



## Research Article

# Using Spatial Demographic Network Models to Optimize Habitat Management Decisions

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**ABSTRACT** Conservation and management activities are always constrained by finite resources. Therefore, decisions such as which sites to protect, whether existing habitat should be restored or whether new habitat should be created, and where on the landscape management efforts should be focused present difficult challenges. An overarching goal of many conservation or management plans is the long-term persistence of populations, which is often dependent on functional connectivity and the maintenance of metapopulation dynamics. Graph theory and network approaches are frequently used tools for modeling functional connections between populations and between habitats. Less often, graph models are used to guide conservation or management decisions. We used spatial networks derived from an amphibian population to determine optimal locations to create new habitat, prioritize existing habitat for restoration, and determine the habitat most critical for maintaining connectivity within the existing metapopulation within Fort Leonard Wood, Missouri, USA, 2012–2014. Using data collected at 206 breeding ponds over 3 years, we constructed demographic networks representing the functional connectivity between ponds by dispersing ringed salamanders (*Ambystoma annulatum*). We incorporated uncertainty in key model parameters through Monte Carlo simulation, and used a graph-theoretical parameterization of the metapopulation mean lifetime model to assess how changes in network structure affect persistence of the network. We conducted addition and removal experiments within our Monte Carlo simulations to rank and prioritize locations for pond creation, ponds for restoration, and ponds for preservation. Salamanders bred in 106 ponds in  $\geq 1$  year; 2.4% of ponds functioned predominantly as sources and 51% of occupied ponds functioned predominantly as sinks. The importance of a pond to the network was correlated with the number of emigrants dispersing from a pond, the number of ponds reached by these dispersers, and the frequency a pond functioned as a source. Creating new ponds at optimal locations increased the persistence of the network an average of 15.4% compared to randomly selected locations, whereas selective restoration of currently unoccupied ponds resulted in an average increase of 31.4% in network persistence, as compared to randomly selected unoccupied ponds. Through Monte Carlo simulation, we constructed biologically informed demographic connectivity networks for use as a spatial conservation or management planning tool. Although our approach was implemented with an amphibian and a breeding pond network, it is generalizable to any species occupying discrete habitat patches. © 2017 The Wildlife Society.

**KEY WORDS** *Ambystoma annulatum*, amphibian, demographic networks, dispersal, functional connectivity, graph theory, metapopulation dynamics, source-sink.

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Many wildlife populations have been steadily declining in recent decades because of multiple interacting factors (Reading et al. 2010, Inger et al. 2015, Ripple et al. 2015, Grant et al. 2016). Among the most pervasive of these influences is anthropogenic change, specifically in the form of habitat loss, degradation, and fragmentation. As a consequence of habitat alteration, functional connectivity among populations is often reduced or eliminated, jeopardizing

dizing metapopulation dynamics and the long-term persistence of populations on the landscape (Hanski 1998, Hanski and Ovaskainen 2000). There is a clear need for management and conservation to operate on entire landscapes (Lindenmayer et al. 2008), requiring inclusion of spatial population dynamics and functional connectivity to maintain extinction-colonization processes (Hess 1996). This seemingly straightforward requirement is fraught with challenging questions and decisions. Which sites should be prioritized for protection? Should existing habitat be restored, or should new habitat be created? Where (spatially) should management efforts be focused? Objectively answering one or all of these questions can require extensive and detailed empirical data that may not exist or may come with considerable uncertainty (Margules and Pressey 2000).

Numerous tools derived from a number of theoretical frameworks (e.g., graph, circuit, metapopulation, and decision theory) have been developed to address these questions, but graph theory has provided methods and tools that have readily been adopted by ecologists and conservationists to critically assess landscape-level connectivity (Urban et al. 2009, Galpern et al. 2011). Graph theory is the study of graphs or networks, which consist of nodes (e.g., habitat patches) connected by edges (e.g., dispersal between patches). Graphs generally represent simplifications of often complex systems, but the body of mathematics developed around understanding connections and flows within graphs has made this theory a powerful tool across many disciplines (Gross and Yellen 2006). Numerous conservation-related issues have been addressed by graph theory, including functional connectivity, patch importance, and importance of connections between patches (Galpern et al. 2011). An appeal of graph theory is that input data requirements can be minimal while still facilitating patch- or landscape-level inferences (Urban et al. 2009). However, graph models can also incorporate a great deal of biological realism and complexity (Schick and Lindley 2007, Kininmonth et al. 2011). Of relevance to management and conservation of populations at a landscape-scale, clear connections exist between graph theory and metapopulation theory through the graph-theoretic implementation of the metapopulation mean lifetime model (MLT; Kininmonth et al. 2010).

The MLT model was developed and used by Frank and Wissel (1998, 2002) to model metapopulation persistence in heterogeneous landscapes while incorporating variation in patch size and inter-patch distance. Drechsler (2009) formulated an analytical solution to the MLT based on network properties, which was further modified by Kininmonth et al. (2010) to incorporate a graph theory model of dispersal that could accommodate asymmetric dispersal between patches in the network and the strength of connections formed by dispersal. In short, the MLT model is a summary of 4 network properties: the ratio of dispersal range and network size, the ratio of environmental correlation range and network size, the number and size of the patches, and the geometric mean of the number and size of patches (Drechsler 2009). The distillation of these elements to a single value (MLT) is particularly appealing

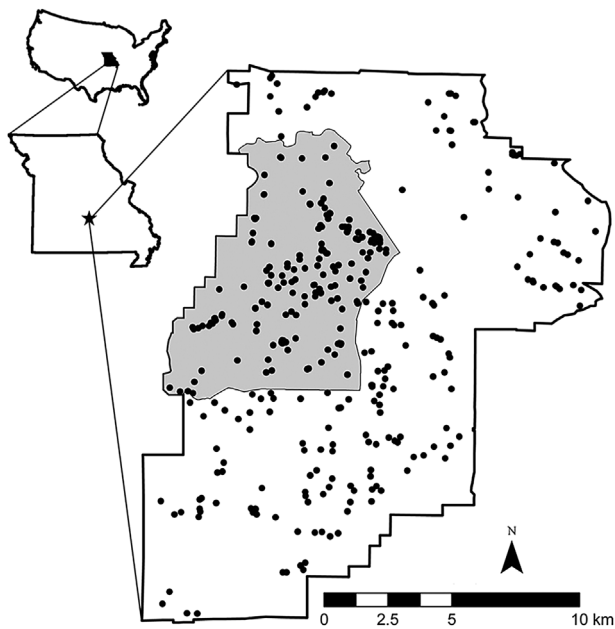
because it allows MLT to be used as an objective function for optimization problems. This formulation has been used to gain insight into the influences of network topology on metapopulation persistence (Kininmonth et al. 2010), and as tool for marine reserve design (Kininmonth et al. 2011).

Although graph theory models have been extensively used in the context of conservation of marine systems (Tremblay et al. 2008, Andrello et al. 2015, Cabral et al. 2016), application to other systems have been more limited. One system that can be particularly well-suited to applications of graph theory models are pond-breeding amphibians. When amphibian breeding ponds are viewed as discrete habitat patches (Marsh and Trenham 2001), amphibian populations can readily be modeled using graph-theoretic approaches to infer ecological processes such as population persistence (Fortuna et al. 2006), source-sink dynamics (Peterman et al. 2013), or species richness (Ribeiro et al. 2011). Graph-theoretic approaches have also been used to inform land-planning decisions related to amphibian populations (Foltête et al. 2014, Clauzel et al. 2015). As such, graph and metapopulation theory provide powerful and relevant frameworks for ecological inference and conservation of amphibians.

We build upon this body of research by modeling functional connectivity and metapopulation dynamics among amphibian breeding ponds. Specifically, we developed a framework for including species- and population-specific demographic parameters, and uncertainty in these parameters, to provide optimal management decisions. Our goal was to demonstrate how MLT can be used as an objective global measure of demographic networks and how MLT can be used to address 3 critical questions related to the conservation and management of spatially structured populations. Where are the best locations to create new habitat to maximize connectivity and persistence of the metapopulation? Which existing habitats, if restored, would provide the most benefit to the metapopulation? Which populations are most critical to the long-term persistence of the metapopulation? We predicted that use of MLT in these contexts would result in improved population resiliency relative to random or haphazard management decisions. Additionally, we used our connectivity model to assess the source-sink status of populations (Pulliam 1988) and relevant network properties.

## STUDY AREA

We conducted our study at Fort Leonard Wood (FLW), Missouri, USA (37.92°N, 92.17°W), an active military training facility encompassing 24,852 ha in the northern Ozark Highland (Fig. 1). Annually, FLW received about 110 cm of rainfall. Average temperatures during the summer exceeded 26°C, and average temperatures during the winter were below 12°C. The area has a varied topography with elevation changes between ridges and ravines ranging from 230 m to 398 m. The area was 80% forested, consisting predominantly of oak-hickory forests (*Quercus* spp. and *Carya* spp.) or short-leaf pine plantations (*Pinus echinata*). There were over 450 deliberately constructed or incidentally created water bodies (e.g., tire ruts) at FLW that ranged in



**Figure 1.** Potential breeding ponds for ringed salamanders in Fort Leonard Wood, Missouri, USA, 2012–2014. Ponds are indicated by black dots and the Focal Area is shaded gray.

size from 1 m<sup>2</sup> to 42,549 m<sup>2</sup>. Most of these ponds were small (<0.04 ha), fishless, constructed wildlife ponds; however, there were several large ponds and small lakes (>1 ha) stocked with fish (sunfish [Centrarchidae], mosquitofish [*Gambusia* spp.], and fathead minnow [*Pimephales promelas*]). We sampled 206 ponds, representative of the variation in ponds present, in a 7,140-ha area in the west-central portion of FLW (i.e., Focal Area). The Focal Area encompasses the range of pond sizes, including small ponds and stocked lakes, and dominant land cover types (i.e., deciduous and coniferous forests, open fields, and developed areas). Fourteen species of amphibians bred in FLW ponds, including 3 species of ambystomatid salamander (Semlitsch et al. 2015).

## METHODS

We focused on the ringed salamander (*Ambystoma annulatum*), a species endemic to the Ozark and Ouachita mountains of Missouri, Arkansas, and Oklahoma, USA (Petranka 1998). Breeding occurs in the fall and larvae overwinter in ponds before metamorphosing in late spring or early summer (Semlitsch et al. 2014). Previous research at FLW reported that ringed salamanders breed in fishless ponds with more permanent hydroperiods that are located within forested habitat (Peterman et al. 2014).

### Field Sampling and Estimation of Density

To estimate the density of larval ringed salamanders, we conducted repeated surveys of ponds within the Focal Area as described in Peterman et al. (2014). We sampled all Focal Area ponds using dip net sweeps and funnel traps standardized to pond surface area (Shulse et al. 2010) from February to March (2012–2014). We calculated pond area assuming all ponds were ellipses, and measured the

major axes of each pond with a rangefinder in the field. At each site, each year, we conducted 3 independent dip net surveys, and typically 3 trapping sessions (ponds surveyed = 139, 169, and 151 in 2012, 2013, and 2014, respectively), although we excluded some sites from trapping because of their location (e.g., roadbed ditch) or shallow water depth ( $n = 18, 24, \text{ and } 31$  in 2012, 2013, and 2014, respectively). Previous analyses with these data reported that detection did not vary by sampling method (Peterman et al. 2014, Anderson et al. 2015). We therefore included all sites surveyed in analyses regardless of whether we used funnel traps. We identified all captured salamander larvae (Trauth et al. 2004), counted them, and returned them to the pond. We calculated mean larval density by dividing the number of larvae captured at a pond by the sampling effort. We assumed that dip net sweeps and funnel traps sampled a comparable area of 1 m<sup>2</sup>. We then multiplied mean larval density by pond area to calculate larval abundance at each pond. We used larvae captured in this study, as did Ousterhout et al. (2015), because N-mixture models fit to our data resulted in imprecise abundance estimates with individual detection rates being poorly explained by methodological or environmental covariates (Peterman et al. 2014). We assumed that in most instances, our use of mean density was a conservative measure of the actual number of larvae present in a pond.

We resurveyed all sites where we detected larvae by dip netting ponds (20–30 Apr 2012; 25–28 Apr 2013; 16–18 May 2014) to measure the size of recent metamorphs and late stage larvae (hereafter metamorphs; Anderson et al. 2015). We searched all ponds during a single visit, and scaled the number of dipnet sweeps to pond surface area in the same manner as in the larval surveys. We measured body size of metamorphosed, or nearly metamorphosed, salamanders because it is a significant predictor of adult fitness and small metamorphs have substantially lower juvenile survival (Scott 1994, Altwegg and Reyer 2003, Earl and Whiteman 2015). We photographed up to 20 metamorphs at each pond, and approximated total length (TL) by measuring from the snout to the tip of the tail using Image J 1.45s (Rasband 2013). We used TL for analyses instead of snout-vent length (SVL) because it had fewer missing values based on image analysis (TL had 3% missing observations, SVL had 50% missing observations) and was highly correlated with SVL ( $r = 0.96$ ). Missing SVL observations were primarily due to uncertainty of the vent location. We excluded individuals with obvious tail damage from the TL measurement database.

Reproductive effort, as determined by quantifying the number of larvae present in a pond, varies considerably among ponds and from year to year. For this study we used the maximum density (larvae/m<sup>2</sup>) observed at each pond in each year, and then multiplied this density estimate by the pond area. To accommodate year-to-year variation in our model, we calculated the mean and standard deviation of larval abundance at each pond across the 3 sample years. All field sampling methods were approved by the University of Missouri Animal Care and Use Committee (permit no. 7403), and was permitted by the Missouri Department of Conservation.

## Modeling Steps

We used 5 steps in the modeling process.

1. Specify population-specific values for population size and size of metamorphs.
2. Specify the probability that a metamorph survives to adulthood to reproduce, the probability that surviving individuals will remain philopatric to their natal pond, and the mean distance that individuals will disperse.
3. Calculate the number of individuals dispersing between all populations.
4. Determine the contribution and influence of each population to the MLT.
5. Repeat steps 1–4 for the specified number of Monte Carlo (MC) iterations, generating new values for the parameters in steps 1 and 2 from their specified distributions.

Because of uncertainty in each of the parameters in steps 1 and 2, we modeled them as stochastic, and drew new values at each MC iteration. We assessed population size and size of metamorphs separately for each population at each iteration. We drew values for these parameters from a normal distribution with a mean and standard deviation determined from 3 years of field-collected data. We truncated the normal distribution for population size at 0. Survival probability of metamorphic ringed salamanders to adulthood is also unknown. However, there is evidence that size at metamorphosis can affect survival (Altwegg and Reyer 2003, Van Buskirk 2007). We therefore estimated metamorphic survival at each pond following the equation provided by Altwegg and Reyer (2003):

$$\text{logit}(\text{survival}) = -1.366 + 0.87 \times \text{TL}_i \quad (1)$$

where  $\text{TL}_i$  is the standardized total length ( $\bar{x} = 0$ ,  $\text{SD} = 1$ ) of late-stage larvae and recent metamorphs collected at pond  $i$ . The proportion of ringed salamanders that remain philopatric to their natal pond is unknown. We therefore relied on Gamble et al. (2007) to guide our estimate of a plausible distribution for this parameter, setting the mean to  $0.85 \pm 0.10$  (truncating the upper limit at 1.0). Because previous research in this system reported minimal influence of the landscape matrix on genetic connectivity of ringed salamanders (Peterman et al. 2015, 2016; Burkhart et al. 2017), we modeled dispersal and connectivity as an exponential decay of distance. We drew mean dispersal distance from a normal distribution with a mean of 1,700 m ( $\pm 500$  m SD) derived from genetic-based dispersal estimates for ringed salamanders at FLW (Peterman et al. 2015). We calculated the probability of successful dispersal from population  $i$  to population  $j$  as

$$m_{ij} = \begin{cases} \exp(-\alpha d_{ij}) & \text{if } i \neq j \\ 0 & \text{if } i = j \end{cases} \quad (2)$$

where  $d_{ij}$  is the distance between populations and  $\alpha$  controls the dispersal range, with  $1/\alpha$  being the average dispersal distance. We standardized the probabilities in  $m_{ij}$  so each row

$i$  summed to 1:

$$m'_{ij} = \frac{m_{ij}}{\sum_j} \quad (3)$$

The number of individuals dispersing from population  $i$  to each  $j$  is multinomially distributed

$$n_i \sim \text{Mult}(e_i, m'_i) \quad (4)$$

where  $e_i$  is the number of emigrants from population  $i$ :

$$e_i = \text{Abundance}_i \times \text{logit}(\text{survival}_i) \times (1 - \text{philopatric}_i) \quad (5)$$

$m'_i$  is the vector of successful dispersal probabilities from population  $i$  to every  $j$ . Matrix  $M$  is comprised of vectors of emigrants,  $n_i$ . Summing across columns,  $j$ , of matrix  $M$  gives the number of emigrants leaving population  $i$ , whereas summing across rows,  $i$ , gives the number of immigrants entering population  $j$ :

$$\text{emigrants}_i = \sum_{n=1}^j M_{ij} \quad (6)$$

$$\text{immigrants}_j = \sum_{n=1}^j M_{ij} \quad (7)$$

We then calculated the MLT of the network following equations described by Frank and Wissel (2002) and Drechsler (2009), as implemented by Kininmonth et al. (2010). First, we calculated an extinction rate,  $v_i$ , as

$$v_i = \varepsilon A_i^{-\eta} \quad (8)$$

where  $\varepsilon$  and  $\eta$  are parameters relating the local extinction rate to pond area,  $A$ , measured in hectares. Without specific knowledge of how habitat variability affects local extinction ( $\eta$ ), or how extinction may change with pond area ( $\varepsilon$ ), we followed Hale et al. (2015) and conservatively set  $\varepsilon$  and  $\eta$  to 1 and 0.5, respectively. We used the graph theory model of dispersal described by Kininmonth et al. (2010) to measure colonizability and colonization strength:

$$C_i^{\text{in}} = \frac{1}{\mu} \sum_{n=1}^i M_{ij} \quad (9)$$

$$C_i^{\text{out}} = \frac{1}{\mu} \sum_{n=1}^i M_{ij} \quad (10)$$

where  $\mu$  is the number of immigrants required for successful dispersal, defined as 2 in this analysis. Colonizability,  $C_i^{\text{in}}$ , describes the ability of a particular pond ( $i$ ) to be colonized by individuals dispersing from all other ponds ( $j$ ) on the landscape. Colonization strength,  $C_i^{\text{out}}$ , describes the ability of individuals from a particular pond ( $i$ ) to colonize all other ponds ( $j$ ) on the landscape. We then multiplied colonizability and colonization strength by the extinction rate of a pond,  $1/v_i$ :

$$u_i^{\text{out}} = \frac{C_i^{\text{out}}}{v_i} \quad (11)$$

$$u_i^{\text{in}} = \frac{C_i^{\text{in}}}{v_i} \quad (12)$$

The harmonic mean of  $u_i^{\text{in}}$  and  $u_i^{\text{out}}$  then gives the colonization-extinction ratio

$$U_i = \left( \frac{1}{2} (u_i^{\text{in}})^{-2} + \frac{1}{2} (u_i^{\text{out}})^{-2} \right)^{-1/2} \quad (13)$$

The aggregated colonization-extinction ratio of the entire network is then

$$q = \prod_{i=1}^N \left\{ \max(U_i, \sqrt{2}) \right\}^{1/N} \quad (14)$$

where  $N$  is the number of populations in the network. We then calculated the geometric mean of the local extinction rates as

$$z = \prod_{i=1}^N v_i^{1/N} \quad (15)$$

With these values, the MLT of a network can then be calculated. Because  $q > 2.5$  in all networks considered in this study, we used the approximate equation of Drechsler (2009):

$$\text{MLT} = \ln(zT) \approx N \left( \frac{1}{q} + \ln(q) - 1 \right) \quad (16)$$

We then determined the importance of population  $i$  to the network as the amount of change ( $\Delta\text{MLT}$ ) in MLT when we added population  $i$  (in the case of habitat creation and restoration) or removed population  $i$  (to assess population importance):

$$\Delta\text{MLT} = \frac{(\log_{10}(\text{MLT}_{\pm i} + 1) - \log_{10}(\text{MLT} + 1))}{\log_{10}(\text{MLT} + 1)} \quad (17)$$

In this study, we used  $\Delta\text{MLT}$  to determine 1) the best location on the landscape to create a pond and establish a new breeding population; 2) which currently unused breeding ponds, if restored, would increase MLT the most; and 3) the breeding populations that, if lost, would result in the greatest reduction in MLT. We conducted all modeling and analyses in R (version 3.3.0; R Core Team 2017). Code to implement these analyses can be found in the R package *ssmc* (<https://github.com/wpeterman/ssmc>).

### Assessment of Suitable Landscape Features for Pond Construction

For this analysis, we assumed that all 462 uniquely georeferenced ponds at FLW were constructed and that the physical landscape and soil properties at each of these ponds represented suitable conditions for future pond construction. The goal of this assessment was to identify the common characteristics of created ponds at FLW that hold water. This assessment was done without regard as to whether a pond had been used for breeding, as this would have unnecessarily reduced the number of ponds evaluated. We determined the slope, soil type, and distance from road for all ponds at FLW using a geographic information system

(ArcGIS v.10.2). We obtained soil data from the web soil survey database (<http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>; accessed 5 Dec 2014), and downloaded road, land cover (30-m resolution), and elevation data (9-m resolution) from the Missouri Spatial Data Information Service (<http://msdis.missouri.edu/>; accessed 5 Dec 2014). We calculated percent slope from the 9-m resolution elevation data. We determined the optimal soil types to be those that occurred at  $>25\%$  of ponds, and optimal slope and distance from road were values less than the 95% upper quantile of all observations. Although all observed habitat values at existing ponds could have been used to determine suitable areas for future pond construction, we found that doing so failed to discriminate much of the landscape because of the wide range of values present at existing ponds. The chosen cutoffs adequately constrained the range of values for each habitat variable. Because forested habitat surrounding ponds is critical to occupancy and abundance of *Ambystoma* species breeding at FLW (Peterman et al. 2014), we further restricted the suitable landscape to forested areas that were  $\geq 200$  m from existing ponds on the landscape. We implemented this restriction to minimize clustering of ponds on the landscape.

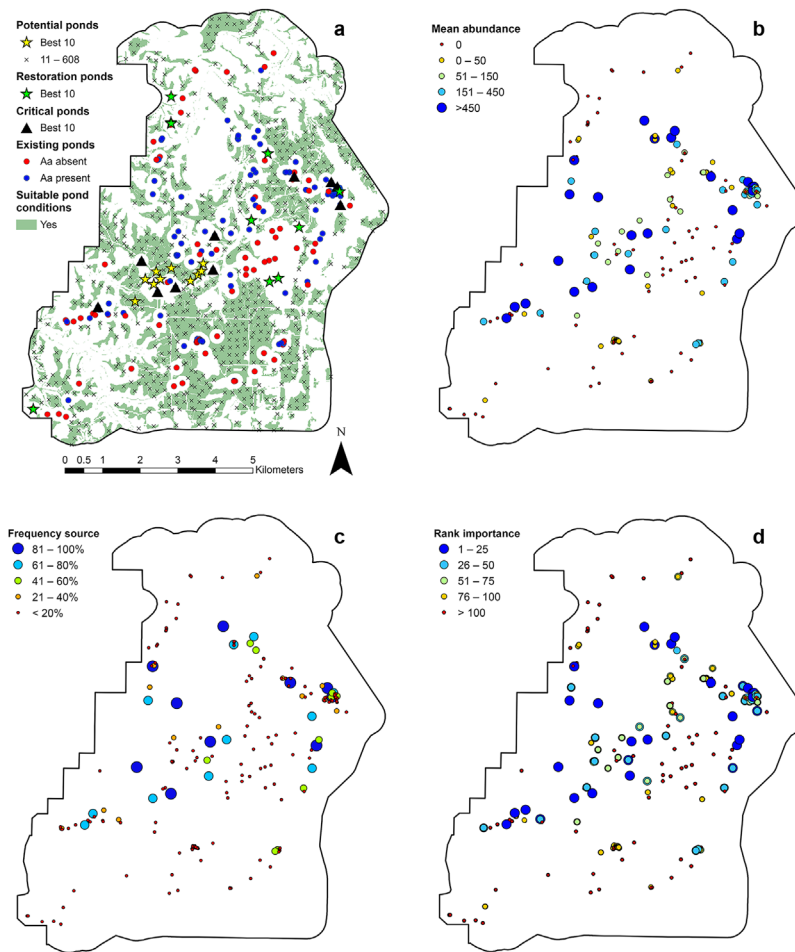
### Evaluation of Habitat

Within the region identified as suitable for pond construction, we generated 608 random points, with each being separated by at least 200 m (Fig. 2a). To assess the potential contribution that each of these random locations could provide to the population network, we iteratively added and removed each, calculating  $\Delta\text{MLT}$  for each population at each MC iteration. We assume that the area, population size, and metamorph size of potential populations were equal to the median of all occupied breeding populations during a given MC iteration (i.e., a typical population is created). We avoid using the average of these measures because of extreme positive skew. However, use of the mean in preliminary simulations did not substantively change the patterns found in the final analysis. Following 5,000 MC iterations, we calculated the average change in  $\Delta\text{MLT}$  and multiplied this by the frequency that each potential location was likely to be colonized by  $\geq 2$  individuals,  $c$ :

$$\Delta\text{MLT}_{\text{col}} = \Delta\text{MLT} \times c \quad (18)$$

We used this adjusted  $\Delta\text{MLT}_{\text{col}}$  measure to determine the rank-order importance of each potential location to the population network. A larger  $\Delta\text{MLT}_{\text{col}}$  is indicative of a site that, if created, is more likely to be colonized and to have a greater positive influence on the population network.

We followed the same analysis steps described above for determining the optimal locations to create new breeding habitats to identify existing habitats for restoration. We used  $\Delta\text{MLT}_{\text{col}}$  to identify existing, unused, pond habitats that would provide the most benefit to the population network if they were restored so that they supported a population with typical abundance and metamorph size. This analysis assumes that there is a known structural (e.g., vegetation), functional (e.g., hydroperiod), or biological (e.g., presence of



**Figure 2.** Summaries of demographic network model results for ringed salamanders within Fort Leonard Wood, Missouri, USA, 2012–2014. We present the best locations to create ponds, the best locations to restore existing ponds, the most critical ponds to the mean lifetime of the network, the presence or absence of ringed salamanders in existing ponds, and the areas deemed suitable for future potential pond creation (a). We also present the mean abundance of larval salamanders, determined through field sampling (b), the frequency that a pond functions as a source population, determined through 5,000 Monte Carlo iterations (c), and the rank importance of existing ponds to the network, determined by the amount of change in metapopulation mean lifetime (MLT) when a pond is removed from the network (d).

fish) reason that a pond is currently unused, and restoration efforts can feasibly mitigate the issue. For each of 5,000 MC iterations, we set the abundance and metamorph population size of each unused breeding pond to be equal to the median of existing breeding populations for that MC iteration. We calculated  $\Delta\text{MLT}$ ,  $\Delta\text{MLT}_{\text{col}}$ , and rank-order importance as described above.

To assess the contribution and importance of each breeding population to the metapopulation, we conducted 5,000 MC iterations, removing each population in turn during each iteration. We determined the rank-order importance by calculating the average  $\Delta\text{MLT}$  for each population across MC iterations. During this analysis, we also determined the average number of philopatric individuals, the number of immigrants into and emigrants leaving each population, and whether a population acted as a source (immigrants < emigrant) or a sink (immigrants > emigrants). Such a source-sink designation does not account for births or deaths (Pulliam 1988, Runge et al. 2006), but empirical estimates of adult survival are lacking for our study

population. Finally, we summarized the distance between functionally connected populations.

The modeling approach used in this study relies on several stochastic parameters. We used global sensitivity analyses to assess the influence and contribution of philopatry, survival to adulthood, and mean dispersal distance on MLT (Saltelli et al. 2008). Specifically, we calculated Sobol' sensitivity indices using the R package sensitivity (Baudin et al. 2016, Pujol et al. 2016). Sobol' sensitivity analyses are variance-based analyses that rely on Sobol' sequences to maximally cover parameter space (Saltelli et al. 2008). Analyses estimate first- and total-order indices. First-order indices report the variance explained by each parameter in isolation. Total-order indices report the variance explained by each parameter plus its interaction with all other parameters.

## RESULTS

We surveyed 206 ponds from 2012 to 2014, and detected ringed salamanders in 106 ponds. The average abundance of larvae in occupied ponds was estimated to be  $600 \pm 2,034$

( $\bar{x} \pm \text{SD}$ ) and the median was 81 (interquartile range = 22–320). Overall, there was a high degree of congruence between abundance (Fig. 2b), the frequency that a population functioned as a source (Fig. 2c), and the overall rank importance of a population to the network ( $\Delta\text{MLT}$  when a pond was removed; Fig. 2d). Ponds with higher abundance tended to function as sources more frequently (Pearson correlation;  $\rho = 0.84$ ,  $P < 0.001$ ) and were generally more important (lower rank) to the MLT of the network (Kendall's rank correlation;  $\tau = -0.780$ ,  $P < 0.001$ ). The most critical breeding populations are distributed along a southwest to northeast axis in the center of the Focal Area (Fig. 2a). These 10 ponds often functioned as sources (mean frequency =  $79.9\% \pm 19.4\%$ ) with emigrants dispersing to many ponds (mean connectivity =  $45.5 \pm 25.2$  ponds). Of the 106 occupied ponds, only 5 (2.4%) functioned as sources >90% of the time, whereas 54 (50.9%) functioned as sinks >90% of the time. The remaining 47 (44.3%) occupied ponds produced emigrants in excess of immigrants, on average, 44.5% ( $\pm 25.3\%$ ) of the time. Although abundance is important for populations acting as sources, and acting as a source tends to increase the importance of a population, these measures are not completely congruent. The average rank in mean abundance of the 5 source ponds was 7.2 (range = 2–13), but these same source ponds had an average rank importance to MLT of 3 (range = 1–5). Nonetheless, the rankings produced by these 2 measures at occupied ponds were significantly correlated ( $\tau = 0.82$ ,  $P < 0.001$ ). Therefore, there is generally corroboration between population abundance and rank importance, but our results highlight the importance of spatial location and functional connections to maximizing metapopulation persistence. The average length of all connections in our network was  $2,092 \text{ m} \pm 1,542$ , the average maximum connection length was  $6,592 \text{ m} \pm 1,386$ , and the average distance between all ponds was  $3,769 \text{ m} \pm 2,050$  (max. = 11,434 m). Peterman et al. (2016) determined the average distance between connected populations based on a genetic connectivity network on this same landscape was  $2,510 \text{ m} \pm 2,140$ .

Our analysis of the landscape features that corresponded with existing created ponds on the landscape determined that slopes  $\leq 17\%$ , proximity to existing roads ( $\leq 675 \text{ m}$ ), and gravelly or silt-loam soils were most essential. This combination of features within forested habitat resulted in 31% percent (2,323 ha) of the Focal Area being suitable for construction of ponds likely to hold water and be used by ringed salamanders for breeding. Of the 608 potential pond locations on the landscape that we assessed, creation of a pond at any of the best 10 locations increased MLT of the network an average of 15.4% ( $\pm 4.95\%$ ) as compared to 10,000 random combinations of 10 potential locations. These optimal locations were clustered in the center of the Focal Area and close to ponds with large existing ringed salamander populations (Fig. 2a, Fig. S1, available online in Supporting Information). In contrast, we found that the best potential ponds for restoration were more widely distributed across the Focal Area (Fig. 2a). Restoration of any of the 10 best currently unoccupied ponds increased MLT of the

network an average of 31.4% ( $\pm 5.67\%$ ) as compared to 10,000 random combinations of 10 potential restoration ponds (Figs. 2a and S2).

Global sensitivity analyses indicated that the variation in MLT explained by the proportion of the population that remains philopatric was 0.40 (95% CI = 0.36–0.44) and the proportion explained by the probability of surviving to adulthood was 0.58 (95% CI = 0.56–0.61), as determined by the first-order Sobol' indices (Table 1, Fig. 3). Surprisingly, mean dispersal distance had low explanatory power (0.02, 95% CI =  $-0.03$ – $0.08$ ; Table 1, Fig. 3). The total-order indices did not differ substantially from the first-order indices and their sum only marginally exceed 1.0 (1.07), indicating that little of the variance in our stochastic model is attributable to interactions between model parameters (Table 1).

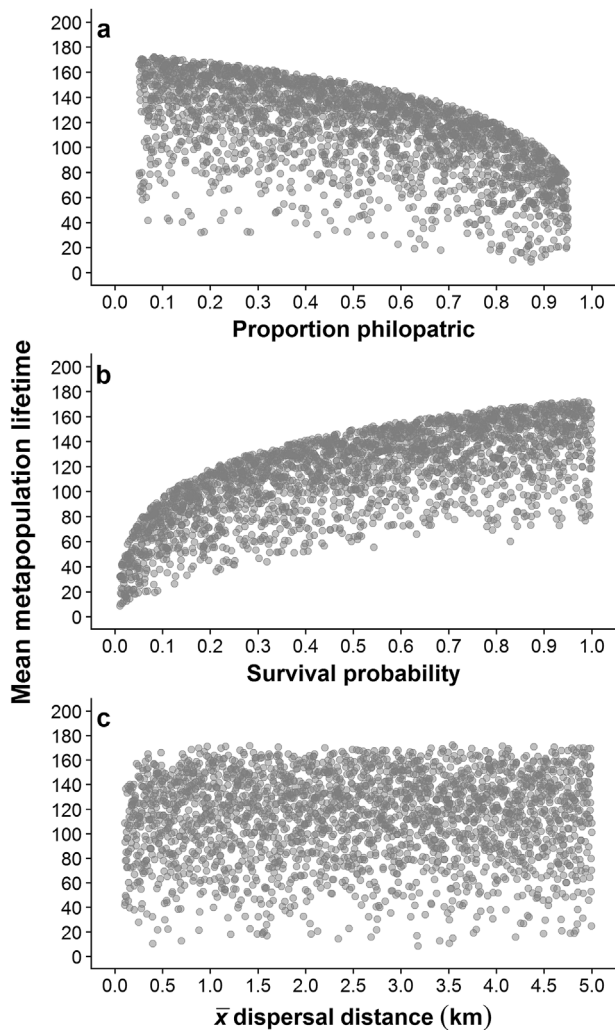
We also assessed the rank correlation between pond-level model outputs from occupied ponds. The number of emigrants produced by a pond ( $\tau = -0.79$ ), average number of ponds reached by emigrants dispersing from a pond (i.e., outdegree;  $\tau = -0.79$ ), and the frequency that a pond functioned as a source ( $\tau = -0.78$ ) were all highly correlated with the importance of a pond to the network. In other words, ponds that readily produce many emigrants in excess of the number of immigrants and that are highly connected to other ponds through emigration have the most influence on the MLT of the network. Directly affecting the number of emigrants available to disperse is the probability of surviving to adulthood. Lower survival rates lead to fewer dispersing salamanders, which reduces connectivity within the network and lowers MLT (Fig. 3).

## DISCUSSION

We demonstrated how the metapopulation mean lifetime model can be used as a network restoration and conservation planning tool. We found that MLT, as a global measure of metapopulation persistence, effectively allowed us to optimize locations for habitat creation, restoration, and preservation. Management and conservation of spatial

**Table 1.** Summary table of variance explained and 95% confidence intervals for Sobol' sensitivity analysis, a global sensitivity analysis conducted to assess the effect and contribution of philopatry, survival probability, and dispersal distance on the mean metapopulation lifetime of the network for ringed salamanders within Fort Leonard Wood, Missouri, USA, 2012–2014. First-order indices report the variance explained by each parameter in isolation, whereas total-order indices report the variance explained by each parameter plus its interaction with all other parameters.

Sobol' index	Parameter	Variance explained	95% CI
First order	Proportion philopatric	0.40	0.36–0.44
	Survival probability	0.58	0.56–0.61
	Dispersal distance	0.02	$-0.03$ – $0.08$
Total order	Proportion philopatric	0.42	0.39–0.45
	Survival probability	0.59	0.55–0.63
	Dispersal distance	0.05	0.05–0.06



**Figure 3.** Influence of philopatry (a), survival probability (b), and mean dispersal distance (c) on the mean lifetime of the network, as determined from sensitivity analyses for ringed salamanders within Fort Leonard Wood, Missouri, USA, 2012–2014. We allowed all 3 parameters to vary during the sensitivity analysis, but we fixed abundance and average metamorph size at the mean values observed during field sampling.

populations presents many challenges and trade-offs (Drechsler and Wissel 1998). With minimal resources or knowledge of the system, conservationists, and resource managers may default to preserving the largest populations, or focus restoration efforts adjacent to large existing populations. In the absence of a specific management plan for pond-breeding amphibians at FLW, habitat management, restoration, or creation efforts have largely been focused on areas adjacent to known existing populations (K.L. Lohraff, FLW, personal communication). Our analyses of ringed salamander breeding ponds at FLW demonstrate that this can be an effective, although potentially sub-optimal strategy. These large populations provide functional connectivity to the network, resilience to loss of habitat, and can ensure that newly created or restored habitat is quickly colonized. However, a closer assessment of mean abundance, source status, and importance to the metapopulation demonstrate that these are not synonymous

measures. The populations that are most important to the metapopulation generally have higher abundances and act as sources more often. However, spatial location and functional connectivity are not integrated into estimates of abundance or source-sink status as they are in the estimation of MLT, highlighting the importance of understanding spatial dynamics in conservation and management decisions.

Estimates of functional connectivity in our model are dependent on specification of key life-history parameters. Despite decades of research on amphibian behavior and ecology, precise estimates of life-history parameters remain elusive. We relied heavily on the primary literature to inform these parameters, but lack of empirical data for ringed salamanders specifically, and wide variation in reported estimates for amphibians generally, makes precise specification tenuous. Although it would be ideal to develop a spatially explicit population model to more directly understand how populations are functionally connected (Dunning et al. 1995), such models are often data intensive, can be highly sensitive to parameter misspecification, and are often applicable to a limited number of species (Conroy et al. 1995, Turner et al. 1995). To accommodate uncertainty or variation in these parameter estimates, we used a Monte Carlo simulation approach. This necessarily adds complexity and computation time to analyses but allows inferences to be made from thousands of random plausible parameter combinations. Doing so provided a realistic representation of the potential variation within the network, giving confidence that our model results are resilient to annual variation or imprecision in model parameter specification.

Habitat creation and restoration are challenging endeavors. The task of creating ponds to match the form and function of natural ponds can be particularly difficult (Zedler 1996). Size, depth, basin slope, and hydroperiod are among the numerous factors that must be considered when constructing ponds, especially when a primary goal of pond construction is amphibian reproduction (Calhoun et al. 2014). Perhaps one of the most critical aspects of pond construction is location and landscape context because colonization is dependent upon animals dispersing from existing ponds on the landscape (Shulse et al. 2010). Therefore, created ponds must be situated near existing ponds, within the dispersal distance of target amphibian species, and within habitat conducive for amphibian dispersal. Further, the existing pond must support amphibian breeding populations that produce enough dispersing individuals to provide the greatest likelihood that randomly dispersing juveniles successfully reach newly created habitat. As we have demonstrated in this study, MLT can be a powerful tool for critically assessing potential pond locations, providing a degree of confidence that a new pond can realistically be colonized and an assessment of the potential contribution to the metapopulation network. Although we assumed uniform resistance of the landscape to dispersal (Peterman et al. 2015, 2016), connectivity could be modeled as a function of landscape resistance (Compton et al. 2007). Rather than determining probability of successful dispersal from Euclidean distances, electrical



resistance (McRae 2006), kernel resistance distance (Compton et al. 2007), or least cost path distance could be used as long as the calculated resistance distances can be logically linked to a species' dispersal ability. Such measures would likely increase computational demands and time needed to complete a simulation.

Our finding that newly constructed ponds should optimally be clustered and located proximally to critical existing ponds (i.e., source ponds with many connections to other ponds) is supported by simulation studies of Kininmonth et al. (2011) who reported that new habitat patches should be situated next to each other and adjacent to highly connected critical hubs in the network. Although this clustering of ponds on the landscape appears to be optimal for maximizing the lifetime of the metapopulation, it is unclear how or if temporal and spatial population dynamics would affect, or be affected by, such decisions. Both Ousterhout et al. (2015) and Peterman et al. (2014) reported spatial autocorrelation in ringed salamander abundance at 500–1,000-m scales. There is potential that ponds created near existing sites could become spatially or temporally synchronous, which may alter the role or contribution of such ponds to the metapopulation (Fox et al. 2017).

It is not always feasible or practical to create new habitat, and we found that restoration of existing ponds can result in up to twice the improvement to network MLT as the creation of new ponds. The reasons for ringed salamanders failing to breed in nearly half of the wetlands in the Focal Area are varied, and are unknown in many cases. The presence of fish and short or ephemeral hydroperiods are 2 of the primary reasons that ringed salamanders fail to breed or successfully recruit from a pond (Peterman et al. 2014, Anderson et al. 2015, Semlitsch et al. 2015), both of which can be modified through direct management (Walston and Mullin 2007, Calhoun et al. 2014). It is important, however, to carefully assess all relevant structural habitat features to ensure that restoration efforts provide more than partial remediation. The presence and amount of forest cover, for instance, is also an important consideration (Peterman et al. 2014, Anderson et al. 2015). Forest cover and structure are not practical to restore directly but are important considerations when further refining the suitability of existing ponds for restoration.

Our pairing of the MLT model with Monte Carlo simulation provides a framework for including variation or uncertainty in population or demographic parameters. It is important to note that field validation of our MLT model has not yet occurred. Experimentally, the model could be validated by prioritizing the creation or restoration of a predetermined number of ponds based upon MLT results with an equal number of ponds being created or restored based on random selection. Metapopulation mean lifetime itself is a measure of the persistence of the metapopulation. Success or failure of the metapopulation is likely an untenable metric of assessment, but the rate that control and experimental ponds are colonized, as well as the number of colonizers, would provide a heuristic approach that could be compared to MLT model predictions such as in-degree

(i.e., the number of populations contributing immigrants) and the number of immigrants.

Graph theory has seen extensive development and growing applications in ecology and conservation (Urban et al. 2009, Beier et al. 2011, Galpern et al. 2011, Rayfield et al. 2011), including habitat creation, restoration, and reserve design (Kininmonth et al. 2011, Clauzel et al. 2015, Mimet et al. 2016). Only recently has a more formal methodological framework for using graph theory for land-use planning been proposed (Foltête et al. 2014). Our approach is generally in line with this framework, although we did not explicitly reference Foltête et al. (2014) during the development or implementation of this study. The appeal of graph-theoretic approaches for conservation planning is often the minimal data requirements and computational efficiency. However, it is possible to incorporate relevant biological and ecological information into graph models to represent the importance of habitat patches or populations, and the strength and direction of connections between patches, more realistically (Tremblay et al. 2008, Kininmonth et al. 2010). By including taxon-specific estimates of dispersal distance, emigration probability, and mortality, we identified key demographic parameters that affected source-sink designation. Connectivity through dispersal is clearly important for maintenance of metapopulation dynamics and persistence (Hanski 1998), but dispersal distance had little influence on MLT in our network. In contrast, the proportion of the population that dispersed and the probability of surviving to adulthood had a much greater effect on MLT. These are critical insights into the spatially structured metapopulation of ringed salamanders at FLW that would not be possible if we had used a simpler graph-theoretic approach.

## MANAGEMENT IMPLICATIONS

Our use of the metapopulation mean lifetime model and Monte Carlo simulation provides a relevant and powerful framework to modeling functional demographic connectivity for making robust spatial management and conservation decisions related to habitat creation, restoration, and preservation. In all scenarios, decisions that increase MLT are likely to have the greatest benefit to ringed salamanders, with restoration of existing pond habitat potentially having more benefit than creation of new ponds. A clear understanding of source-sink dynamics and functional connectivity provides a solid foundation upon which to make conservation and management decisions, and our study highlights how limited or uncertain life-history and population data can be successfully leveraged to gain insight into these processes. Although we used ringed salamanders as an example application of this approach to management and conservation of pond-breeding amphibians, the approach is generalizable to any system with discrete habitat patches.

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## DATA ACCESSIBILITY

Code and functions to conduct the analyses in this paper are available in an R package called *ssmc* (Source-Sink Monte Carlo; Peterman 2017) that is available on GitHub (<https://github.com/wpeterman/ssmc>). This study used version 0.1.3, available at <https://doi.org/10.5281/zenodo.596859> (Peterman 2017).

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