $p < 1$).

We conducted 3 separate analyses. First, we combined detection information

from transect and leaf litterbag searches into a single survey event ('combined'

dataset). In this dataset, the probability of detection represents the likelihood that the

species was detected by either survey method during a survey event, and the

resulting estimate of occupancy should provide an unbiased estimate of the true

occupancy state of the site. Second, we analyzed a single dataset in which each

detection/non-detection observation was separate for the two methods employed

during a survey event ('method-covariate'). By modeling "method" as a covariate in

the PRESENCE models, we were able to obtain detection estimates for each survey

method, using knowledge of sites where the species was detected by the other

method. Finally, we analyzed separate datasets ('method-specific') for each method,

in which the probability of detection represents the likelihood that the species was

detected by only one method. This dataset represents the data that would be

collected if only one method was implemented, and thus may reveal a potentially

biased estimate of the site occupancy, suggesting that the sampling method itself

may be flawed.

These analyses allowed us to investigate possible heterogeneity in detection

probabilities caused by sampling bias associated with each survey method. The two

methods may differ in their detection probabilities, but if the methods are able to

detect a species, then the detection-adjusted estimates of occupancy should be the

same among all the analyses. Drastic differences in the occupancy estimates would

suggest a bias in the actual sampling method (i.e., if one method was unable to detect, or had very low probability of detecting the target species at occupied sites). Comparing the method-specific estimates of occupancy with the 'method-covariate' and 'combined' datasets gives an assessment of sampling bias for each survey method (Bailey et al. 2004).

Results and Discussion

For *D. fuscus* and *E. bislineata*, the detection probabilities were higher for transects than leaf litterbags (Table 2.1). For *D. fuscus* this was expected, since submerged leaf litterbags target the larval life stage (Waldron et al. 2003), which was not present during the survey period. We were therefore unable to estimate a method-specific estimate for leaf litterbags for *D. fuscus* (Table 2.1). For *E. bislineata* the probability of detection increased slightly when both methods were used. Both methods appear suitable for detecting this species, as the point estimates of site occupancy were similar across all datasets, though transects alone had a slightly higher probability of detection (Table 2.1). For both *D. fuscus* and *E. bislineata*, incorporating detection probability resulted in an estimate of occupancy that was higher than the naïve estimate (the fraction of sites where the species was detected without accounting for missed detections; naïve $\Psi_{E.\ bislineata}$ = 0.68; naïve $\Psi_{D.\ fuscus}$ = 0.44, Table 2.1).

For *P. ruber*, leaf litterbags were more effective at detecting salamanders than area constrained transects (Table 2.1). Using transects, *P. ruber* was detected at 2 of the 25 sites, and at one site it was found during both survey events. This resulted in a high estimate of p, (though with a large SE) for the method-specific transect dataset. However, when method is modeled as a covariate (Table 1; method-covariate dataset), additional information is provided from leaf litterbag detections,

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which were more efficient at detecting larval salamanders. Including detections from leaf litterbags reduced the estimate of p for the transect method (as *P. ruber* was never detected by both methods at a site). The estimate of occupancy for the method-specific dataset using transects was much lower than the known, naïve estimate of site occupancy (method-specific Ψ = 0.09, naïve Ψ = 0.28). These data indicate the bias in occupancy estimates which would have resulted from using only the transect sampling method, due to the very low probabilities of detecting *P. ruber* (i.e., p = 0.1127 for the transect survey method in the 'method-covariate' dataset). For this species, sampling with leaf litterbags in combination with transects increases the detection probability, eliminates or reduces bias in occupancy estimates that may result for using just one detection method, and also decreases the number of times a site should be visited to obtain an optimal occupancy estimate (i.e., low SE) from 17 to 4 visits (MacKenzie and Royle 2005; Table 2.2).

As expected, using two methods to detect the presence of a species provides a more precise estimate of occupancy than a single method alone (Table 2.1). For example, *P. ruber* was never detected by both methods at the same site, and the estimate of occupancy is more precise for the combined dataset (Table 2.2).

If one method is superior for detecting a species, then the addition of a second method provides redundant information that does not improve the occupancy estimate. The inferior sampling method can still be used, but the optimal number of visits to a site increases substantially (e.g., Table 2.1, 2.2; leaf litterbags are less suitable for detection of *D. fuscus*, and therefore inflate the optimal number of surveys from k = 2 to 17, MacKenzie and Royle 2005). Further, when the detection probability is high, the increase in detection provided by a second method does not change the estimate of occupancy or the optimal number of visits to a site (e.g., Table 2.1,2.2; *E. bislineata*).

Sampling methodologies may vary in their effectiveness of sampling different life stages. Leaf litterbags are designed to preferentially capture larval salamanders (Waldron et al. 2003), and our transect surveys are designed to sample all life stages. In our study, leaf litterbags detected adult salamanders of all three species with low probabilities, and thus leaf litterbags are not likely to provide the data necessary to estimate patterns in stream occupancy by adult salamanders with sufficient power. If occupancy of a habitat by a particular life stage is of primary interest, then the sampling program should be designed primarily using methods that target that life stage. Regardless, interpretation of results should consider that a sampling method may detect all life stages, while having different detection probabilities for each life stage.

Conclusions

In studies designed to assess the status and trends in occupancy of a suite of species across a large area, the allocation of survey effort is a chief concern. For species that are difficult to detect on a given sampling occasion, such as *P. ruber,* the use of an additional method may increase the precision and decrease bias in estimates of occupancy. However, since we found leaf litterbags were expensive to construct (materials cost per bag was $2.50), difficult to maintain in the field, and had lethal effects on non-target organisms (i.e., 2 dead snakes were found tangled in the litterbags), we suggest sampling the leaf litter at a set distance interval (i.e., 1 meter) using an aquarium net, rather than deploy leaf litterbags. Incorporating leaf litter sampling into the transect surveys may be more effective than using leaf litterbags because of increased detections of species that are more likely to be captured within the leaf litter (Bruce 2003; E. Grant, unpublished data).

Regardless, when designing a research or monitoring program, assessment of the potential bias in survey methods should be incorporated into the study design (e.g., this study; Bailey et al. 2004; O'Connell et al., *in press*). In addition, pilot data can guide optimization of data collection to meet a variety of study objectives (Bailey et al. *in press*; MacKenzie and Royle 2005), and will ultimately yield estimates that facilitate comparisons among studies, provided the state variable estimates account for missed detections.

Table 2.1. Detection probability (*p)* and estimates of site occupancy (Ψ) for the

salamanders *Eurycea bislineata*, *Desmognathus fuscus,* and *Pseudotriton ruber*. The

data was analyzed in three ways: using method as a covariate ('Method-covariate'),

separately for each method ('Method-specific'), and combined detections from both

methods for each survey event ('Combined'). Naïve occupancy estimates for *E.*

bislineata (ψ = 0.68)*, D. fuscus* (ψ = 0.44) and *P. ruber* (ψ = 0.28) do not account for

missed detections. Occupancy could not be estimated for *D. fuscus* under the

method-specific leaf litterbag model because there were too few detections for

parameter estimation.

Survey Method	Dataset	*E. bislineata*		*D. fuscus*		*P. ruber*	
		P (SE)	Ψ (SE)	*p* (SE)	Ψ (SE)	*P* (SE)	Ψ (SE)
Transect	Method-covariate	0.621 (0.088)	0.715 (0.099)	0.787 (0.105)	0.460 (0.105)	0.113 (0.298)	0.541 (0.298)
	Method-specific	0.628 (0.121)	0.710 (0.138)	0.886 (0.080)	0.408 (0.100)	0.662 (0.317)	0.091 (0.066)
Leaf litterbag	Method-covariate	0.508 (0.088)	0.715 (0.099)	0.131 (0.071)	0.460 (0.105)	0.226 (0.298)	0.541 (0.298)
	Method-specific	0.545 (0.141)	0.667 (0.168)	0.061 (0.034)	-	0.328 (0.247)	0.371 (0.270)
Both methods	Combined	0.820 (0.078)	0.713 (0.100)	0.838 (0.092)	0.456 (0.104)	0.438 (0.206)	0.416 (0.195)

Table 2.2. Optimal number of surveys (k) given occupancy (ψ) and detection (*p*)

estimates from the method-covariate dataset and the combined model (from Table

1).

Survey Method	*Eurycea bislineata*	*Desmognathus fuscus*	*Pseudotriton ruber*
Transect	3	2	19
Leaf litterbag	4	17	9
Combined	2	2	4

Chapter III: Salamander occupancy in headwater stream networks

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Coauthored with Linda E Green and Winsor H Lowe

Summary

Stream ecosystems exhibit a highly consistent dendritic geometry in which linear habitat units intersect to create a hierarchical network of connected branches.

Ecological and life history traits of species living in streams, such as the potential for overland movement, may interact with this architecture to shape patterns of occupancy and response to disturbance. Specifically, large-scale habitat alteration that fragments stream networks and reduces connectivity may reduce the probability a stream is occupied by sensitive species, such as stream salamanders.

We collected habitat occupancy data on four species of stream salamanders in first-order (i.e. headwater) streams in undeveloped and urbanised regions of the eastern U.S.A. We then used an information-theoretic approach to test alternative models of salamander occupancy based on *a priori* predictions of the effects of network configuration, region and salamander life history.

Across all four species, we found that streams connected to other first-order streams had higher occupancy than those flowing directly into larger streams and rivers. For three of the four species, occupancy was lower in the urbanised region than in the undeveloped region.

These results demonstrate that the spatial configuration of stream networks within protected areas affect the occurrences of stream salamander species. We strongly encourage preservation of network connections between first-order streams in conservation planning and management decisions that may affect stream species.

Introduction

Viewing ecological systems as spatially structured networks has improved our understanding of pattern and process across temporal and spatial scales. Conceptual research has focused on processes in patch-based systems (e.g. metapopulations; see Urban & Keitt, 2001; Calabrese & Fagan, 2004), but there has been little consideration of networks with alternative geometries, such as the dendritic structure common to streams, individual plants, caves and other systems (reviewed in Grant *et al.,* 2007). The branching geometry of these dendritic ecological networks (DENs) can have unique effects on the distribution and abundance of species occupying these systems. For example, the hierarchical nature of stream networks, with small stream branches intersecting at confluences to form larger streams, can influence patterns of dispersal and occupancy of stream-associated organisms (Fagan, 2002; Lowe & Bolger, 2002). These branched networks can also promote population expansion by facilitating movement to adjacent habitats (Fagan *et al.,* 2009), or alter community dynamics by regulating the frequency of species interactions (Cuddington & Yodzis, 2002). If populations in the stream branches are panmictic, branched stream networks will tend to have larger habitat area and lower isolation than traditional metapopulations (e.g. Hanski, 1998). Both characteristics can reduce extinction risk and increase occupancy in branched streams (Fagan, 2002; Lowe, 2002; Fagan *et al.,* 2009).

At the landscape scale, the structure and complexity of a DEN may affect the dispersal of individuals through the network, resulting in vastly different extinction risks for the metapopulation, depending on the number and spatial configuration of branches within the network (Fagan *et al.,* 2009). Stream-dwelling species can move through the network along two pathways: movements upstream and

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downstream within the stream channel (within-network movement), or terrestrial excursions over land between stream branches (out-of-network movement). For most species that are associated with streams, such as fish, stream macroinvertebrates and amphibians, within-network movements are likely the primary dispersal pathway (Finn *et al.,* 2006; Lowe *et al.,* 2006). However, models suggest that some capacity for overland (out-of-network) movements can greatly reduce metapopulation-level extinction risk (Lowe, 2002; Fagan *et al.,* 2009).

Many stream salamander species have the potential for both within- and out-of-network movement. The majority of these species have larvae that are strictly aquatic, but juveniles and adults are generally semi-aquatic or terrestrial (Petranka, 1998). These later life history stages may preferentially move along stream corridors to maintain proximity to moisture, but may also move between adjacent streams by overland pathways (Grover & Wilbur, 2002; Crawford & Semlitsch, 2006; Greene *et al.,* 2008). Due to the contribution of within- and out-of-network movements, we might expect more frequent recolonisation events in streams that have adjacent, connected branches (Fig. 1) than in those that flow directly into larger streams and rivers. Additionally, we would expect species-specific relationships in stream occupancy as a function of ecological and life history traits influencing the likelihood of out-of-network movements. In communities of stream salamanders, competitive and predatory interactions result in habitat partitioning, with smaller species often found furthest from the water's edge despite the increased desiccation risk that results from smaller body size (Hairston, 1987). Body size may be a predictor of propensity for out-of-network movements, and this relationship could be positive or negative for a given species, depending on the relative effects of desiccation risk versus interspecific interactions.

In addition to species ecology and life history, landscape characteristics that decrease local habitat quality or connectivity may influence occupancy in stream networks. Urban development can impact hydrology, geomorphology and stream ecosystem structure and function, which in turn affect local population stability in stream-associated species (e.g. Palmer *et al.,* 2002; Meyer *et al.,* 2005). Specifically, streams in urbanised areas may be more likely to undergo episodic extinctions (Price *et al.,* 2006), resulting in higher variability in occupancy among sites, especially in the branch tips at the upper reaches of a catchment (Fagan, 2002). Further, stream networks in areas of heavy agricultural or urban land use become simplified over time as small streams are lost (Dunne & Leopold, 1978; Sophocleous, 2000), reducing the likelihood of out-of-network movement and recolonisation as branched networks are converted into more linear, unbranched networks (Fagan *et al.,* 2009). Because stream salamanders are most strongly associated with first-order headwater streams (Snodgrass *et al.,* 2007; Peterman, *et al.* 2008), they are likely to be especially sensitive to change in the spatial configuration of stream networks and human activities in the surrounding landscape (Welsh & Olivier, 1998; Lowe & Bolger, 2002).

In this study, we tested the hypothesis that stream network configuration and regional landscape context influence occupancy in four stream salamander species. These species have different combinations of ecological and life history attributes that might affect the propensity for within-network versus out-of-network movements: length of larval period, association of metamorphosed individuals to the aquatic habitat and adult body size. Across all species, we predicted higher occupancy in streams connected to another first order stream (Fig. 1A) than in those flowing directly into larger streams and rivers (Fig. 1B). We also predicted that interspecific

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variation in life history traits would lead to variation in the strength of the relationship

between stream network configuration and occupancy. Finally, we expected lower

occupancy of streams within an urbanised landscape compared to streams located

in a less developed landscape. Our study was motivated by the hypothesis that the

successful management and conservation of sensitive stream species may rely on

explicit consideration of the spatial configuration of protected stream networks.

Methods

Study species

The four study species are in the family Plethodontidae, the lungless salamanders.

Eurycea bislineata (Green) and *E. cirrigera* (Green) are closely-related species

(Jacobs, 1987; but see Petranka, 1998) with extended larval periods (≥ 2 yrs), high

local densities, small body size and a weak association with the stream channel after

metamorphosis. These combinations of characteristics suggest both high occupancy

and an ability to make out-of-network movements. Despite their high surface area to

volume ratio, interactions with larger salamander species generate adult preferences

for microhabitat refuges furthest from the stream channel (L.E. Green, *unpubl. data*).

Perhaps as a result of these antagonistic interactions, *E. bislineata* is known to make

long-distance (> 100 m) terrestrial migrations (MacColloch & Bider, 1975).

Therefore, we expect a relatively strong association with branched networks because

these species (hereafter, *Eurycea* complex) can exchange individuals via both in-

stream larval dispersal and out-of-network movements in the adult stage (Table 1).

Pseudotriton ruber (Latreille) also has an extended larval period (≥ 2 yrs), but low

densities, large body size and a strong adult association with the aquatic habitat that

likely result in low levels of occupancy, especially in unbranched streams (Table 1).

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Finally, *Desmognathus fuscus* (Green) exhibits a short larval period (< 1 yr), high local densities, large body size and a strong adult association with the aquatic habitat. This species was predicted to have an occupancy probability intermediate to the *Eurycea* complex and *P. ruber*, and the strongest association with branched streams (Table 1).

Study sites and field methods

We surveyed 54 first order streams; 11 were located in the National Capital Region (Chesapeake and Ohio Canal National Historic Park, Rock Creek National Park, U.S.A.; hereafter NCR) and 43 were located in Virginia (Shenandoah National Park and the George Washington and Jefferson National Forests, U.S.A.; hereafter VA). The NCR streams were on protected federal lands surrounded by heavily urbanised areas of Washington, D.C. The VA streams were on protected federal lands set within a forested, undeveloped landscape.

Because the data used here were initially collected as part of separate studies by two of the authors (E.H.C.G in NCR and L.E.G. in VA), survey methods differed in the two regions. In both regions, we surveyed transects during the day using two temporary removal passes, capturing and removing salamanders from the transect after each pass to avoid duplicate sampling of individuals. All salamanders were returned to the streams within 2 h. For each stream in the NCR, we surveyed two sets of paired transects (15 m long by 3 m wide) along opposite banks and separated by 15 m of stream length. Each transect pair was separated by 100 m of stream length. For each stream in VA, we surveyed three transects (10 m long by 6 m wide, centred on the stream channel so equal area was surveyed on the right and left banks) separated by 15 m or more of stream length. The total area searched on each stream reach was identical between the regions (180 m^2). Because larval

salamanders may hide in leaf litter in headwater streams, we also sampled the leaf litter in streams at 0.5 m intervals along the NCR transects when litter was present (Mattfeldt & Grant, 2007; Nichols *et al.,* 2008); leaf litter along the entire reach was searched in the VA transects. We surveyed streams in VA in May through August of 2004 and 2005, and in the NCR in June and July of 2005 and 2006.

We used each transect as a survey event in our occupancy analysis, which allows us to estimate the probability of not detecting a species in a transect given that it is present in a stream segment (the detection probability parameter, *p*). This approach assumes that individuals in each transect are part of the same population, an assumption supported by evidence of movement along headwater streams by stream-associated plethodontids (Stoneburner, 1978; Bruce, 1986; Lowe, 2003). While survey methods differed between regions, we were consistent in targeting both aquatic larvae and terrestrial adults of the focal species using multiple transects along each stream. Differences in detection due to methodology are accounted for in our analysis (see *Occupancy analysis*, below). We combined observations of *Eurycea bislineata* (distributed in NCR and VA) and *E. cirrigera* (only VA streams) for analysis based on their close phylogenetic and ecological relationship. Age classes (larvae, juvenile, adult) were also combined for analysis, as the majority of each species was detected in only one age class.

Occupancy analysis

The models of MacKenzie *et al.* (2006) provide a statistical framework for estimating occupancy (Ψ), an instantaneous measure of metapopulation distribution resulting from the balance of extinctions and colonisations. This approach is robust to variation in the probability that a species is detected, given that it is present at a site,

while allowing the incorporation of covariates to test specific hypotheses about factors influencing broader occupancy patterns. At each stream reach, a species can exist in one of three states: 1) present and detected, 2) present but undetected or 3) absent. Because states 2 and 3 cannot be accurately distinguished, researchers must estimate the likelihood of a species being present even when it is not detected. Thus, estimating occupancy requires recording detection-nondetection data during multiple visits to a site within a short time period, during which it is assumed that there is no colonisation or extinction (MacKenzie *et al.* 2006).

Using the most general structure on the state variable occupancy [the global model Ψ (region, network)], we investigated combinations of covariates on the detection probability parameter, *p*, using the program PRESENCE (Hines, 2006). Here, *p* is the probability of detecting a species, given it is present at a site. We tested whether detection was a function of the number of cover objects ("zrocks"; the normalised z-value of the number of rocks and logs >6 cm in diameter turned during the survey), the survey method ("survey"; 15x3 m transects in the NCR or 10x6 m transects in VA) or the additive effect of number of cover objects and survey method. This statistical design allowed us to investigate whether the network configuration or the regional landscape context influenced occupancy patterns while controlling for differences in detection probability resulting from the different survey methods (Bailey *et al.,* 2004).

For the occupancy analysis, we used each stream reach as a site, with three or four transects representing multiple visits in space (in lieu of repeated temporal visits, MacKenzie *et al.,* 2006: 161). We investigated two variables hypothesised to be related to site occupancy: network configuration ("network"), represented by branched (B) versus unbranched (UB) streams (Fig. 1; n = 21 of 54 sites were

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branched), and regional landscape context ("region"; n = 11 NCR sites, 43 VA sites).

We also tested whether occupancy was unrelated to either covariate [notation Ψ (.

)]. We compared models using AIC (Akaike's Information Criterion) and considered

models with ΔAIC less than 2 to be meaningful representations of the relationship

between our covariates and site occupancy (Burnham & Anderson 2002). We tested

for lack-of-fit by evaluating whether the estimated variance inflation factor ($\hat{c}$) was >

1, using the bootstrap method incorporated in PRESENCE (Mackenzie & Bailey,

2004).

Finally, to assess the effect of the stream network configuration (Fig.1), we

calculated model-averaged estimates of occupancy ($\hat{\bar{\psi}}$) for each species in

branched and unbranched streams. Model-averaging can reduce the bias in an

estimator with respect to inference from a 'single-best' model from the model set

(Burnham & Anderson, 2002). Model averaging combines estimates from each

model using their associated model weights, to provide an estimate of the predicted

effect ($\hat{\bar{\psi}}$) that is not conditional on a single model in the set. We used estimates

from each model and the associated model weight to calculate model-average

occupancy estimates for both branched and unbranched stream reaches. For the

additive model [Ψ(network , region)], the estimated occupancy used for model

averaging was chosen from the region where each species had the highest

occupancy, as we expected the difference between branched and unbranched

streams to be largest in the most suitable region for each species.

 Results

The naïve estimate of occupancy is the proportion of sites where a species is

detected, and, unless the detection probability (*p*) equals 1, is always less than the

estimated $\hat{\psi}$. We detected *Pseudotriton ruber* at eight sites in VA and seven sites in NCR (naïve Ψ = 0.28), *Desmognathus fuscus* at 36 VA and nine sites in NCR (naïve Ψ = 0.83) and the *Eurycea* complex at 40 sites in VA and nine sites in NCR (naïve Ψ = 0.91). The VA sites also included some or all of the following sympatric species: *D. quadramaculatus*, *D. monticola*, *D. ochrophaeus* and *Gyrinophilus porphyriticus*. The VA sites had a greater abundance of cover than the NCR sites (mean ± 1 SE = 438 ± 30 versus 45 ± 6 cover objects per transect, respectively; two-tailed *t*-test $t_{8,42}$ = -12.9, P< 0.001). For *P. ruber* and *Eurycea* complex, models including both the number of cover objects (zrocks) and survey method (survey) as covariates on *p* were favoured, while the model for *D. fuscus* included only survey method as a covariate of *p*. We used these covariate structures to investigate occupancy of each species. The global model for all species included the additive effects of region and network. There was little evidence of lack of fit for any species in 5000 bootstrap samples. None of the global models had a variance inflation factor ($\hat{c}$) > 1, indicating no extrabinomial variability unexplained by the global model (Mackenzie & Bailey, 2004). Under the method of MacKenzie & Bailey (2004), one can calculate the Pearson's chi-square statistic (χ^2) for the observed occupancy data under the global model, and find the probability (P) that the calculated statistic is greater than the bootstrapped χ^2 test statistic (*P. ruber* χ^2 = 45030.6, P = 0.48; *Eurycea* complex χ^2 = 51507.2, P = 0.87; *D. fuscus* χ^2 =67673.32, P = 0.67).

Salamanders from the *Eurycea* complex were detected at 91% of sites. Two occupancy models were supported by the data (i.e. ΔAIC < 2.0; Table 2). The *Eurycea* complex had higher model-averaged occupancy (Burnham & Anderson,

2002) in branched streams (Table 3) and higher occupancy in VA than NCR (e.g. a

negative $\hat{\beta}_{Region}$ value; Table 2).

D. fuscus was detected at 83% of sites. The Ψ(region), Ψ(network) and Ψ(.) models were supported by the data, but the model incorporating the additive effect of region and network was not favoured (Table 2). This species had higher model-averaged occupancy in branched streams (Table 3) and higher occupancy in VA than NCR (Table 2).

P. ruber was detected at 28% of sites. Detection for this species was low (estimates using no covariates on the occupancy parameter and only survey method on detection probability [i.e. Ψ(.), p(survey)]: $\hat{p}$ = 0.28 ± 0.05 for transects in NCR; $\hat{p}$ = 0.27 ± 0.13 for transects in VA), and all of the occupancy models considered had some support from the data (Table 2). Based on model rankings, the region appeared to have a greater effect on occupancy than network structure for *P. ruber*. Unlike the other two species, the urban NCR streams had higher model-averaged estimated occupancy for this species than the VA streams (Table 2). Although network structure had less support, the model-averaged occupancy estimates were higher in branched streams (Table 3).

Interpreting the point estimates of occupancy in relation to the network covariate was of primary interest in our analysis. Salamanders from the *Eurycea* complex were more likely to be found in branched than unbranched streams ($\hat{\bar{\psi}}_B$ ± 1 SE =99 ± 3% versus $\hat{\bar{\psi}}_{UB}$ ± 1 SE =90 ± 7%; effect size = 0.13). *P. ruber* also had higher occupancy in branched streams ($\hat{\bar{\psi}}^{\bullet}_B$ = 52 ± 23% versus $\hat{\bar{\psi}}_{UB}$ = 48 ± 18%; effect size = 0.15), though with relatively large uncertainty in the point estimates. For

D. fuscus, point estimates of occupancy in branched and unbranched streams had the smallest effect size ($\hat{\psi}_B$ = 90 ± 8% versus $\hat{\psi}_{UB}$ = 88 ± 7%; effect size = 0.07), though with higher occupancy in branched stream networks.

Discussion

Consistent with our *a priori* hypothesis, models that included the network covariate had support in the data, and occupancy probabilities were higher for branched streams than unbranched streams in the *Eurycea* complex, *P. ruber* and *D. fuscus*. The strength of the association between occupancy and network configuration varied from weak to moderate among species (Table 2). Current model selection methods cannot account for our *a priori* specification of the expected direction of the effect of branched streams on the estimated occupancy (MacKenzie *et al.*, 2006: 119-120), and it is important to note that the higher occupancy probability in branched streams was in the direction we expected based on existing theory in dendritic ecological networks (Grant *et al.,* 2007; Fagan *et al.,* 2009).

Our results support the prediction that different life history characteristics among the species may affect relative propensity to make in-stream versus out-of-network movements, leading to interspecific differences in occupancy in branched and unbranched streams. However, the consistent positive effect of the network covariate (Table 2) suggest that the spatial layout of habitat branches, rather than species-specific life history characteristics, may be a dominant factor in structuring distribution patterns. We predict that higher occupancy in branched streams results from a combination of both in-stream and out-of-network movements. While out-of-network movements may be undertaken by all species considered here, the larger effect sizes of occupancy in branched versus unbranched streams for the *Eurycea*

complex and *P. ruber* suggest that long larval periods may also facilitate in-stream movement between stream reaches.

For *Eurycea bislineata* and *E. cirrigera* (which were combined in our occupancy analysis), we found that occupancy differed between branched and unbranched streams, but that these species had high occupancy across all sites. High levels of occupancy are not surprising because in-stream movements by larvae appear to be common in *Eurycea* populations (Johnson & Goldberg, 1975; Stoneburner, 1978), and are likely to increase occupancy in branched streams. Likewise, out-of-network movements by juveniles and adults may allow colonisation of adjacent streams in both branched and unbranched systems (MacColloch & Bider, 1975; Ashton & Ashton, 1978).

The difference in occupancy between branched and unbranched streams was highest for *P. ruber* and lowest for *D. fuscus*. A recent mark-recapture study of *P. ruber* larvae in North Carolina shows that they can move up to 116 m along first-order streams in less than one month (Cecala *et al., In review*), and this species has a long larval period, long-lived adults and large body size at metamorphosis (Petranka, 1998). Therefore, occupancy of branched streams likely depends on combined movements of both life stages in *P. ruber*; larvae have several years to disperse within the stream channel between branches prior to metamorphosis, and adults benefit from a large body size and associated small surface area:volume ratio that is likely to facilitate out-of-network movements. Adults of *D. fuscus* are smaller in size than *P. ruber* adults, and the larval stage of *D. fuscus* is brief and unlikely to allow extensive in-stream movement. Recently metamorphosed *D. fuscus* individuals are typically small and found near the stream edge, so out-of-network movements may be undertaken by older, larger individuals. The lower effect size in

D. fuscus may thus be indicative of a proportionally smaller pool of potential dispersers to adjacent habitats.

We expected the region in which the protected areas were located would also affect habitat occupancy of each species. Not surprisingly, we found higher occupancy probabilities for *D. fuscus* and *Eurycea* complex in the relatively undeveloped Virginia streams compared to streams within the urbanised region of Washington, DC. However, *P. ruber* exhibited the opposite trend. These species-specific regional differences are likely a function of different microhabitat preferences. We observed large differences in stream substratum (e.g. VA sites had, on average, 57% cobble and 9% fine sediment, while NCR sites had 8% cobble and 50% fine sediment) and *P. ruber* is known to prefer high-silt conditions like those at the NCR sites (Bruce, 2003). There were also differences in salamander community composition that may have contributed to regional differences in occupancy. The study species (*Eurycea bislineata*, *Pseudotriton ruber*, *Desmognathus fuscus*) comprised the entire stream salamander community in the NCR, but the salamander community in the VA sites also included some or all of the following species: *D. quadramaculatus*, *D. monticola*, *D. ochrophaeus* and *Gyrinophilus porphyriticus*. In addition to the regional substratum differences, the presence of *G. porphyriticus* in VA streams may contribute to lower *P. ruber* occupancy, because both species occupy a similar ecological niche and are known to compete (Gustafson, 1993; Bruce, 2003).

Even with the differences in occupancy in our two regions, our results are consistent with theory on spatial population dynamics in dendritic ecological networks (Grant *et al.,* 2007), indicating that occupancy of headwater stream salamanders is shaped by the spatial configuration of stream networks. This suggests that population

persistence in urbanised landscapes may be promoted by connectivity to

neighbouring stream branches. Therefore, we recommend that the integrity of

branched stream networks be considered explicitly in management decisions

affecting urban streams and the species occupying those streams. This study also

highlights the utility of occupancy as a coarse but accessible index for testing

hypotheses for the specific drivers and pathways of dispersal, as well as for how

dispersal contributes to population persistence. Direct observations of dispersing

organisms remain crucial to elucidating movement pathways and the relative

propensity of different species to make in-stream versus out-of-network movements

(e.g. Lowe, 2003). Combined with analyses of large-scale patterns of occupancy like

this one, direct observations of marked animals will greatly expand insight on how

network configuration affects local population persistence in amphibians and other

stream organisms.

Table 3.1 The hypothesised relative dispersal ability of the stream salamander
species in this study. Life history characteristics may result in different propensities to
make in-stream (within-network) versus out-of-network (overland) movements.
These relative movement probabilities may influence patterns of distribution in
streams with or without a confluent first order stream branch. Differences in the table
are for ranking only, hence ++ does not imply that a species is hypothesised to have
twice the dispersal ability as a species with a single +. We combined the two
Eurycea sp. (*E. bislineata* and *E. cirrigera*) for our analysis.

	Movement Pathway	
	Overland	Out of network
Desmognathus fuscus	+	+
Eurycea complex	++	+++
Pseudotriton ruber	+++	+

Table 3.2. Summary of model selection and estimated parameters (and standard errors). ΔAIC is the difference in AIC value for a particular model when compared with the top ranked model; *w* is the AIC model weight; K is the number of parameters in the model and −2*l* is twice the negative log-likelihood value. The "network" covariate was a categorical variable (1 = branched), as was the "region" covariate (1 = NCR). Detection probability was modelled as a function of survey method ("survey") plus the (normalised) number of cover objects ("zrocks"; *Eurycea* complex and *P. ruber* models only). The global model was *Ψ* (network, region),p(survey) *or* p(survey, zrocks). Models in boldface are within 2 ΔAIC units of the top model. A "-" indicates that the effect was not included in the model, or the estimated SE was nonsensical.

Eurycea complex

Model	ΔAIC	w	K	-2*l*	$\hat{\beta}_{Network}$	SE($\hat{\beta}_{Network}$)	$\hat{\beta}_{Region}$	SE($\hat{\beta}_{Region}$)
Ψ(network),p(survey, zrocks)	0.00	0.47	5	250.1	25.142	-	-	-
Ψ(network, region),p(survey, zrocks)	1.20	0.26	6	249.3	25.149	-	-1.015	1.152
Ψ(region),p(survey, zrocks)	2.41	0.14	5	252.5	-	-	-1.812	1.465
Ψ(.),p(survey, zrocks)	2.46	0.14	3	254.5	-	-	-	-

Desmognathus fuscus

Model	ΔAIC	w	K	-2*l*	$\hat{\beta}_{Network}$	SE($\hat{\beta}_{Network}$)	$\hat{\beta}_{Region}$	SE($\hat{\beta}_{Region}$)
Ψ(.),p(survey)	0.00	0.47	3	272.8	-	-	-	-
Ψ(region),p(survey)	1.53	0.22	4	272.3	-	-	-0.761	1.146
Ψ(network),p(survey)	1.61	0.21	4	272.4	0.725	1.341	-	-
Ψ(network, region),p(survey)	3.26	0.09	5	272.0	0.716	1.657	-0.681	1.200

Psuedotriton ruber

Model	ΔAIC	w	K	-2*l*	$\hat{\beta}_{Network}$	SE($\hat{\beta}_{Network}$)	$\hat{\beta}_{Region}$	SE($\hat{\beta}_{Region}$)
Ψ(.),p(survey, zrocks)	0.00	0.37	4	175.4	-	-	-	-
Ψ(region),p(survey, zrocks)	0.27	0.33	3	173.6	-	-	1.277	0.880
Ψ(network),p(survey, zrocks)	1.74	0.16	3	175.1	0.615	1.413	-	-
Ψ(network, region),p(survey, zrocks)	1.95	0.14	6	173.3	0.482	0.869	1.351	0.899

Table 3.3. Model-averaged occupancy probabilities (and standard errors) for

Desmognathus fuscus, *Pseudotriton ruber* and *Eurycea* complex, in branched and

unbranched streams.

	Branched	Unbranched
D. fuscus	0.90 (0.08)	0.88 (0.07)
Eurycea complex	0.99 (0.03)	0.90 (0.07)
P. ruber	0.52 (0.23)	0.48 (0.18)

Figure 3.1 Schematic of stream configurations. "A" represents a branched stream, where the stream reach of interest makes a downstream confluence with another first-order stream; "B" represents an unbranched stream, where the stream reach of interest makes an eventual downstream confluence with a higher order stream. The dotted box indicates a sample site, in which three to four transects were surveyed to characterise occupancy of our focal salamander species.

A   B
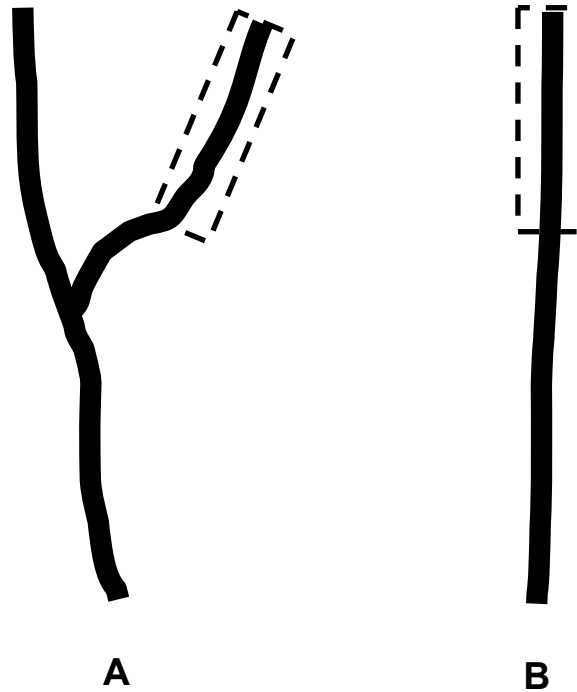
Chapter IV: Visual Implant Elastomer Mark Retention in Amphibian Larvae Through

Metamorphosis

Abstract

Questions in population ecology require the study of marked animals, and marks are assumed to be permanent and not overlooked by observers. I evaluated the retention of Visual Implant Elastomer marks in larval salamanders and frogs through metamorphosis, and assessed the error in observer identification of these marks. I found (1) individual marks were not retained in larval wood frogs, whereas only small marks are likely to be retained in larval salamanders, and (2) observers did not always correctly identify marked animals. Evaluating the assumptions of the marking protocols is important in the design phase of a study, so that correct inference can be made about the population processes of interest.

Introduction

Detailed understanding of animal populations requires precise recognition of captured individuals. Estimation of some ecological parameters, such as movement and survival, or population growth rate, often relies on tracking individuals. To estimate these parameters, marks must be permanent, consistently identified throughout the life of an individual, and have no effect on survival or development. Capturing and marking large numbers of amphibians may be most easily accomplished during the larval stage, especially for 'aggregate' breeders where egg deposition sites are spatially concentrated (e.g., wood frog, *Rana sylvatica*), or species whose terrestrial forms are less likely to be encountered than larvae (e.g., northern two-lined salamander, *Eurycea bislineata*

bislineata, adults are frequently absent from streamside surveys; Grant et al. 2005).

Natural variation in color pattern may be useful in mark-recapture studies of adult

amphibians (e.g., Bailey 2004, Grant and Nanjappa 2006), but may not be useful in

larval animals because color patterns have not completely formed. Retention of marks

added during the larval stage is a critical consideration in any study where individuals

are to be tracked through metamorphosis.

Many species of amphibians are characterized by complex life cycles (Wilbur 1980),

with ontogenetic changes characterized by changes in body form, rapid growth, and

transition from aquatic to terrestrial life forms. In general, the metamorphosis of

salamanders differs from that of frogs and toads. Salamander morphology remains

much the same through metamorphosis, whereas anurans undergo a drastic change in

morphology between tadpole and adult stages, including development of limbs,

resorption of the tail, and development of adult skin (Duellman and Trueb 1986). I

hypothesized that these differences in the mode of metamorphosis may affect the

retention of marks assigned to an individual during the larval stage.

My objectives were to 1) assess the retention of marks through metamorphosis in 3

species of larval amphibians: northern dusky salamander (*Desmognathus fuscus*),

northern two-lined salamander and wood frog, and 2) to quantify bias in observer

identification of marked salamander larvae (northern dusky salamander).

Methods

There are three errors that can be made that would invalidate the assumption that

marks are retained and recorded correctly. First, a mark can be lost physically (mark

loss). Second, a mark may move from the initial marking location (mark migration),

because the mark was administered into the body cavity or too deeply into the space

between the skin and the underlying muscle. I consider both mark loss and mark

migration as separate components of 'mark retention', and I discuss both components of this error herein. Finally, observers may fail to correctly recognize a mark, either by overlooking a mark completely or by misidentifying the mark code ('observer bias').

I marked animals with Visual Implant Elastomer (VIE; Northwest Marine Technology Inc., Shaw Island, Washington). VIE has been used to mark frogs (e.g., Anholt et al. 1998, Nauwelaerts et al. 2000) and salamanders (e.g., Davis and Ovaska 2001, Marold 2001, Johnson and Wallace 2002, Bailey 2004) across a range of sizes and life history stages. VIE is a two-part silicone-based polymer that cures to a pliable consistency, which can be detected with ultraviolet or blue light with amber filtering glasses. The best method for administering VIE marks to amphibians is to inject the VIE just under and parallel to the skin.

In June 2006, I obtained 120 wood frog (*Rana sylvatica*) tadpoles from a backyard swimming pool in Silver Spring, Maryland, USA. I gave 60 animals both a red and a green mark at the base of the tail (Fig. 4.1) with a 29 gauge needle, just above the tail musculature on either side of the tail fin (following Anholt et al. 1998), and an equal number were handled but not injected as unmarked controls. To administer the marks, I anesthetized all individuals (including control animals) in a buffered (pH 7.0) 500 mg/L tricaine methylsulfonate (MS-222). All study animals were allowed to recover in clean water and then added to one of two 10 L tanks. I fed animals frozen, thawed organic romaine lettuce and fish food flakes. After 20 days, I captured 20 tadpoles at random from the marked treatment group, and assessed the retention of marks. After each surviving animal metamorphosed I recorded marks for the marked group on two separate days following metamorphosis. I used a 2-tailed *t*-test to test the hypothesis that marking had no effect on either (1) time to metamorphosis or (2) size at metamorphosis in the wood frog tadpoles, and a linear regression to relate mark loss (as

an explanatory variable with three levels: zero, one or two marks retained) to time to metamorphosis.

In April 2006, I collected 30 larval northern dusky salamanders from streams in the Chesapeake and Ohio Canal National Historic Park, Maryland, USA. In June 2006, I collected 30 larval two-lined salamanders from a different stream in the same park. I chose twenty individuals of each species at random to receive marks. I gave eight northern dusky salamanders and five northern two-lined salamanders one mark, and 12 northern dusky salamanders and 15 northern two-lined salamanders were given two marks. Animals were given a unique mark by combining 2 VIE colors (red, green) and 4 marking locations (anterior to each hind limb and posterior to each front limb, Fig. 4.1), with a 29 gauge needle. I handled, but did not inject, all animals that were not marked. I kept animals in individual containers in an environmental chamber maintained at 15 C and fed them frozen, thawed bloodworms until metamorphosis. I did not use a microscope while I marked either frogs or salamanders, because I was interested in the feasibility of the technique for marking large numbers of small animals in remote field locations.

I chose sixteen of the 30 northern dusky salamanders (11 marked, 5 unmarked) at random for the observer bias study. Thirteen observers participated in the study: 4 with prior experience identifying marks in the field, and 9 naïve observers. Naïve observers were primarily graduate students at the University of Maryland, and did not have experience with VIE marking techniques. Observers were given a brief introduction to VIE marking techniques and mark identification, and were allowed to practice with color standards until they were comfortable using the VIE lights. Recently Northwest Marine Technology, Inc. switched from a blue-LED light and amber filtering glasses to a violet-LED light which was intended to facilitate mark identification. Both lights were tested for

their efficacy in mark identification in my study. Observers were informed of the marking procedure, and that animals may have been given between 0 and 4 marks, with two colors of VIE (red and green). Observers were provided a schematic of the marking locations. After all observers had viewed the animals, salamanders were re-randomized and presented to the same observers, who viewed the salamanders with the other light. Observers were unaware that they were presented with the same set of individuals for each light. An observation was scored as correct when an observer recorded all marks on an individual salamander that matched the true mark combination. Because I expected the probability of recording an incorrect mark to increase with the complexity of the marking code (1 versus 2 marks), I used separate logistic regression models for each light (blue and violet) to determine if the proportion of correct identifications was related to the number of marks. I used a two-tailed paired t-test to test whether observers took more time to identify marks by light, or whether the light (blue vs. violet) was related to the proportion of correctly identified salamanders. I transformed the proportion of correctly identified salamanders with an arcsine-square root. I separated observers into naïve and experienced observer groups, to further evaluate the impact of training on correct mark identification.

I evaluated mark migration in northern two-lined salamanders on 4 occasions prior to their metamorphosis. On each occasion, I recorded the marks on each animal twice on the same day, which allowed me to separate mark migration from observer error in mark identification. After each animal metamorphosed, I recorded the position of marks remaining in each salamander. This also was done twice on a single day to assess bias in mark identification. I used multistate modeling to evaluate my observations on mark retention in northern two-lined individuals. One can consider mark migration to be equivalent to an animal's code making a transition, with probability Ψ, among states

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'correct' and 'incorrect' between two observation periods (Ψ_{CI}; Williams et al. 2002).

Marks that were loose in the body cavity or administered too deeply under the skin may change position over different observation periods, resulting in some animals first experiencing mark migration, and then 'recovering' their marks. Because I observed some animals that recovered their marks (i.e., were observed to be marked incorrectly in one period, and marked correctly in a subsequent time period), I also estimated the transition probabilities from 'incorrect' to 'correct' mark codes (Ψ_{IC}). To estimate the transition probabilities Ψ_{CI} and Ψ_{IC}, I used the recaptures-only multistate model in program MARK (White and Burnham 1999). I created a 5-period 'capture history' for each animal, recording whether the read code matched the given code (on day 0) at 16, 43, 96 and 116 days after marking. I fit all models where survival was allowed to vary by time (since several animals died at each time period) but was equal for all animals (i.e., there was no effect of mark migration on survival), and I set the capture probability (*p*) equal to 1. The initial transition probability from incorrect to correct (Ψ_{IC}) was set to zero for all models, because all individuals started the study with a correct mark code.

I used 6 multistate models (Table 4.1), representing different hypotheses of the nature of mark migration in larval salamanders. Model 1 is the most general model, with transition probabilities state independent and allowed to vary among observation periods. Model 2 allows transition probabilities to vary by state only (constant across all observation periods). Model 3 specifies a constant transition probability among states, but allows variation across observation periods. Model 4 allows a different Ψ_{CI} in the first time period (versus time periods 2-5) and $\Psi_{CI}=\Psi_{IC}$ for each subsequent time period. Model 5 is similar to Model 4 except that it does not require $\Psi_{CI}=\Psi_{IC}$. Model 6 specifies a constant transition probability among states (i.e., $\Psi_{CI}=\Psi_{IC}$) with no time variation. I use AIC corrected for small sample size (AICc; Burnham and Anderson 2002) to rank the

candidate models. Models within 2.0 ΔAICc were considered to have support. I

expected Model 4, which specified a different transition probability (Ψ_{CI}) in the first time

period and equivalence among states ($\Psi_{CI}=\Psi_{IC}$) to be the most likely (e.g., have the

lowest AICc)..

Results

Of the 120 wood frog tadpoles, 42 of the 60 marked and 45 of the 60 unmarked

tadpoles successfully metamorphosed. After 20 days, 50% of marked tadpoles had lost

one of the two marks, though no individuals lost both marks. Among marked individuals

that metamorphosed, 67% lost at least one mark, and 21% lost both marks. There was

no relationship between time to metamorphosis and number of marks retained (R^2 =

0.03). The location of the marks did not change in any individual, though as the tail was

resorbed, marks moved further up the animal's dorsum. Marks were visible for at least 2

weeks following metamorphosis. Marks in 2 individuals were still visible 6 months after

metamorphosis under darkened dorsal pigment. There was no difference between

marking treatments in time to metamorphosis ($\bar{x}\pm 1SE$: unmarked = 28 $\pm$ 10 days,

marked = 31 $\pm$ 13 days; t_{88} = 0.132, P = 0.188) or the size at metamorphosis ($\bar{x}\pm 1SE$:

SVL (for both marked and unmarked groups) = 14 $\pm$ 2 mm; t_{68} = 0.67, P = 0.542).

Naïve and expert observers correctly identified 69 and 83% of marked northern

dusky salamanders, respectively. In all but 2 of 130 total observations of unmarked

individuals (13 observers*5 unmarked northern dusky*2 lights), observers correctly

identified unmarked individuals. Overall, observers using the blue light and amber

glasses took less time (t_{10} = 3.24, P = 0.008), and had a higher proportion of correctly

identified marks (t_{10} = 2.54, P = 0.029; 0.80 $\pm$ 0.07% for the blue light versus 0.66 $\pm$

.05% for the violet light). The difference between lights was larger in naïve observers

(0.79 $\pm$ 0.08% for the blue light, 0.60 $\pm$ .04% for the violet light) than in experienced

observers (0.84 $\pm$ 0.08% for the blue light, 0.82 $\pm$ 0.10% for the violet light). Whereas

naïve observers had higher correct identification under the blue light (t_{10} = 2.38, P =

0.039), experienced observers did not prefer either light (t_{10} = 0.15, P = 0.882). The

probability of correct identification was not related to the number of marks on an

individual; the variable describing number of marks (1 versus 2 VIE marks) was not

significant in a logistic regression model conducted separately for each light (blue light:

χ^2 = 0.290, P = 0.591; violet light: χ^2 = 0.601, P = 0.438). Odds ratios were small for two

marks with both lights (blue light 1.255 (95% Wald CI = [0.549, 2.870]); violet light 1.317

(95% Wald CI = [0.656, 2.643]). In 5 of 11 marked northern dusky salamanders, marked

animals were incorrectly identified as not having a mark by at least one observer (range

1-5 observers), but at least one observer correctly identified marks in all animals.

Most of the northern two-lined salamanders died prior to metamorphosis, likely

caused by a *Saprolegnia* fungus (D.E. Green, National Wildlife Health Center, *pers.*

comm.). Marking did not contribute to mortality or susceptibility to the disease because

control animals died at the same rate. Marks migrated from their original position at

some point over the study period in five of 17 marked individuals that survived through

the second observation period (43 days after marking; Table 4.2). There was no

consistent pattern of mark migration, but marks tended to accumulate near the vent,

which has been observed in adult animals in the field. A sixth individual (animal 17) had

one mark migrate after 146 days. In 3 individuals, a mark was recorded in a different

position in one time period, only to return to the original location in a later period (Table

4.2; animals 09, 12, 18). Viewing each salamander twice in the same day (i.e., during

each observational period) ruled out the possibility that this effect was due to mark mis-

identification. Relatively large marks (i.e., ~2mm or larger) were more likely to migrate:

seven individuals were given large marks, of which 5 experienced mark migration over

the course of the study. All individuals with mark migration had one mark that split into two, and one of these 2 marks then migrated to a different position.

The most general model (Model 1), with transition probabilities different in each state and time period, was not well supported (e.g., ΔAICc > 0, Table 4.1), whereas Models 5 and 2 had similar levels of support (ΔAICc < 2.0). The estimated transition probability (Ψ_{CI}, from correctly marked to incorrectly marked) was highest during the first observation period (estimate $\pm$ SE; Ψ_{CI} = 0.185 $\pm$ 0.075), and was smaller in the subsequent observation periods (Ψ_{CI} = 0.048 $\pm$ 0.033) under Model 5, with a different Ψ_{CI} in the first time period (versus time periods 2-5), and $\Psi_{CI}=\Psi_{IC}$ for each subsequent time period (Table 4.1). The 'recovery' probability (Ψ_{IC}, the transition probability between an incorrect and a correct mark) was relatively high (estimate $\pm$ SE; Ψ_{IC} = 0.375 $\pm$ 0.171). The model I expected *a priori* to be most likely (Model 4) was not well supported (Table 4.1; ΔAICc >2.0, AICc weight = 0.079), though the top model (Model 5) still allows a different transition in the first observation period, (with Ψ_{CI} not equal to Ψ_{IC}; Table 4.3).

The probability of mark migration in the two-lined salamander larvae resulting in an incorrect mark decreased after the initial marking period (Table 4.1, 4.3). Consider Table 4.2 as an example. If the 6 animals are recaptured 16 days after marking, 5 of the individuals would be mis-identified (due to mark migration). If the same 6 animals were recaptured 43 days after marking, only 3 of the individuals would be misidentified (due to mark migration). Some individuals "recovered" their marks over time (Table 4.2), which may be unique in the mark-recapture literature.

Only 7 (4 marked and 3 unmarked) northern two-lined salamanders survived and successfully metamorphosed, thus there was no apparent effect of marking on survival to metamorphosis. All metamorphosed animals retained their marks in the correct

positions. All northern dusky salamanders successfully metamorphosed, but marks

migrated in 25% (5 of 20) of individuals.

Discussion

Mark retention and observer bias in mark identification have not been routinely

tested or reported in amphibian mark-recapture studies, despite the potential for bias in

demographic parameter estimates caused by mark loss or misidentification (Bailey

2004). Perhaps more importantly, an assessment of mark retention of larval animals

through metamorphosis is needed if long-lived animals will be tracked for multiple years.

Such an assessment will allow researchers to address potential problems in the design

phase of a study. For larval amphibians, I suggest 1) assigning small VIE marks if

individual identifiers are needed because large marks may split and migrate, leading to

incorrect mark codes, and 2) using 2 observers (or having a single observer view an

animal's mark twice) to check both the application of mark codes and recording of codes

on recaptured animals. Further, assigning marks with a small number of locations or

VIE colors (especially early in the study) and recording age and detailed size information

may allow subsequent identification of suspect marks. This type of data may allow

estimation of the joint probability of a mark migrating and being read as an invalid code.

The identity of an individual changed for every observation period after the mark

migrates (unless the mark is 'recovered' in a later period; e.g., Table 4.2, animals 09, 12,

18), unlike observer (e.g., resighting) errors that are independent between time periods,

in the case of my larval salamanders with mark migration. The size of the VIE mark may

influence the retention of a given mark code; large marks split and migrated to different

positions within an animal. Therefore, I suggest taking care to assign marks that are

small, if the assumption that marks are retained is to be met.

The effect of tag migration on estimates of demographic parameters may depend on goals of the study and thus the capture-recapture model being considered. For example, in two-sample, closed population abundance estimators such as the Lincoln-Petersen model (Williams et al. 2002), only identification of the number of previously marked individuals is required. In this model, individual marks are not needed (and mark migration is not an issue, if the mark is not physically lost). In a study lasting longer than 2 capture occasions, survival from period t to $t+1$ generally requires individually marked animals, especially when investigating factors that influence survival (e.g., size, sex, age). Tag migration may result in an individual having a lower capture probability after initial marking (similar to a trap shy response; Pollock et al. 1990), leading to a positive bias in abundance estimators under open population models (e.g., the Jolly-Seber model; Williams et al. 2002), due to a negative bias in the capture parameter estimate, p (Weiss et al. 1991, Schwarz and Stobo 1999). Survival estimates under the Jolly-Seber model are robust to heterogeneity in capture probabilities, and in long-lived species, the bias in survival estimates declines over time (Schwarz and Stobo 1999). Mark migration that results in a new individual can be identified by comparing with the list of known marks in the population, provided that the investigator added the marks. It is important to consider ways of reducing or detecting the error when mark migration results in an individual which has a mark matching a 'true' code of a different animal in the population,.

Errors in recording marks may be common (e.g., Stevick et al. 2001, Milligan et al. 2003). Mark loss or misidentification has the potential to bias estimates of demographic parameters, however, field studies may have insufficient power to detect these errors (Schwarz and Stobo 1999). When mark misidentification, mark loss, or mark migration cannot be controlled during the design phase of a capture-mark-recapture study, these

errors must be incorporated into the modeling of the capture histories (e.g., Lukacs and

Burnham 2005), which can deal explicitly with the biases caused by incorrectly

identifying marked animals (at a cost of reduced estimator precision). Reducing the

potential for these errors in the data collection phase of a capture-mark-recapture study

is advised, because an increase in estimated variance of population size, for example,

may occur when error rates are as small as 5% in genetic mark-recapture studies,

(Lukacs and Burnham 2005).

Management implications

Tracking amphibians through metamorphosis is an important component of

investigations into factors limiting amphibian populations. Care must be taken when

using visual implant elastomer marks to individually identify larval amphibians, and I

suggest investigation of mark migration and the impact of mark size on mark migration in

other studies applying this marking method. Despite the cost associated with additional

observers (or observations by a single observer) of each captured animal, errors in mark

identification can be identified only with repeat observations of each individual. Care

must be taken in the design phase of a mark-recapture study to ensure that all model

assumptions are met, because violation of any of the assumptions of mark recapture

models can result in either large variances of estimated parameters or incorrect

inference.

Table 4.1. Results of model selection for the 6 multistate models analyzed using program MARK, describing mark migration in northern two-lined salamanders (*Eurycea bislineata bislineata*). Transition (Ψ) probabilities, which may occur between states 'Correct' (C) and 'Incorrect' (I), are estimated under several competing hypotheses. In all models, survival is assumed equal among states ($S_C = S_I$) but allowed to vary across observation periods (time, *t*), the capture probability (p) is set to 1, and the transition probability, Ψ_{IC} for the first time period is set to 0 (since all individuals were known to have a correct mark code in the first observation period). AICc = Akaike's information criterion, adjusted for small sample size (Burnham and Anderson 2002), Num. Par = number of parameters estimated in the model.

Model	Model Name	Δ AICc	AICc Wt	Model Likelihood	K	Deviance
5	S (*t*) Ψ (state, t_1,t_{2-5})	0.000	0.460	1.000	7	16.694
2	S (*t*) Ψ (state)	1.018	0.276	0.601	6	20.037
6	S (*t*) Ψ (.)	2.325	0.144	0.313	5	23.618
4	S (*t*) Ψ (t_1,t_{2-5})	3.517	0.079	0.172	6	22.536
1	S (*t*) Ψ (state*t*)	5.773	0.026	0.056	11	12.620
3	S (*t*) Ψ (*t*)	7.994	0.008	0.018	8	22.310

Table 4.2. Marks moved in the following marked northern two-lined salamander (*Eurycea bislineata*) animals that survived through at least 2 sample periods (43 days post-marking). + indicates that the mark matched the original mark given, whereas - indicates the mark did not match the given mark (i.e., that a mark had moved elsewhere in the body). xx indicates that the animal died prior to the sample period.

	Days after marking			
Animal ID	16	43	96	146
15	-	-	xx	xx
12	-	+	+	xx
18	-	-	+	xx
09	-	+	+	-
23	-	-	-	-
17	+	+	+	-

Table 4.3. Estimates for the survival and transition probabilities with the best multistate model (Model 4; S(*t*) Ψ (state, t_1,t_{2-5})) in program MARK. For the analysis, I fixed the capture probability (*p*) equal to 1, and the transition probability between incorrect and correct marks (Ψ_{IC}) equal to zero for the first period (day 16 after marking), indicated by – in the table.

Days after marking (*t*)	Parameter	Estimated probability	SE (Estimate)
16	Survival (S)	0.964	0.036
43		0.926	0.050
96		0.680	0.093
146		0.471	0.121
Initial	Transition (Ψ_{CI})	0.185	0.075
> day 16		0.048	0.033
Initial	Transition (Ψ_{IC})	-	-
> day 16		0.375	0.171

Figure 4.1. Marking locations on tadpoles (top) and salamander larvae (bottom).
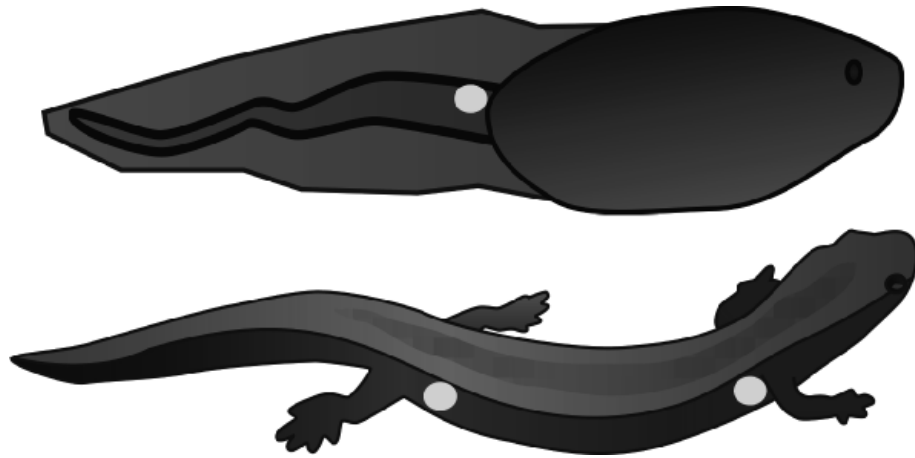
Chapter V: Dispersal behaviour in stream salamanders suggests a mechanism for population stability.

Coauthored with James D. Nichols, Winsor H. Lowe and William F. Fagan

Abstract

Despite the implications of network structure for the evolution of dispersal strategies and resulting population and community dynamics, quantifying dispersal in real populations has proven tremendously difficult (Nathan 2001). Of particular concern are specific, rarely observed dispersal pathways that may affect network dynamics(Holland and Hastings 2008, Ranta et al. 2008) and distributional patterns (Levey et al. 2005, Muneepeerakul et al. 2008) and promote metapopulation stability (Gyllenberg et al. 1993, Ruxton 1994, Dey and Joshi 2006) in populations with low growth rates. While populations of amphibians are generally in decline worldwide, those of stream salamanders have not been observed to undergo enigmatic extinctions (Hairston 1987, Green 2003, Stuart et al. 2004). Here we show the first direct evidence of movement behavior in a stream salamander, demonstrating age- and route-dependent variation in dispersal rates that suggest a mechanism for system-level stability. We find a strong upstream bias in movement and evidence of high rates of overland movement to adjacent headwater streams, suggesting a mechanism for the persistence of stream salamander populations despite population declines in other systems (Stuart et al. 2004). Our results indicate that the network geometry of stream systems affects the basic movement behavior of stream organisms. This link between landscape geometry and movement has significant implications for understanding spatial aspects of demography, evolution, and community assembly in streams and rivers.

Introduction

The hierarchical geometry of streams, hedgerows and plants separate these ecological networks from other spatially structured networks (Grant et al. 2007). In these dendritic networks, dispersal can follow two pathways: along network branches (within-network movement), or overland between branches (out-of-network movement). Variation in dispersal pathways may be related to species- or age-specific habitat associations, and may have strong effects on population persistence, evolutionary dynamics, and patterns of community composition. In species that are restricted to movement along riparian corridors, dispersal is constrained by the structure of the network (Rissler et al. 2004). Theory predicts population stability and local extinction risk in these species will be highly sensitive to network position and direct connections among populations (Labonne et al. 2008). Even in species that rely on streams for most of their life history, a capacity for overland movement is predicted to increase population stability and decreases extinction risk significantly (Hill et al. 2002, Ranta et al. 2008). Many habitat conditions vary along the stream continuum (Vannote et al. 1980) and consequently, dispersal along this continuum is more likely to expose stream organisms to novel conditions than dispersal between branches at the same hierarchical level. Furthermore, dispersal distances between branches are generally shorter by overland routes than along stream corridors. This is especially true in the uppermost portions of the network (i.e., the headwaters), suggesting that headwater specialists, including many amphibians and invertebrates, should evolve overland dispersal strategies.

While declines of amphibians have been widely documented in other habitats, the existing data on stream salamanders in the Appalachian mountains of the Eastern United States suggest stable populations (Green 2003), without evidence for large-scale, enigmatic declines like those affecting amphibians worldwide (Stuart et al. 2004). In

stream salamanders, both occupancy (Rissler et al. 2004, Grant et al. 2009) and abundance (Lowe and Bolger 2002) are higher in streams with a confluent (i.e., connected) stream branch in the headwaters. While the propensity for an organism to disperse among habitat branches in a stream network can have a profound influence on metapopulation stability in theoretical models (Gyllenberg et al. 1993, Hill et al. 2002, Ranta et al. 2008), empirical data for such movement probabilities in stream-associated organisms (and for declining amphibians in particular (Lips et al. 2003)) is lacking.

Plethodontid salamanders are a model for studies of evolutionary divergence and diversification, and have their greatest species diversity in upland, headwater areas of streams in North and Central America (Wake and Larson 1987, Wiens 2007). Therefore, we would predict that their dispersal behavior is adapted to the spatial layout of headwater habitats. We expected upstream-biased movement that would allow a species to maintain its position in the headwater. Upstream biased movement appears common in stream organisms (Bruce 1986, Macneale et al. 2005), and overland dispersal has been observed in stream invertebrates (Macneale et al. 2005). Stream salamanders have a complex life cycle where aquatic larvae metamorphose into juveniles and adults that are largely terrestrial (Wilbur 1980). In the Appalachian mountains of eastern North America, both occupancy and abundance of stream salamanders are higher in branched headwater streams than in streams flowing directly into larger streams or rivers (Lowe and Bolger 2002, Rissler et al. 2004, Grant et al. 2009). These observations suggest that connectivity between streams promotes population stability, but until now no data have been available to test this prediction and identify pathways of dispersal between streams.

In each of two confluent stream pairs in Shenandoah National Park, Virginia, USA, we marked individuals of all age classes of salamanders in three 40 m reaches, separated by <500 m either along the stream length or across terrestrial habitat. Each

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reach was surveyed in May, June, July and September in 2007-08. Using multistate

mark-recapture modeling (Lebreton et al. 2009), we compared the probabilities of within-

network vs. overland movements. Combining data from two species of stream

salamander (*Desmognathus fuscus, D. monticola*) having similar life histories and close

association with the stream channel (Organ 1961), we followed 2470 individually marked

salamanders over the 2 yr study.

   We used the closed robust design multistate model (Lebreton et al. 2009) to

estimate the probabilities of survival and transition among 'states'. In our analysis, we

defined each state as a combination of age class and stream reach (Lebreton et al.

2009). The transition probability ψ_t^{rs} is therefore the probability an individual in state *r*

(age a_t in reach l_t) at time *t* is found in state *s* (age class a_{t+1} in reach l_{t+1}) in time *t+1*,

conditional on survival from *t* to *t+1*. Two of five candidate models, representing our

hypotheses about stream salamander movement were supported by the data and had a

combined 93% of the model weight. Because of the uncertainty in model support (Table

1: model selection results), we calculated model-averaged estimates for the transition

probabilities (ψ_t^{rs}) across all models.

   Newly metamorphosed juveniles, those that were larvae in time *t-1*, had the

highest probabilities of dispersing to other stream segments, with both a strong

upstream bias in movement and a higher probability of moving overland between

reaches than along the stream corridor (Fig. 5.1). Post-metamorphic juveniles, those that

were juveniles in time *t-1*, had higher site fidelity, and smaller probabilities of moving

between reaches. Like newly metamorphosed juveniles, they were more likely to move

upstream than downstream, and had a non-negligible probability of moving overland to

an adjacent reach (Fig. 5.1). Adults exhibited the highest site fidelity, with movement

probabilities near 0 (Fig. 5.1).

Though the origin and evolution of salamanders in the family Plethodontidae is debated (Ruben and Boucot 1989), they likely diversified in headwater streams (Vieites et al. 2007), and we would predict that their dispersal behavior may be an adaptation to the spatial layout of these habitats. Our data, which represent the first direct observations on stream salamander movement, provide a mechanism for increased salamander occupancy and abundance in complex stream networks relative to simpler networks (Lowe and Bolger 2002, Grant et al. 2009). High rates of upstream and overland dispersal by juveniles, and low rates of within-network dispersal along the stream corridor, support our prediction that the dendritic structure of stream systems affects the basic movement behavior of headwater specialists (Grant et al. 2007). These data also support general theory predicting increased metapopulation persistence in networks with even a small amount of overland dispersal (Holland and Hastings 2008, Fagan et al. 2009), especially in species with low intrinsic population growth rates (Brown and Kodric-Brown 1977, Gyllenberg et al. 1993). Accordingly, the observed dispersal probabilities in our system suggest a mechanism for the perceived stability of stream salamander populations (Tilley 1980, Hairston 1987, Green 2003), which may contribute to their persistence in headwater stream habitats.

Methods summary

Data for *D. monticola* and *D. fuscus* were combined for analysis, as larval and juvenile individuals are hard to differentiate in the field. In this way, we are assuming that the movement ecology of these two species is similar with regards to overland and within-stream movement probabilities. This is a reasonable expectation, as these movement probabilities likely stem from the similarity in life-history characteristics (Organ 1961) (e.g., short larval period, close association with the stream channel and overlapping body sizes within each life stage).

We used the Huggins formulation of the closed robust design multistrata model, implemented in program MARK (White and Burnham 1999), to estimate survival (S_t^r) and capture (p) probabilities at each site, and transition probabilities (ψ_t^{rs}) among age-reach states. The survival probability is the probability that an animal alive at time t survives to time t+1 and remains in the study system (i.e., does not die or permanently emigrate), while the recapture probability (p) is the probability of capturing a marked individual conditional on it being present in the sampled population at t. The transition probability (ψ_t^{rs}) is the probability that an animal in one state at time t is present in a different state at time t+1, conditional on survival from time t to time t+1. It is important to note that our use of the robust design (using 3 temporary removal passes on each survey occasion) estimates the surface-active population at each sampling occasion and not the total population in the system.

We investigated 5 models (Supporting Online Material) representing our hypotheses about stream salamander movement, and used AICc to rank models based on their support in the data (Burnham and Anderson 2002). We used model-averaging to incorporate model uncertainty into our inferences and to reduce the bias in the estimator ($\hat{\psi}_t^{rs}$) with respect to inference from a 'single-best' model from the model set.

Methods (Supporting Online Material)

Individuals were classified into three ages: larvae, juvenile, and adult. Animals were assigned to either the juvenile or adult age class based on the distribution of sizes: *Desmognathus fuscus* individuals were classified as adults when their SVL exceeded 36 mm, and *D. monticola* individuals when their SVL exceeded 45 mm (Orser and Shure 1975, Bruce 1989, Bruce and Hairston 1990).

We used program U-CARE (Choquet et al. 2003) to perform the goodness of fit test on the global model. The global multisite test indicated some lack of fit in one of the stream groups, and an investigation of Test3.Sr indicated the problem was likely due to 'transients' – animals that were traveling through the study area (or experienced a handling effect), leading to extremely low probabilities of being present in future occasions. Within each age class, we therefore used different survival parameters for the period following initial capture and all subsequent periods. Because of low capture probabilities of larval individuals, we borrowed information across age classes to estimate the capture probability within the closed population removal model.

Our global model included stream pair, stream reach, age class, and sampling season as covariates on survival probabilities (S_t^r); we included stream pair, stream reach, temporary removal pass, and sampling season as covariates on capture probabilities (p). Recapture probabilities were constrained to zero to reflect our use of temporary removal passes within each sampling occasion. Covariates on the age-reach transition probabilities (ψ_t^{rs}) focused on the type of movement (no movement, upstream, downstream or overland), and we conditioned on the type of age transition (remain as larvae, remain juvenile, remain adult, transform from larvae to juvenile, recruit from juvenile to adult). All transitions which were not possible (e.g., from adult to larvae; overland movement of larvae) were fixed = 0. Because all larvae were observed to metamorphose prior to July, larval transition probabilities for July-September were fixed = 0.

We used a sequential modeling approach, where we first found parsimonious models for the closed-population capture probabilities and then survival probabilities, and we used the resulting parameterizations to test models of state transition probabilities. Models of capture probabilities included additive models of stream pair, reach,

temporary removal pass, and sampling month. Because numbers of captured larvae did

not always decline with removal pass, we borrowed capture information across all life

stages. This primarily affected the larval capture probabilities (see also Jung et al.

2005). Models of survival probabilities included additive effects of stream configuration,

reach, life stage, and month. We did not expect stream configuration to affect either

capture or survival probabilities.

The modeling proceeded as follows: (1) using the most general model, we used the

small-sample Akaike's Information Criterion (AICc) to rank models including different

combinations of covariates to determine the most parsimonious structure on the

detection probability parameter. Using this set of covariates, we proceeded to

investigate the covariate structure on the survival probability. Finally, we used the most

parsimonious structure on p and ϕ to investigate our hypotheses of stream salamander

transition among stream reaches and age classes. We calculated model-averaged

estimates of the transition probabilities (ψ_t^{rs}). Model averaging combines estimates

from each model using their associated model weights, to provide an estimate of the

predicted effect that is not conditional on a single model in the set (Burnham and

Anderson 2002).

We were not able to explicitly separate movements between the uppermost reaches

of our stream pairs. However, in order to travel between the two uppermost reaches via

within-stream moves, an individual would have to survive and move first from the upper

to the lower reach ($\phi_{t-1}^{upper1-lower} = S_{t-1}^{upper1}\psi_{t-1}^{upper1-lower}$), and then survive and move from the

lower reach to the adjacent upper reach ($\phi_t^{lower-upper2} = S_t^{lower}\psi_t^{lower-upper2}$). Across all age

classes, this sequence of probabilities (ϕ_t^{rs} = 0.0001) is much lower than the overland

survival-transition probability calculated for the same 2 time periods (ϕ_t^{rs} = 0.0474), in

which an individual could either survive and remain in the uppermost reach

$(\phi_{t-1}^{upper1-upper1} = S_{t-1}^{upper1}\psi_{t-1}^{upper1-upper1})$ and then survive and move to the adjacent reach

$(\phi_{t}^{upper1-upper2} = S_{t}^{upper1}\psi_{t}^{upper1-upper2})$, or vice versa. This suggests that, though movement

between the uppermost stream reaches is possible via within-stream movements, they

comprise a small fraction of the observed overland movement probabilities.

Figure 5.1. Monthly movement probabilities (and SE) for each age transition in the stream networks sampled in Shenandoah National Park, VA, USA.

Larvae - Larvae

0.000
(0.001)

0.000
(0.000)

Larvae - Juvenile

0.115
(0.052)

0.949
(0.053)

0.169
(0.069)

0.035
(0.023)

0.041
(0.020)

0.790
(0.069)

Juvenile - Juvenile

0.027
(0.006)

0.992
(0.017)

0.041
(0.009)

0.008
(0.004)

0.010
(0.004)

0.965
(0.017)

Juvenile - Adult

0.075
(0.009)

0.073
(0.009)

Adult - Adult

0.992
(0.004)

0.989
(0.007)
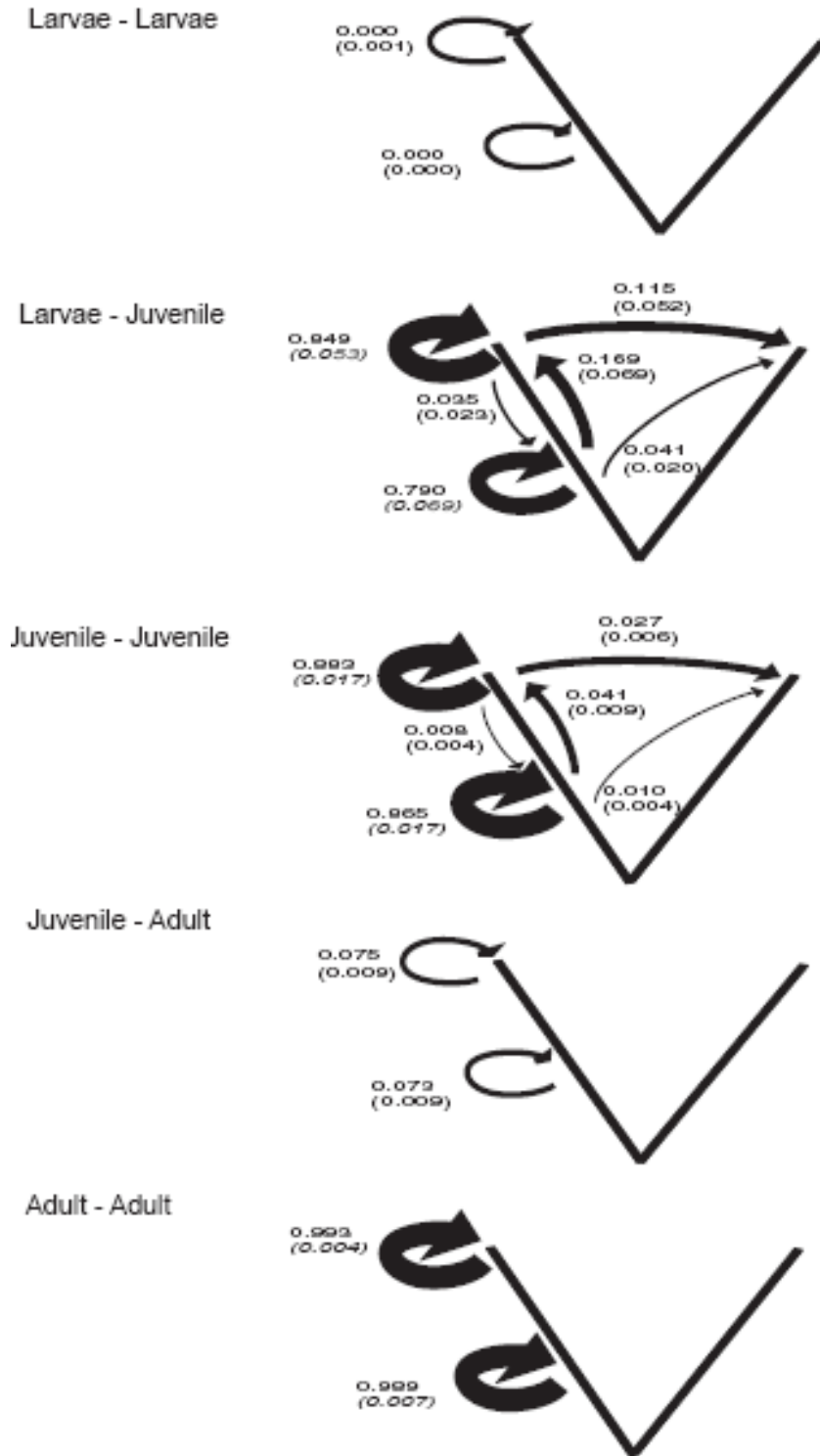
Table 5.1. Model set used for model-averaging. All models included the most

parsimonious detection [p (tx,pass,season)] and survival [ϕ (a,month)] structures, and

all transition probabilities were conditioned on age transition (larval to larval; larval to

juvenile; juvenile to juvenile; juvenile to adult; adult to adult). Model definitions follow

Table 5.2.

Model	AICc	ΔAICc	*w*	K	Deviance
ψ (move2)	20674.14	0.00	0.67	23	20627.81
ψ (move3)	20676.10	1.96	0.25	24	20627.74
ψ (move)	20678.69	4.55	0.07	22	20634.39
ψ (move3(Up=Dn))	20685.70	11.56	0	23	20639.37
ψ (move(Up=Dn))	20688.71	14.57	0	21	20646.43

Table 5.2. Candidate model set. All models included the most parsimonious structure

on p (stream reach, temporary removal pass (1-3), sampling month) and ϕ (age class,

sampling month). All transition probabilities were conditioned on age transition (larval to

larval; larval to juvenile; juvenile to juvenile; juvenile to adult; adult to adult), and

constrained to reflect our hypotheses of stream salamander movement among our study

reaches.

Model	Description
ψ (move)	Movement overland from the upper reach equivalent to overland movement from the lower reach.
ψ (move2)	Different overland movements from upper and lower reaches.
ψ (move3)	Different overland movement for upper and lower transects; overland movement between upper transects allowed to be different than overland movement from the adjacent upper transect to the lower transect.
ψ (move(Up=Dn))	No bias in within-stream movement; different overland movement from the upper and lower reaches
ψ (move3(Up=Dn))	No bias in within-stream movement; different transition for lower and upper transects in overland movement; overland upper->lower different than overland lower ->upper.

Appendix: Riverine Landscapes: Ecology for an Alternative Geometry

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Coauthored with: William F. Fagan, Heather J. Lynch, Emma C. Goldberg, Peter J. Unmack

Abstract

Ecologists interested in spatial processes are increasingly turning to models and sampling efforts that are spatially explicit. By definition, such explicitness necessitates a conceptualization of the underlying geometry of the landscapes in which important ecological processes (e.g., habitat loss, fragmentation, transport) are seen to operate. Perhaps because humans are fundamentally a terrestrial species, the default perspective in much of ecology—and in theoretical ecology in particular—is of two-dimensional terrestrial landscapes in which habitat patches of various types are interspersed within a habitat matrix.

However, riverine landscapes (including riparian systems as well as creeks and rivers themselves) exhibit fundamentally different geometric properties than do 2-D terrestrial landscapes. These geometric properties likely have important consequences for population, community, and ecosystem ecology, but they have been relatively little explored. Drawing upon several examples, we lay out a rationale for increased research on the linkages between the branching geometry of riverine landscapes and ecological dynamics, focusing on the fundamental issue of the 'branchiness' of riverine networks. Given the rich biodiversity of riverine landscapes and the pervasive threats that these key systems face, extensive opportunities exist for theoretical and empirical research in this alternative geometry.

Dendritic Networks as a Problem in Spatial Ecology

Whether one considers the evolution of new species, the dynamics of invading species, or the maintenance of biodiversity, spatial processes play central roles in ecology. A key aspect of such spatial processes is the degree to which subunits of a system or network are connected to one another, because connectivity is often a linchpin for population persistence, patterns of biodiversity, and ecosystem function (Calabrese and Fagan 2004).

Thus far, however, ecological studies of landscape connectivity have dealt almost exclusively with 'planar' geometries, wherein habitat units or patches (such as forests, fields, and cities) extend in two dimensions and can completely 'fill up' a landscape. In contrast, other natural landscape geometries have received far less attention. For example, dendritic networks, such as river systems, which consist of effectively linear (rather than 2D) habitat units sequentially arranged, have inherently different geometries than planar landscapes (Fagan 2002, Grant et al. 2007) (Fig. Appendix.1). River systems (and their associated riparian zones: Gregory et al. 1991, Malanson 1993, Naiman and Décamp 1997) are perhaps the most obvious dendritic networks in nature, but caves, plant structures, and animal migratory pathways exhibit similar topologies. Geometry is a critical feature of these dendritic networks because it is intimately tied to network dynamics. For example, branching, hierarchical networks may slow down movement altering opportunities for interactions between individuals or network components (Cuddington and Yodzis 2002, Campos et al. 2006).

Despite their potential importance, the unique contributions of dendritic geometry to the dynamics and emergent functions of networks have only rarely been studied by theoreticians (Johnson et al. 1995,Charles et al. 1998a,b, Fagan 2002, Anderson et al. 2005, Muneepeerakul 2007).   Empirical studies addressing dendritic geometry are also

scarce, but the extant few highlight the potential importance of hierarchical geometry for species persistence and patterns of biodiversity (Bornette et al. 1998, Crabbe and Fausch 2000, Cottenie and de Meester 2003). For example, in the Amazon, river confluences exhibit dramatically higher diversities of predatory 'electric' fishes than do other reaches (Fernandes et al. 2004), suggesting a key link between connectivity and community structure. Likewise, in Sonoran stream networks, fish species with highly fragmented distributions have exhibited markedly increased rates of local extinction compared to species whose historical distributions were more connected (Fagan et al. 2002, 2005a,b).

Unique features of dendritic landscapes and their consequences for ecological theory

Given the profound lack of research on the ecology of dendritic geometries, even fundamental issues remain unresolved. For example, within a branching network, what are the relative contributions of linear components and branching frequency to individual movements, population persistence, and species diversity? When species move through a dendritic landscape, do transient changes in density influence population persistence, competition, predation, and the transmission of pathogens, and what is the contribution of network geometry to those changes? What are the functional differences between 'rooted' networks (e.g., rivers or ant trails) and other dendritic geometries where hierarchical branching occurs on both ends (e.g., avian flyways)? These and many other interesting problems remain to be explored.

Clearly issues of dendritic geometry are related in certain ways to the increasingly popular 'network theory' approaches that have been used in studies of telecommunication (Albert et al .2000), epidemiology (Grenfell and Bolker 1998),

foodwebs (Brose et al. 2004, Garlaschelli et al. 2003), and elsewhere. However, several

key differences set the problem of dendritic geometries apart from network theory more

generally (Grant et al. 2007). The most important of these is that dendritic ecological

networks exist as physical entities whereas in network theory the 'branches' or links of a

network represent rates or magnitudes of connections among entities (e.g., patches).

Dendritic networks require separate investigations because organisms actually live and

interact in those alternative geometries (Grant et al. 2007). Consequently, the important

issues in the ecological dynamics of dendritic networks are not easily addressable via

graph theory or similar approaches that are so popular with network theorists (Vincent

and Myerscough 2004, Grant et al. 2007). Instead, to explore these issues theoretically

one must often build model landscapes of patches arranged in a variety of branching,

hierarchical fashions and then simulate populations or communities of species that

interact on those landscapes (e.g., Fagan 2002, Muneepeerakul et al. 2007).

Despite commonalities with other network-related topics, dendritic ecological

networks present several unique complications that, together, constitute a novel

research frontier in spatial ecology. Four of these sources of complexity are:

1) Intrinsic effects of configuration

Even without any additional complications (i.e., even if the three sources of

complexity listed below are not present), the hierarchical, branching arrangement of local

communities *per se* can affect ecological patterns and dynamics in dendritic networks.

In dendritic geometries, confluences and spatial sequencing are important

considerations because they can act as impediments to spatial averaging as the scale

changes (Guo et al. 2003, Kuby et al. 2005). For example, temporal variation in a

natural process (e.g., water retention) may have starkly different consequences

depending on whether the process occurs upstream or downstream within a river

network (Guo et al. 2003).

<u>2) Directional biases</u>

River networks feature directionally biased flows (e.g., river flows) that introduce systematic anisometries and noncommutativities into problems of dispersal in branching networks (e.g., the 'distance' or 'ease of travel' from patch A to B is not necessarily the same as from patch B to A). Directionality has received some theoretical attention via advection-diffusion models focusing on questions of population persistence, critical patch sizes, and the 'drift paradox' (Anderson et al. 2005, Lutscher et al. 2005, Pachepsky et al. 2005), but these studies considered linear habitats, not branching geometries.

<u>3) Out-of-network connections</u>

Some processes in dendritic networks are out-of-network by nature. For example, forest fires and other disturbances, which need not follow the geometry of river networks, represent situations in which out-of-network processes are mismatched against the geometry of organisms' in-network dispersal (Fagan 2002). Likewise, human trucking of salmon and overland 'walking' by invasive snakehead fish are good examples of situations where out-of-network movement is critical to network-level dynamics. Some species (e.g., fish) are restricted to travel along the network, while others (e.g., stream insects) may make occasionally make overland movements.

<u>4) Transient connectivity</u>

The connectivity among patches in a river network may be transient (i.e., time-dependent) rather than static. For example, river networks featuring regional droughts (Arizona) or episodic flooding (Amazonia) exhibit reduced or enhanced connectivity, periodically altering opportunities for dispersal and redistribution of resources.

To investigate how hierarchical, dendritic geometries influence ecological dynamics and patterns of biodiversity will require the development of a series of models of varying complexity, detail, and focus. Explicit dendritic landscapes should be at the

core of these models, providing a common framework that transcends differences in model structure and purpose. For example, to explore the interface between dendritic geometry and network dynamics, one could vary the geometric properties of those landscapes (e.g., branching frequency, rooted versus non-rooted topology, hierarchical form of spatial heterogeneity) and impose one or more of the four complications above to examine their joint impacts on ecological patterns and dynamics. Of the four sources of complexity, the last item, transient connectivity, is arguably the most novel and most likely to yield results that generalize in important ways to network problems far beyond theoretical ecology. In such models, a difference or differential equation (such as those routinely used to study local population dynamics and species interactions) could operate within each compartment, and the compartments would then be linked to other compartments within the hierarchy. Given their complexity, such models will typically be solved via extensive numerical simulations, but in some cases variable aggregation methods may be useful (Charles et al. 1998a,b). Across model runs, outputs could can be interpreted in terms of scaling laws for such metrics as population persistence times, average abundance or occupancy, or rates of spatial spread (Muneepeerakul et al. 2007, unpublished ms.). This approach is commonly used in ecohydrology (Rodriguez-Iturbe and Rinaldo 1997).

The 'branchiness' of a river network influences colonization opportunities and extinction risk

To illustrate the importance of dendritic geometry for ecological systems, we focus in this chapter on one important geometric factor, namely the 'branchiness' of a river network. Extending some ideas about riverine metapopulation dynamics that were initially laid out in Fagan (2002), we first use a simulation model to explore how branchiness of a network alters opportunities for recolonization and consequently

extinction risk. We then draw upon a database of fish distributions to illustrate the effects of network branchiness in a real system where fragmentation is already known to be an important driver of extinction risk.

Modeling the effects of network branchiness for metapopulation dynamics

We investigated the relationship among network branchiness, movement probabilities, and extinction risk of a metapopulation within networks of 15 stream reaches ('habitat patches'). In our model, all patches are of equal habitat quality, and we assume a uniform distribution of a population in the network. After investigating extinction risk in general, we look closer at a particular metapopulation scenario using parameter values guided by a mark-recapture study of a stream salamander species, *Gyrinophilus porphyriticus* (Lowe 2003).

We created two 15-patch dendritic networks with different topologies: (1) a fractal network ('Full') with bifurcations at each branch node, and (2) a network with reduced complexity ('Pruned'), where only one bifurcation is present at each depth in the network (Fig Appendix.2). The first configuration corresponds to the model in Fagan (2002), whereas the second configuration results in a network with branches of differing length from the mainstem (Fig Appendix.2). Realistic networks in nature may fall between the dendritic network topologies considered here (Dunne and Leopold 1978). Location in the network is indexed by specifying a network 'depth,' or location along the mainstem of the network, and the horizontal position in the network (Fig Appendix.2). In our ordering schema, starting from the downstream terminus of the network, a patch in position (3,2) is located 3 steps along the mainstem, and 2 branches from the leftmost patch (at the first bifurcation point, keep left, at the second, keep right).

For each model run, we initialized full occupancy of all patches in the network, and fixed the time-specific extinction probability in each patch for each model run. At

each time step, we allowed colonization of extinct patches via three movement routes: (1) upstream, (2) downstream and (3) overland, out-of-network colonization from one of the two closest neighboring patches within the same depth. We investigated three probabilities for extinction probability (0.1, 0.01, 0.001), and four movement probabilities (0, 0.1, 0.01, 0.001). The model was run for a maximum of 10000 time steps (or until full extinction of the network) for all parameter combinations, and each combination was replicated 100 times. We investigated all combinations of extinction and movement probabilities, though we present here results for the case with upstream = downstream movement probabilities.

For the Full dendritic network, the presence of out-of-network connectivity has a large effect on the time to extinction. This effect was most prominent with high levels of within-network movement, suggesting that out-of-network movement is not the sole driver of extinction risk (Fig. Appendix.3, left panels). When per-patch extinction risk was low (0.001), the network persisted for a wide range of both within- and out-of-network dispersal probabilities (Fig. Appendix.3, left panels). At intermediate levels of extinction probability (0.01), the network had a reduced time to extinction when there was at least a small amount of out-of-network movement compared to the scenario without out-of-network movement. The metapopulation persisted when both within network dispersal was high (0.1), and out-of-network dispersal was moderate to high (0.01 – 0.1). Extinction risk in the Pruned network was similar to that in the Full network (Fig. Appendix.3, right panels), but featured a damped pattern that was especially evident at intermediate levels of extinction probability (Fig. Appendix.3, left middle panel, extinction = 0.01). With high extinction probability (0.1), the Pruned network goes extinct rather quickly (not different axis scale), regardless of the level of out-of-network dispersal.

Finally, we compared 15-patch networks in two configurations (Full vs. Pruned networks) guided by empirical within-network movement data on a species of stream salamanderLittle is known about rates of out of network movements in stream amphibians, though populations of some species are more closely associated with stream networks with confluent first order branches (Lowe and Bolger 2002, Rissler et al. 2004, Grant and Green, *unpublished data*), suggesting that this type of movement may be naturally low in some species. Stream networks in altered landscapes typically lose complexity via loss of small headwater streams (Dunne and Leopold 1978). In species which are adapted to live in streams, the loss of network complexity may result in an increased extinction risk, especially when within network movements are the predominant mode of dispersal. Some species may be capable of making out of network movements, which may be important for stabilizing populations (a type of 'weak link,' Csermely 2004). Further, in undisturbed populations, stream salamanders likely have low rates of extinction (Hairston and Riley 1993), though with increasing landscape disturbance, rates of extinction are likely higher (Price et al. 2006). Using our model, we found that at low rates of extinction (0.01), both network complexities have similar extinction risk when there is a small amount of out of network dispersal (Fig. Appendix.4, top). However, at higher extinction rates (0.1), the Full dendritic network has a greater potential for population persistence, when out-of-network movements are proportional to or greater than other modes of dispersal (Fig. Appendix.4, bottom).

From our simulation results, it is apparent that the spatial layout of populations within a stream network helps determine the risk of metapopulation extinction. Consequently, understanding how network complexity interacts with population extinction risk may be important for managing stream network habitats. More complex patterns of extinction (e.g., correlated disturbances, Fagan 2002, Lowe 2002) and biases in animal movements or habitat preferences in the network (e.g., preference for higher

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order branch locations) may alter the results from our simple model discussed here. However, we expect that more realistic models will strengthen the relationship among movement probabilities and network complexity, especially considering variation in out-of-network colonization probabilities.

For most species that live in dendritic networks, empirical estimates of movement probabilities is a critical information need for managing populations in these habitats, though these estimates are largely unavailable at large scales. As our results suggest, the specific combination of movement probabilities are important for assessing metapopulation extinction risk. While out-of-network connectivity generally increases the time to metapopulation extinction, the effect of increasing this movement is mediated by the within-network movement probabilities. Few long-term data exist to test our model in existing dendritic network systems at large scales, though recently established monitoring programs that recognize the potential importance of the spatial layout of dendritic networks should yield useful empirical data.

Finally, we note that the modeling approach employed here may be useful for planning repatriation, translocation or stocking programs in dendritic stream networks. Viewing out-of-network dispersal as a translocation or stocking event, alternative scenarios could be explored in advance of field work. Extensions to our model could specify stocking or translocation frequency via modification of the out-of-network colonization probability, consider the impact of stocking location within the network hierarchy, and allow for a greater range of colonization distances (e.g., allowing for long distance dispersal events in the network).

Network branchiness and extinction risk for desert fishes

A key prediction emerging from the above modeling scenarios is that 'branchier' networks should facilitate recolonization among subpopulations and thereby buffer the

system as a whole from regional extinctions. To test this prediction in the real world, we investigated the link between network branchiness and local extirpation risk in an assemblage of fish species native to the Sonoran Desert ecoregion.

Occurrence records for this group of species are summarized in the Sonoran Fishes (or 'SONFISHES') database, initially developed by the late ichthyologist W. L. Minckley. This GIS database provides extensive distributional data for native freshwater fishes in the southwestern USA and northwestern Mexico. Within the Sonoran ecoregion, the Lower Colorado River basin, and within that, the Gila River, feature the most detailed biogeographical coverage and the greatest density of collecting records. Parts of this landscape are highly fragmented due to a lack of perennial water due to the interplay among precipitation, discharge and substrate, and more recently as a result of diversion and desiccation by human activities (Brown et al., 1981). Moreover, even when contiguous stretches of surface water exist, the widespread introduction of multiple, non-native, invasive fish species induce a type of 'biological fragmentation' due to larvivory, in which non-native species prey on juvenile native fish and greatly limit their recruitment (Unmack and Fagan 2004).

The SONFISHES database encompasses ~160 years (from 1843 to ~2005) and contains incidence, identity, and collection data for the complete holdings of the major museum collections from this region, numerous smaller collections of southwestern fishes, records from the Non-Game Branch of the Arizona Game and Fish Department, and peer-reviewed and 'gray' literature sources. Due to the intensity and time span of sampling, SONFISHES summarizes virtually all that is known about past and present distributions of fishes in the region and represents an unusually comprehensive resource for examining changes in species spatial distributions over time.

Previous analyses of the SONFISHES database have demonstrated that, among 25 fish species native to the Lower Colorado River basin, the degree to which a species'

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distribution was fragmented historically is a strong predictor of the frequency of local

extirpations that the species has since experienced (Fagan et al. 2002a, 2005a,b).

Although a species' historical frequency of occurrence (i.e., number of localities at which

it was found) is also correlated with the risk of extirpation on local scales (e.g., 5km or

25km reach lengths), historical fragmentation of occurrences is a far stronger predictor

of variation in extinction risk among species (Fagan et al. 2002), and this dependence

manifests on small through large spatial scales (5 to 2500 km reach lengths; Fagan et al.

2005a). Thus the physical arrangement of species' populations and not just the number

of those populations has been an important determinant of extinction risk in the Sonoran

ecoregrion.

Here we seek to expand on this understanding by quantifying the relationship

between the branching geometry of river networks in particular watersheds and the

observed frequency of local extinctions in those watersheds. To quantify network

branchiness, we will adopt two measures of riverine geometry from the theoretical

hydrology literature (Rodriguez-Iturbe and Rinaldo 1997, Dodds and Rothman 1999,

Turcotte et al. 1998).   However, before introducing the branchiness metrics themselves,

we first define some important hydrological terms that provide context..   Using the

conventional methodology for characterizing watershed geomorphology (Strahler 1967),

a stream's '*order*' is an index that relates to both flow capacity and network position.

Starting from tiny trickles far upstream (1st order streams), stream order increases when

two streams of equal order merge together. For a given stream of order *n*, a *'major side

tributary'* is a stream of order *n-1* that merges with the parent stream partway along its

course (rather than at its upstream confluence). Likewise, a '*stream segment*' is defined

as a contiguous reach of stream with the same order (i.e., a stream segment is bounded

by upstream and downstream confluences where order changes). In idealized

watersheds, these concepts are related by Tokunaga's Law (Dodds and Rothman 1999) which states

$$T_n = T_1 R_T^{n-1} \qquad (1)$$

where T_n is the expected number of tributaries of order n in a given watershed, T_1 is the average number of major side tributaries per stream segment, and R_T is a multiplicative factor describing the average rate at which numbers of side tributaries of successively lower orders accumulate in a watershed. Example calculations of these branchiness metrics appear in Dodds and Rothman (1999). Although Equation (1) is typically used in theoretical hydrology problems, the metrics T_1 and R_T, which quantify different, but complementary, aspects of stream network complexity, can also be calculated for real watersheds via tedious effort.

To characterize the branchiness of different river networks, we quantified T_1 and R_T for 13 watersheds within the Gila River drainage (central Arizona and western New Mexico, USA, plus small portions of northern Sonora, Mexico). We used watersheds defined at the HUC-8 scale (Hydrological Unit Code – 8; Seaber et al. 1987), and given the monotony involved in calculating the branchiness metrics, chose a subset (52%) of the HUC-8 watersheds that spanned the range of watershed complexity evident in the Gila drainage. We focused our analyses on six species of small- and medium-sized fish: *Agosia chrysogaster*, *Catostomus insignis*, *Gila intermedia*, *Meda fulgida*, *Rhinichthys osculus*, and *Tiaroga cobitis*. These species were all widespread in the Gila River drainage historically, and, unlike other fish native of the region, were not restricted to particular elevational zones (e.g., *Onchorhynchus* spp.) or river flow volumes (e.g., *Xyrauchen texanus*, *Ptychocheilus lucius*). We then used logistic regression to quantify relationships between watershed branchiness and the observed frequency of extirpation at the local scale (=5 km of reach).

Gila River watersheds vary substantially in branchiness, whether that geometric complexity is measured in terms of the average number of major side tributaries (T_1) or the rate at which reaches accumulate lower order tributaries (R_T). On average, a given stream segment in Gila River watersheds has T_1 = 1.00 major tributaries (range: 0.85 – 1.42) and finer scale branching occurs at an average rate of R_T = 2.21 branches per segment (range: 1.44- 3.15)

For four of our six focal species, the frequency of local extirpation was strongly and significantly dependent on one or both measures of network branchiness (Fig. Appendix.3). *Catostomus* and *Rhinichthys* both exhibited lower local extinction risk in those watersheds with relatively high T_1 scores, whereas observed extinction risk in *Gila* and *Tiaroga* were more strongly related to R_T. In contrast, extinction risk in neither *Agosia* nor *Meda* was significantly related to watershed branchiness, although extinction risk for *Agosia* trended downward with increasing branchiness for both R_T and T_1.

In a system like the Sonoran ecoregion, where connectivity may be determined largely by in-stream proximity of individual populations, it is intuitive that the extent of fragmentation in populations is a strong predictor of extinction risk, and this has been borne out by several analyses (Fagan et al. 2002, 2005a, b). Our analysis here suggests that watershed 'branchiness' may contribute to those previously observed relationships between fragmentation and extinction risk, with branchier watersheds being less prone to local population extinctions. Consequently, conservationists and resource managers may want to consider the branching geometry of riverine networks when seeking to identify watersheds that will yield a high probability of local population persistence for Sonoran fishes.

Conclusion

Although this chapter has focused on riverine geometry, river networks are only one example within a broader class of ecological networks involving dendritic geometries. For example, caves feature network-like geometry, but exist in three dimensions rather than just two (Curl 1986, Palmer 1991). Likewise, avian flyways, ungulate migratory pathways, and ant trails possess branching, hierarchical geometries but exist at a functional level (for migration or resource acquisition) rather than in a structural sense (Watmough and Edelstein-Keshet 1995, Speirs and Gurney 2001, Hindmarch and Kirby 2002, Jackson et al. 2004, Xia et al. 2004). The architecture of individual plants also involves dendritic geometries that may alter species interactions and drive emergent food web dynamics (Kareiva and Sahakian 1990, Cuddington and Yodzis 2002). Unfortunately, links between geometry and dynamics in these other dendritic systems have received even less theoretical attention than have river networks. Consequently, the ecology of alternative geometries will afford rich research opportunities for years to come.

Figure Appendix.1 A dendritic landscape (left) differs fundamentally from the standard

two dimensional landscape often featured in spatially explicit investigations in ecology.
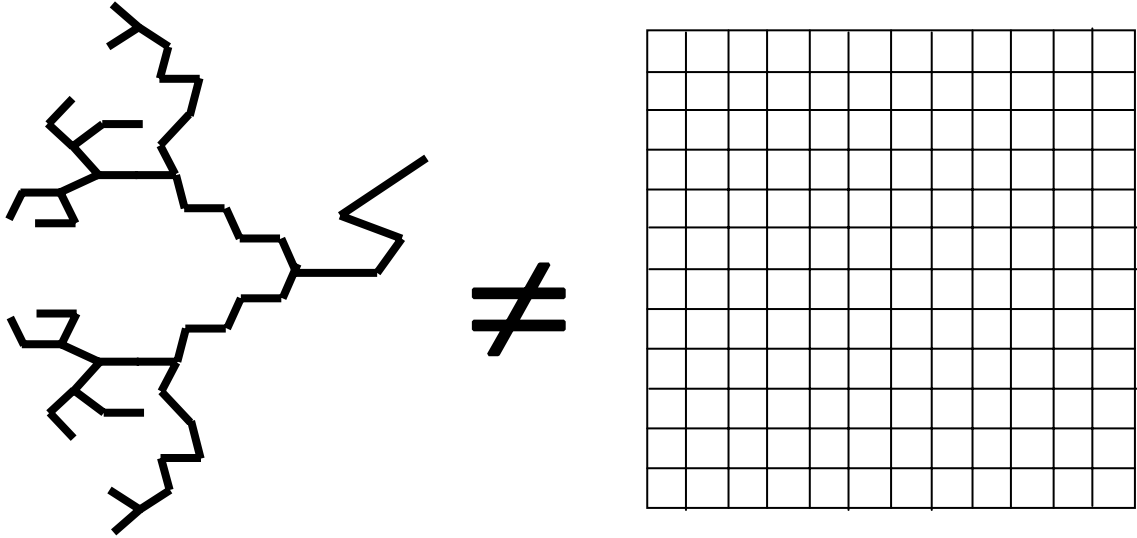
Figure Appendix.2 Fifteen patch network configurations (A = Full, B = Pruned) considered in investigating extinction risk in dendritic metapopulations. The network depth is used to index position in the network.
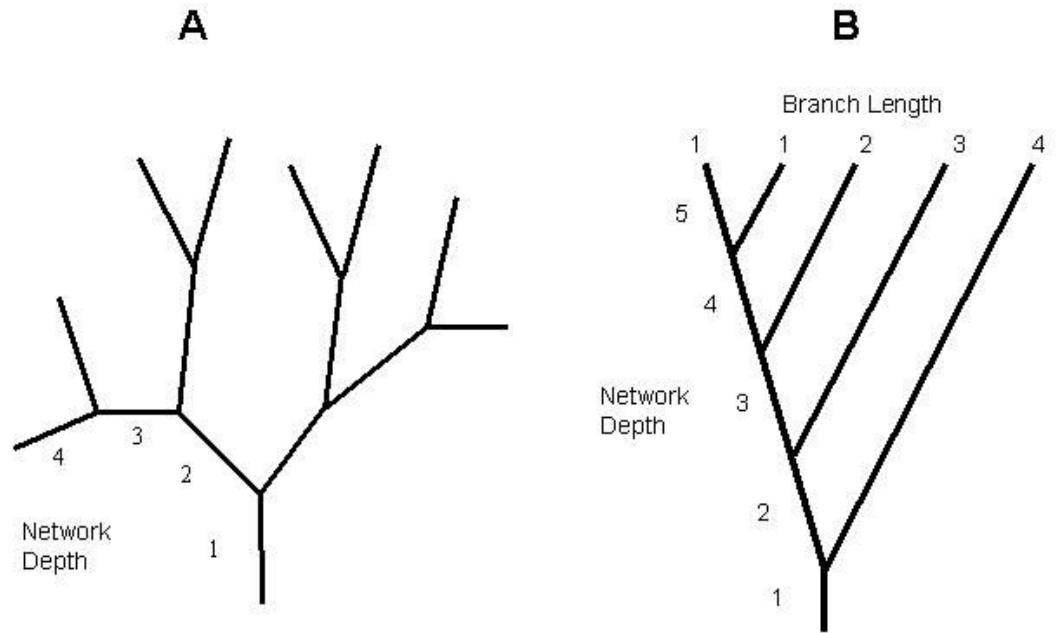
Figure Appendix.3 Effects of river network 'branchiness' on extinction risk in 15 patch dendritic metapopulations. Panels on the left are from a full dendritic network, and on the right are from the pruned network. Three extinction probabilities were modeled (0.001, top row; 0.01, middle; 0.1 bottom row), under combinations of within and out of network dispersal probabilities (0, 0.001, 0.01, 0.1).
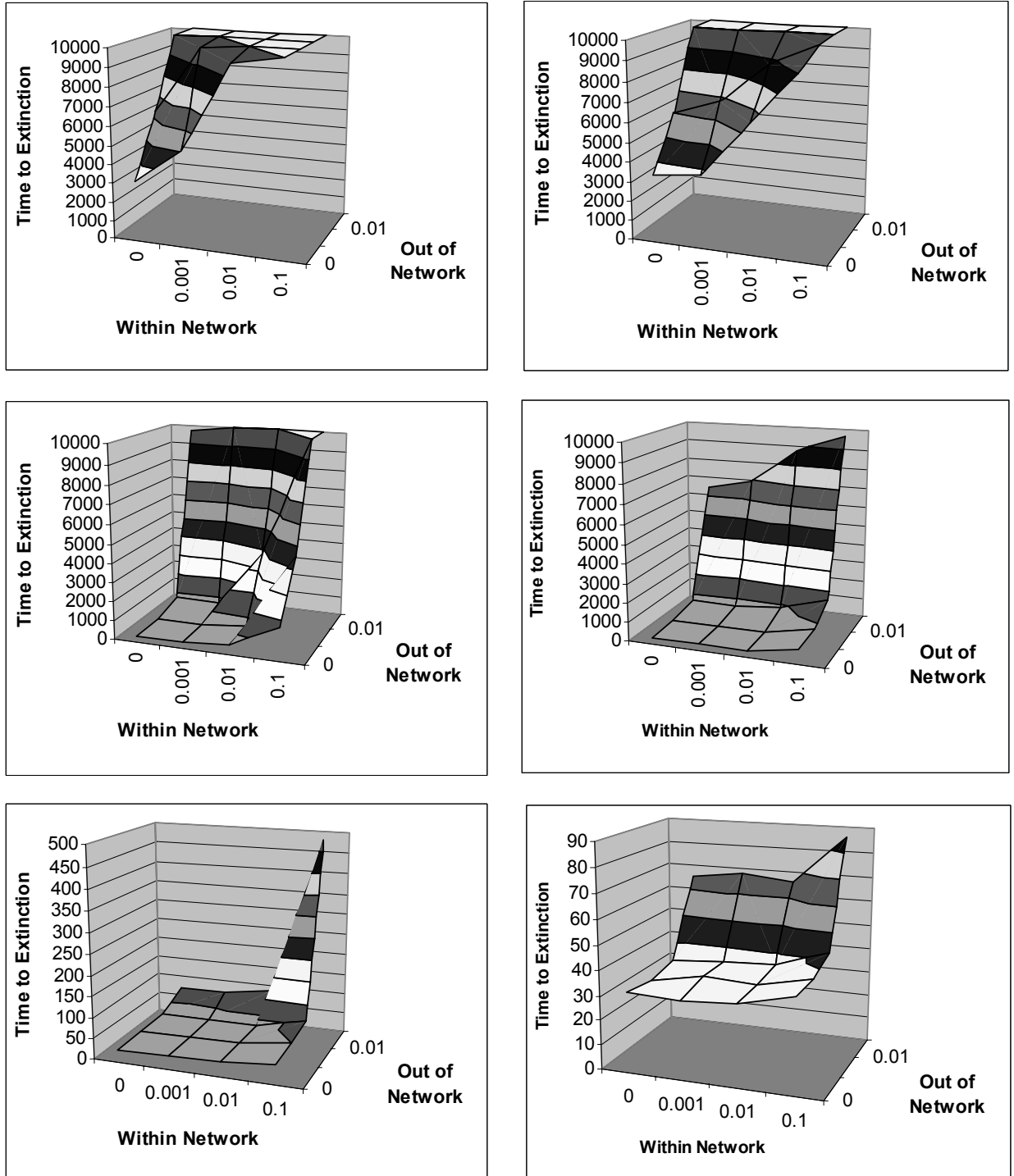
Figure Appendix.4 Effects of river network 'branchiness' on extinction risk for the spring salamander *Gyrinophilus porphyriticus* under different levels of out of network dispersal (upstream dispersal probability = 0.15, downstream dispersal probability = 0.05). Top panel, extinction probability = 0.01. Bottom panel, extinction probability = 0.1.
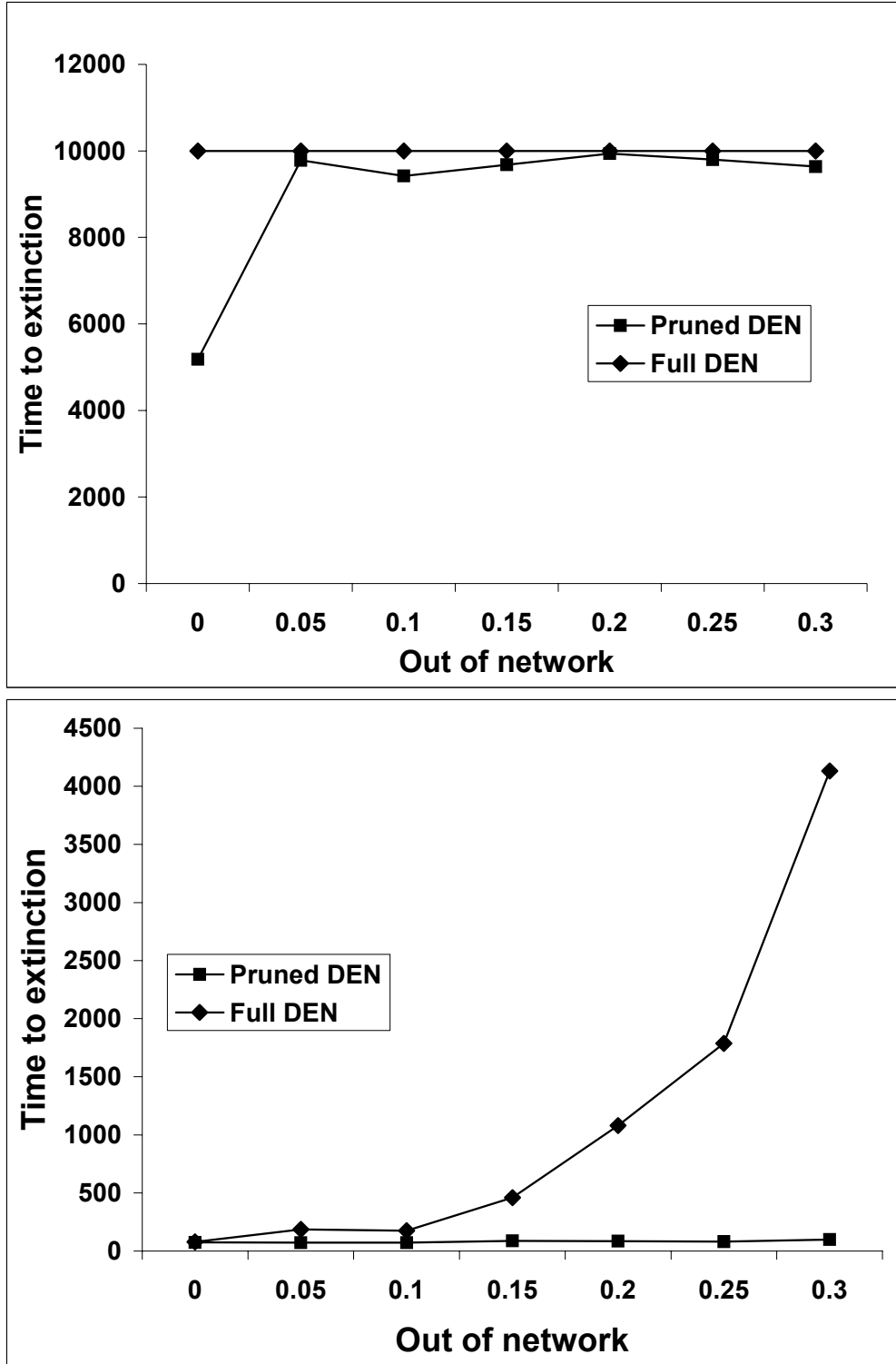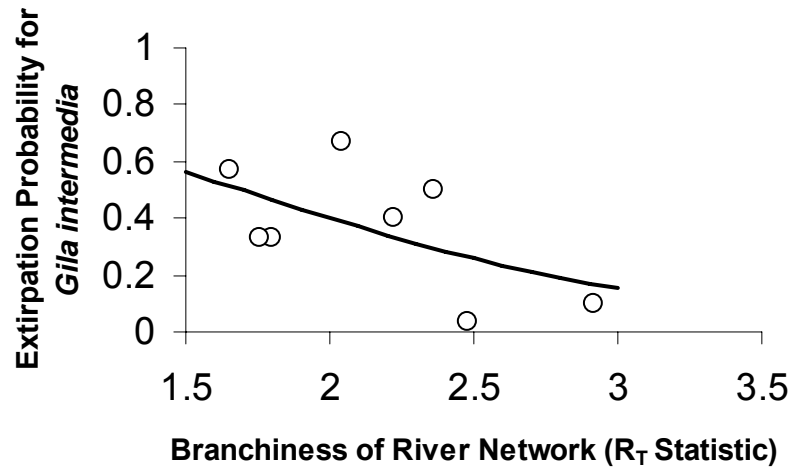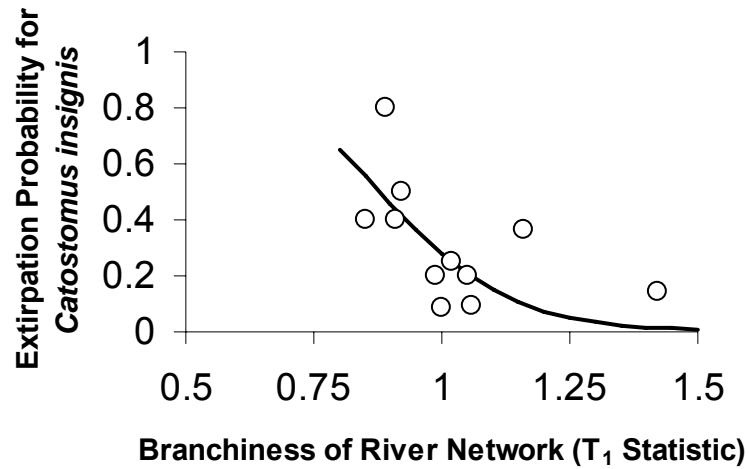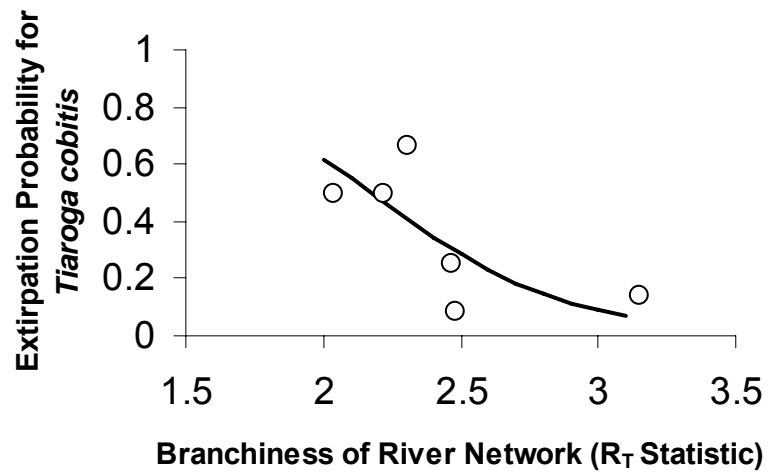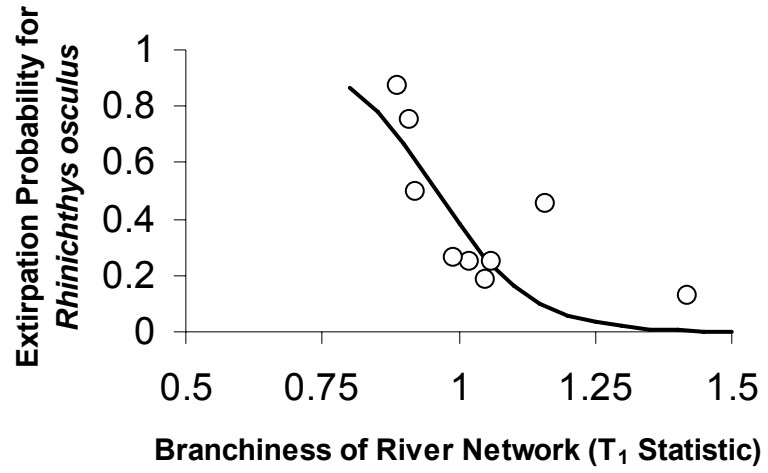
Figure Appendix.5 Measures of river network branchiness as predictors of extinction risk in fish species of the Gila River in the Sonoran Desert ecoregion. Extirpation probability calculated at the scale of 5km reaches.

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