APPLIED ISSUES

Salamander occupancy in headwater stream networks

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SUMMARY

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

2. 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.

3. 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.

4. 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.

5. These results demonstrate that the spatial configuration of stream networks within protected areas affects 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.

Keywords: dendritic ecological network, headwater stream, occupancy, protected areas, stream salamander

Introduction

Viewing ecological systems as spatially structured networks has improved our understanding of pattern and process across temporal and spatial scales. Con-

ceptual 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, Lowe & Fagan, 2007). The branching geometry of 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.*, in press), 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.*, in press).

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.*, in press). Stream-dwelling species can move through the network along two pathways: movements upstream and 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.*, in press).

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, Lowe & Likens, 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 than in those that flow directly into larger streams and rivers (Fig. 1). Additionally, we would expect species-specific relationships in stream occu-
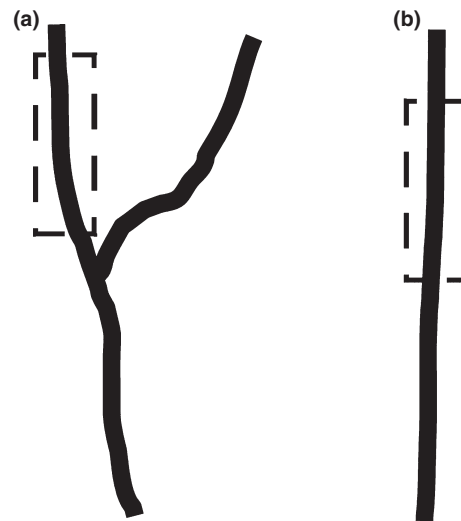

Fig. 1 Schematic of stream configurations. (a) A branched stream, where the stream reach of interest makes a downstream confluence with another first-order stream and (b) an unbranched stream, where the stream reach of interest makes an eventual downstream confluence with a higher-order stream. The dotted box indicates a sample site, in which three to four transects were surveyed to characterise occupancy of our focal salamander species.

pancy 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, Paul & Taulbee, 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.*, in press). Because stream salamanders are most strongly associated with first-order headwater streams (Snodgrass *et al.*, 2007; Peterman, Crawford & Semlitsch, 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 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 years), high local densities, small body size and a weak association with the stream channel after metamorphosis. These combina-

tions 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 years), 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). Finally, *Desmognathus fuscus* (Green) exhibits a short larval period (<1 year), 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

Table 1 The hypothesised relative dispersal ability of the stream salamander species in this study

	Movement pathway	
Species	In-stream	Out-of-network
Desmognathus fuscus	+	+
Eurycea complex	++	+++
Pseudotriton ruber	+++	+

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.

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, DC. 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). We combined observations of *E. 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: (i) present and detected; (ii) present but undetected or (iii) absent. Because states (ii) and (iii) 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'; 15 × 3 m transects in the NCR or 10 × 6 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, Simons & Pollock, 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 branched), and regional landscape context ('region'; $n = 11$ NCR sites, 43 VA sites). We also tested whether occupancy was unrelated to either covariate [notation $\Psi(\cdot)$]. We compared models using Akaike's information criterion (AIC) and considered models with ΔAIC < 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 ($\bar{\psi}$) 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 $\hat{\bar{\psi}}$. We detected *P. ruber* at eight sites in VA and seven sites in NCR (naïve $\Psi = 0.28$), *D. fuscus* at 36 VA and nine sites in NCR (naïve $\Psi = 0.83$) and the *Eurycea* complex at 40 sites in VA and nine sites in

NCR (naïve $\Psi = 0.91$). The VA sites also included some or all of the following sympatric species: *D. quadramaculatus*, *D. monticola*, *D. ochrophaeus* and *Gyrinophilus porphyriticus* (Green). The VA sites had a greater abundance of cover than the NCR sites (mean $\pm$ 1 SE = 438 $\pm$ 30 versus 45 $\pm$ 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-squared 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*: $\chi^2 = 45030.6$, $P = 0.48$; *Eurycea* complex: $\chi^2 = 51507.2$, $P = 0.87$; *D. fuscus*: $\chi^2 = 67673.32$, $P = 0.67$).

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).

Desmognathus fuscus was detected at 83% of sites. The Ψ(region), Ψ(network) and $\Psi(\cdot)$ 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).

Pseudotriton 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. $\Psi(\cdot)$, p(survey)]: $\hat{p} = 0.28 \pm 0.05$ for transects in NCR; $\hat{p} = 0.27 \pm 0.13$ for transects in VA), and all of the occupancy models considered had some support from

Table 2 Summary of model selection and estimated parameters (and SE)

Model	ΔAIC	w	K	$-2l$	$\hat{\beta}_{\text{Network}}$	SE($\hat{\beta}_{\text{Network}}$)	$\hat{\beta}_{\text{Region}}$	SE($\hat{\beta}_{\text{Region}}$)
Eurycea complex								
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								
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								
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

ΔAIC, difference in AIC value for a particular model when compared with the top ranked model; w, AIC model weight; K, number of parameters in the model; $-2l$, twice the negative log-likelihood value; –, effect was not included in the model or the estimated SE was nonsensical.

The 'network' covariate was entered as a categorical variable (1 = branched), as was the 'region' covariate (1 = NCR). Detection probability was modelled as a function of survey method ('survey'; all models) 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.

Table 3 Model-averaged occupancy probabilities (and SE) 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)

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 ($\hat{\bar{\psi}}_{\text{B}} \pm 1$ SE = 99 ± 3% versus $\hat{\bar{\psi}}_{\text{UB}} \pm 1$ SE = 90 ± 7%; effect size = 0.13). *Pseudotriton ruber* also had higher occupancy in branched streams ($\hat{\bar{\psi}}_{\text{B}}$ = 52 ± 23% versus $\hat{\bar{\psi}}_{\text{UB}}$ = 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 ($\hat{\bar{\psi}}_{\text{B}}$ = 90 ± 8% versus $\hat{\bar{\psi}}_{\text{UB}}$ = 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 DENs (Fagan *et al.*, in press; Grant *et al.*, 2007).

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) suggests 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 *E. 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 (K. R. Cecala, S. J. Price & M. E. Dorcas, unpubl. data), 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 (*E. bislineata*, *P. ruber*, *D. 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 *G. 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 DENs (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 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.

Acknowledgments

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