

The importance of local and landscape-scale processes to the occupancy of wetlands by pond-breeding amphibians

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Abstract Variation in the distribution and abundance of species across landscapes has traditionally been attributed to processes operating at fine spatial scales (i.e., environmental conditions at the scale of the sampling unit), but processes that operate across larger spatial scales such as seasonal migration or dispersal are also important. To determine the relative importance of these processes, we evaluated hypothesized relationships between the probability of occupancy in wetlands by two amphibians [wood frogs (*Lithobates sylvaticus*) and boreal chorus frogs (*Pseudacris maculata*)] and attributes of the landscape measured at three spatial scales in Rocky Mountain National Park, Colorado. We used cost-based buffers and least-cost distances to derive estimates of landscape attributes that may affect occupancy patterns from the broader spatial scales. The most highly ranked models provide strong support for a positive relationship between occupancy by breeding wood frogs and the amount of streamside habitat adjacent to a wetland. The model selection results for boreal chorus frogs are highly uncertain, though several of the most highly ranked models indicate a positive association between occupancy and the number of neighboring, occupied wetlands. We found little evidence that occupancy of either species was correlated with local-

scale attributes measured at the scale of individual wetlands, suggesting that processes operating at broader scales may be more important in influencing occupancy patterns in amphibian populations.

Keywords Functional connectivity · *Lithobates sylvaticus* · Occupancy model · *Pseudacris maculata* · Rocky Mountain National Park · Spatial distribution

Introduction

Spatial variation in the distribution (i.e., occupancy of sampling units) of populations of plants and animals is often a consequence of processes that operate at multiple spatial scales (Ricklefs 1987; Jacquemyn et al. 2002). At the scale of the sampling unit, occupancy is influenced by local processes associated with attributes such as habitat quality, productivity and levels of competition and predation, and ecologists have traditionally focused their research at this scale (Dunning et al. 1992; Johnson et al. 2002; Van Buskirk 2005). However, at broader spatial scales, processes such as migration (movement of individuals among patches of resources) and dispersal (movement of individuals between local populations) also affect patterns of occupancy (Dunning et al. 1992; Sjögrén Gulve 1994; Boscolo and Metzger 2011; Dullinger et al. 2011).

The degree to which the landscape resists or facilitates the movement of individuals is referred to as landscape connectivity (Taylor et al. 1993). Two components of landscape connectivity have been identified (O'Brien et al. 2006). Structural connectivity refers to the spatial arrangement of habitat patches or of local populations (e.g., the number of patches of habitat, the size of the patches, and the proximity of patches to one another). Functional

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connectivity refers to the response of organisms to the spatial arrangement of patches or local populations. Two populations near one another (connected structurally) will only be connected functionally if individuals are motivated and able to move across the landscape that separates them. Because structural measurements are easily derived, analyses of species' spatial distributions often only consider the role of structural connectivity (Taylor et al. 2006; Ziegler et al. 2011). In contrast, accounting for functional connectivity requires information on the decisions that guide individuals' movements and the effects of landscape attributes on those movements. Fortunately, this information is available for many species (Rosenberg et al. 1998; Rizkalla and Swihart 2007; Eggers et al. 2010), and covariates that account for functional connectivity are now more frequently included in analyses of occupancy data (Joly et al. 2001; O'Brien et al. 2006; Zeigler et al. 2011).

Because their different life stages (embryo, larvae, juvenile and adult) use resources at various spatial scales, populations of pond-breeding amphibians are valuable for evaluating the influence of local and broad-scale (e.g., landscape connectivity) processes on occupancy patterns. The embryonic and larval life stages of most amphibian species are exclusively aquatic, and consequently, conditions within a wetland must facilitate the survival and development of embryos to metamorphosis for a wetland to be consistently occupied (Werner et al. 2009). The area used by juveniles and adults, however, often extends well beyond the boundaries of the wetlands in which they breed (Rittenhouse and Semlitsch 2007a), and individuals may spend much of the year in terrestrial environments, moving across the landscape to access seasonal resources (e.g., refugia from drying, overwintering sites, areas with a sufficient prey base; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). If seasonal resources are not accessible, a wetland may not be occupied despite having suitable local conditions for breeding and recruitment (Johnson et al. 2002). Finally, wetland occupancy is also affected by local colonization and extinction dynamics (Sjögren Gulve 1994). Wetlands that are functionally connected to other occupied wetlands may have higher occupancy probabilities, because dispersers are more likely to find them (Sjögren Gulve 1994; Knapp et al. 2003). Successful dispersers may colonize previously unoccupied wetlands, rescue local populations from extinction, or ameliorate the effects of inbreeding depression (Smith and Green 2006; Werner et al. 2009).

Many studies have explored the relationships between local- and landscape-scale covariates on occupancy patterns in amphibians (Knapp et al. 2003; Mazerolle et al. 2005; Van Buskirk 2005; Cunningham et al. 2007). More recently, these types of studies have included covariates that measure the functional connectivity of the landscape

(e.g., resistance surfaces, least cost paths, and cost-based buffers; Ray et al. 2002; Zanini et al. 2008; Janin et al. 2009). The results are highly variable with studies finding strong support for many covariates measured at several spatial scales (Mazerolle et al. 2005; Van Buskirk 2005). Consequently, generalizations about the covariates or processes that most strongly influence patterns of occupancy in amphibian populations are not apparent (Zanini et al. 2009), and acquiring reliable information for management and conservation strategies may only be possible through focused studies on local populations of interest.

Historic observations of amphibians in the Kawuneeche Valley (KV) of Rocky Mountain National Park (RMNP), Colorado, include four anurans [boreal toad (*Anaxyrus boreas boreas*), boreal chorus frog (*Pseudacris maculata*; hereafter chorus frog) northern leopard frog (*Lithobates pipiens*), wood frog (*Lithobates sylvaticus*)] and a caudate [tiger salamander (*Ambystoma tigrinum*)]. The KV is the only location in RMNP where all of these species have been observed (Corn et al. 1997), but surveys over the last 30 years in RMNP indicate that the boreal toad and northern leopard frog have either declined dramatically or been extirpated (Corn et al. 1997; Muths et al. 2003). Much less is known about the spatial distributions of the other species.

Operation of a water diversion ditch and the loss of beaver have altered hydrologic processes in the KV and other montane valleys in the park (Peinetti et al. 2002; Westbrook et al. 2006). With respect to amphibian populations, the consequences of these alterations include a reduction in hydroperiod for many wetlands, a decrease in the spatial extent of wetlands (Westbrook et al. 2006), and a likely decline in landscape connectivity. This study was initiated to improve our understanding of the environmental factors that influence wetland occupancy for amphibians in the KV. Specifically, our objective was to evaluate hypothesized relationships between occupancy of wetlands by breeding chorus frogs, wood frogs, and tiger salamanders and environmental covariates. We measured covariates at three spatial scales and used methods that consider both structural and functional connectivity to derive estimates of covariates. Due to a small number of detections, we only include summary statistics for tiger salamanders.

Methods

Study area

The study area is the KV in Rocky Mountain National Park, Colorado, and includes the adjacent mountainsides up to 3048 m elevation (total area = 7587 ha; Fig. 1). The majority of the study area is upland, and the dominant land

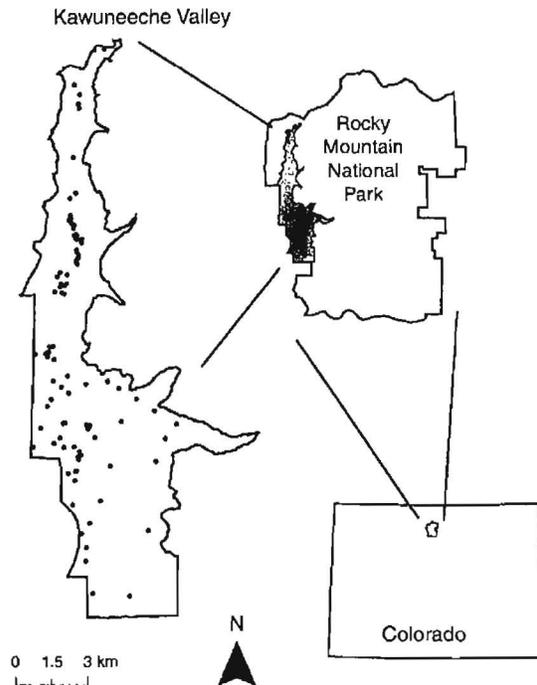


Fig. 1 Map of the study area, the Kawuneeche Valley, in Rocky Mountain National Park, Colorado. The black circles represent sampled wetlands ($n = 95$)

cover classes are lodgepole pine (*Pinus contorta*) forest (57 % of the study area) and mixed coniferous (*Abies lasiocarpa*, *Picea engelmannii*) forest (34 %) (Salas et al. 2005). The valley bottom is bisected by the Colorado River and is composed primarily of riparian areas (5 %) and wetlands with herbaceous vegetation (e.g., *Carex* spp., forbs and various grasses; 4 %) (Salas et al. 2005).

Amphibian surveys

We used aerial photographs and field reconnaissance to identify 383 wetlands in the study area. We ordered them from north to south and selected a sample using a systematic sampling design with a random start. Identification of wetlands using aerial photography is uncertain (Baker et al. 2006), and some wetlands contained no standing water on the first sampling occasion. These wetlands were removed from the sample, which resulted in a final sample of 95 wetlands. In ArcGIS 9.2 (ESRI 1999–2006), we used aerial photography of the study area and field notes to map each wetland and calculate its surface area.

We conducted three surveys at each wetland. We started surveys 6 days after the first detection of a wood frog egg mass and finished all surveys before observing metamorphosed

individuals of either species. The number of days between surveys at a wetland ranged from 1 to 22. During each survey, two to five field workers walked the perimeter of the wetland and as far out as 10 m from the perimeter in search of amphibians of all life stages. We also searched accessible shallows (depth of water less than 60 cm) for larvae with aquarium nets (10 × 15 cm opening). For each survey, we recorded the life stages of each species that was detected.

Occupancy model

We used the single-season occupancy model (MacKenzie et al. 2002, 2006) to test hypothesized relationships between occupancy and environmental covariates. The model includes two parameters: p_{ij} , the probability the species is detected at site i on survey j given that it is present at the site, and ψ_i , the probability the species occupies site i . Incorporation of covariates in occupancy models allows hypothesized relationships between ψ_i and site characteristics to be evaluated, as well as suspected relationships between p_{ij} and characteristics of sites and surveys.

We addressed assumptions of the occupancy model in both the design and analysis phases of the project. First, the models assume the occupancy status of a site does not change within a sampling season (MacKenzie et al. 2006). Movements of adult or juvenile frogs into or out of a wetland between surveys could violate this assumption. Therefore, we counted only detections of egg masses and tadpoles in the analyses, life stages that were confined to wetlands during the sampling period. The occupancy model also assumes that the detection of a species during a survey is independent of detections during other surveys (MacKenzie et al. 2006). We suspected that detection of a species at a wetland would make the detection probability of the species higher in subsequent surveys, because field workers would remember where to look. To address this issue, we evaluated a model in which detection probability on surveys after initial detection were different from detection probability on or prior to the survey of original detection. Finally, the occupancy models assume that detection and occupancy are independent across sites (MacKenzie et al. 2006). The most likely cause of a violation of this assumption in this study is spatial dependency in occupancy status induced by spatial autocorrelation in environmental attributes that make a wetland suitable or unsuitable to a species or by movement between neighboring wetlands. In our analyses, we evaluated models that represented these processes.

Hypotheses for detection probability

Prior to model building, we developed hypotheses for temporal and spatial variation in detection probability. We

identified three covariates likely to cause variation in detection probability across surveys: the number of workers during a survey (NUMBWORK), the day of the survey (SAMPDAY), and the length of the survey (SAMPTIME). In all mathematical models, we related covariates to detection probability using the logit link function (MacKenzie et al. 2006). We hypothesized two functional forms for the relationship between NUMBWORK and detection probability; we hypothesized that detection probability would increase linearly as NUMBWORK increased or detection probability would increase with increases in NUMBWORK to a threshold. We used a pseudo-threshold equation to represent the threshold relationship, and all models with this relationship were of the following form:

$$\log \text{it}(\theta) = \beta_0 + \beta_1 \log_e(x_1 + 0.005),$$

where θ represents the parameter of interest (detection probability or occupancy probability) and x_1 represents the covariate of interest. We added 0.005 to covariate values to eliminate values of 0. We denoted these models as $p(\text{NUMBWORK_LIN})$ and $p(\text{NUMBWORK_THRESH})$ and use this format (covariate name followed by the functional form of the relationship) to label model structures.

SAMPDAY represents the day on which a survey occurred (the first day of surveys was identified as day 1). We hypothesized a linear and quadratic relationship between detection probability and SAMPDAY. We expected detection probability to be highest early in the sampling season when egg masses of both species are present. The linear relationship represented the hypothesis that detection probability would be highest for surveys early in a sampling season and decline linearly for subsequent surveys. The quadratic relationship represented the hypothesis that detection probability would be lowest during the middle of each sampling season and higher on surveys that were early and late in each sampling season. Toward the middle of each sampling season, egg masses were less abundant or absent and tadpoles were small. Therefore, we expected detection probability to be lower. All quadratic relationships in this analysis were of the following form:

$$\log \text{it}(\theta) = \beta_0 + \beta_1(x_1) + \beta_2(x_1^2).$$

Finally, we hypothesized that the amount of time workers surveyed a pond (SAMPTIME) would affect detection probability and modeled this relationship using linear and threshold functions. We expected detection probability to be higher for surveys with relatively large values of SAMPTIME and that detection probability may reach an asymptote at the highest values of SAMPTIME.

In addition to evaluating the effects of covariates on detection probability, we evaluated the hypothesis that detection probability was constant across sampling

occasions ($p[.]$). As noted above, we also evaluated the hypothesis that detection probability on surveys after initial detection was different from detection probability prior to initial detection ($p[\text{INITDET}]$).

Hypotheses for occupancy probability

We explored relationships between occupancy probability and covariates at three spatial scales: local (attributes of the wetland), intermediate (attributes of the landscape at the scale of migration; on average, 230 m from a wetland for wood frogs and 150 m for chorus frogs) and broad (attributes of the landscape at the scale of dispersal; on average, 570 m from a wetland for wood frogs and 400 m for chorus frogs). We define migration as seasonal movements by adults and juveniles between their natal wetland and areas of the landscape with seasonal resources (Semlitsch 2008). We define dispersal as movement that results in an individual permanently leaving its natal wetland and becoming a member of another local population (Semlitsch 2008). Dispersal tends to occur over a larger area than migration.

Local scale

At individual wetlands, we measured three variables: hydroperiod (HYDRO), percent of the wetland surface area with emergent vegetation (EMERVEG), and the surface area of the wetland (AREA). We used field measurements of water depth and annual observations of hydroperiod from previous years of fieldwork in the study area to assign each wetland to one of four categories: 1 (wetlands have the shortest hydroperiod and dry annually), 2 (wetlands have an intermediate hydroperiod and dry frequently), 3 (wetlands have a long hydroperiod and dry rarely), or 4 (wetlands have the longest hydroperiod and never dry). In Colorado, wood frogs use small, ephemeral wetlands for breeding (Corn et al. 1997) and are associated with wetlands of intermediate or short hydroperiod across their geographic range (Egan and Paton 2004; Cunningham et al. 2007). Chorus frogs use wetlands of temporary and permanent hydroperiod for breeding (Werner et al. 2009), and in the KV, they oviposit at approximately the same time as wood frogs but metamorphose faster (approximately 50 days; Matthews and Pettus 1966). Therefore, we expected chorus frogs to occupy wetlands across a broader range of hydroperiods.

We proposed several a priori hypotheses to explore the relationship between hydroperiod and occupancy in both species: (1) Occupancy will be equal across wetlands of all hydroperiod categories (null model, denoted as $\psi[.]$), (2) Occupancy will vary between wetlands of different hydroperiod category ($\psi[\text{HYDRO } 1, 2, 3, 4]$), (3) Occupancy in wetlands of category 2 and 3 will be equal and

higher than the probability of occupancy in wetlands of category 1 and 4 ($\psi[\text{HYDRO } 1, 2 = 3, 4]$), and (4) Occupancy in wetlands of categories 1, 2 and 3 will be equal and higher than the probability of occupancy in wetlands of category 4, ($\psi[\text{HYDRO } 1 = 2 = 3, 4]$).

We expected the amount of emergent vegetation in wetlands would be important for wood and chorus frog occupancy, because both species attach egg masses to emergent vegetation and it provides cover for tadpoles (Egan and Paton 2004; Hartel et al. 2009). During each survey, we estimated the percent of each wetland's surface with emergent vegetation using the following categories: 0–25, 26–50, 51–75, and 76–100 %. For model building, we used the estimate most frequently assigned to each wetland and evaluated the following hypotheses regarding the relationship between cover from emergent vegetation (EMERGVEG) and occupancy: (1) Occupancy will vary between wetlands in each emergent vegetation category ($\psi[\text{EMERGVEG } 1, 2, 3, 4]$), (2) Occupancy in wetlands with greater than 25 % emergent vegetation will be higher than in wetlands with lower percentages of emergent vegetation ($\psi[\text{EMERGVEG } 1, 2 = 3 = 4]$), (3) Occupancy in wetlands with greater than 50 % emergent vegetation will be higher than in wetlands with lower percentages of emergent vegetation ($\psi[\text{EMERGVEG } 1 = 2, 3 = 4]$), and (4) Occupancy will be greater in wetlands with intermediate percentages of emergent vegetation (i.e., a quadratic effect; Hartel et al. 2009) ($\psi[\text{EMERGVEG } 1, 2 = 3, 4]$).

Finally, we expected larger wetlands to have higher occupancy probabilities, because they can support larger populations that are less affected by demographic stochasticity and local extinction events (Goodman 1987). In addition, colonization rates may be higher because emigrants may be more likely to find larger wetlands. We hypothesized a linear and threshold relationship between occupancy probability and wetland surface area.

Intermediate scale

We used data from this scale to evaluate the hypothesis that sufficient amounts of seasonal habitat types must be accessible from a wetland for it to be consistently occupied by breeding wood and chorus frogs. Studies of wood frogs suggest a general pattern of seasonal migration. After the breeding season, or upon metamorphosis for juveniles, frogs migrate to moist forested areas, wetlands, stream edges and ravines (Vasconcelos and Calhoun 2004; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007b). These landscape features facilitate hydroregulation and may support higher densities of prey (Rittenhouse and Semlitsch 2007b). As winter approaches, wood frogs migrate to areas with unsaturated soils relatively near breeding wetlands

(Regosin et al. 2003, 2005). If sufficient amounts of seasonal habitat types are not accessible, the wetland may have a low probability of occupancy. Relative to wood frogs, information on migratory behavior in chorus frogs is limited. Spencer (1964) reported that the majority of adults and juveniles from a high-elevation population in northern Colorado remained near their natal wetland or migrated only a short distance (≤ 300 m) to adjacent wet meadows.

To evaluate relationships between occupancy and the amount of seasonal habitat adjacent to the wetland, we: (1) developed a cost surface (Table 1; for details on our methods, see S1 in the Electronic Supplementary Material, ESM), (2) delineated a cost-based buffer (Ray et al. 2002; Zanini et al. 2008) around each wetland, (3) estimated the amount of seasonal habitat within each buffer and (4) used these estimates as covariates in the occupancy models. Most previous studies of occupancy relationships in amphibians have used circular buffers around wetlands with the implicit assumption that movement from wetlands is equal in all directions (Fig. 2; Joly et al. 2001; Fortin and Dale 2005; Zanini et al. 2008). However, many species of amphibian avoid moving through particular land cover types (deMaynadier and Hunter 1999), and the cost of movement, in terms of body condition and survival, varies among land cover types (Rothermel and Semlitsch 2002; Sztatecsny and Schabetsberger 2005; Rittenhouse et al. 2008). We used cost-based buffers (see S2 in the ESM), because they account for variable costs of movement through different land cover types. The result is a buffer that extends farther from the wetland when the intervening landscape is less resistant to movement (Fig. 2). The measurement unit, cost meters, is the product of the

Table 1 Weighted-average costs of movement for wood frogs, *Lithobates sylvaticus*, and boreal chorus frogs, *Pseudacris maculata*, adults and juveniles (in parentheses) through 7 of the 26 land cover classes in the study area. These land cover classes were selected to show a range of costs (see the ESM, for the full list of land cover classes with movement costs). Classes 22 and 23 are the most common land cover classes and comprise over 80 % of the study area

Land cover class	Brief class description	Cost	
		Wood frog	Chorus frog
5	Herbaceous wetland	3 (6)	3 (5)
13	Shrub upland	1 (2)	1 (1)
22	Sub-alpine mixed conifer	4 (8)	6 (8)
23	Lodgepole pine	4 (9)	6 (9)
52	Lakes and reservoirs	Barrier	Barrier
501	Small streams	4 (6)	4 (6)
502	Rivers and large streams	8 (14)	10 (14)

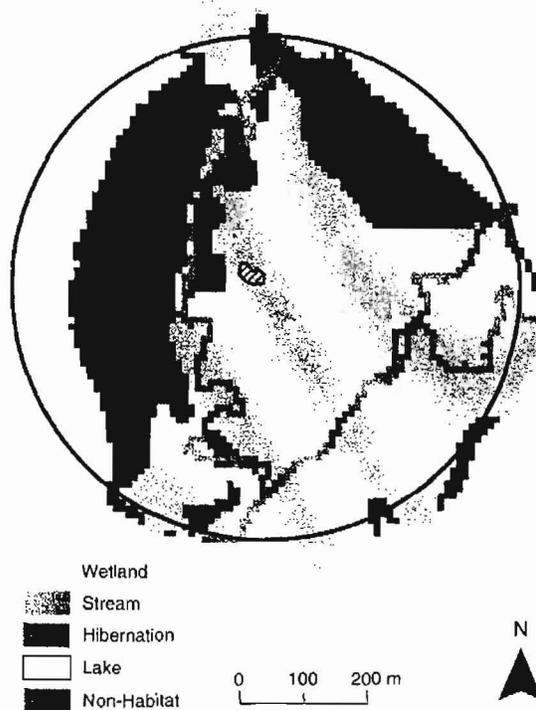


Fig. 2 Circular and cost-based buffers for estimating the amount of seasonal habitat types adjacent to breeding wetlands. The *small, hatched area with a black outline in the center of the figure* is a wetland. The *black circle* represents a circular buffer around the wetland, and the *shaded area* delineates a cost-based buffer. Within the buffer, cells of different color represent different habitat types or areas of non-habitat. Cells with no color within the buffer are permanent lakes and, because they likely contained fish, were considered complete barriers to wood and chorus frogs

Euclidean distance of a path through a landscape and the relative cost of movement through each land cover type along the path. For example, traveling 3 m through a land cover type with a relative cost of movement of 3 would equate to 9 cost meters. Measures of the amount of adjacent seasonal habitat based on cost-based buffers provide a better explanation of the spatial variation in occupancy in amphibians (Ray et al. 2002; Zanini et al. 2008) and other species [e.g., wood crickets (*Nemobius sylvestris* Bosc.); Brouwers et al. 2010].

Within each buffer, we derived estimates of the following covariates for wood frogs: (1) the area of wetland vegetation within 400, 600 and 1000 cost meters of the breeding wetland (WETVEG400, WETVEG600, and WETVEG1000), (2) the length of stream within 400, 600, and 1000 cost meters of the breeding wetland (STREAM400, STREAM600, and STREAM1000), and (3) the amount of upland within 400, 600, and 1000 cost

meters of the breeding wetland (UPLAND400, UPLAND600, and UPLAND1000). We used cost-based buffers of three sizes to account for uncertainty in the scale of seasonal migration. For wood frogs, 400, 600 and 1000 cost meters were equivalent to approximately 130, 210 and 350 meters in straight-line distance. We estimated the same covariates for chorus frogs but, because of their body size and evidence that they travel shorter distances from wetlands during seasonal migrations (Rittenhouse and Semlitsch 2007a), used smaller spatial scales (200, 400 and 800 cost meters). For chorus frogs, 200, 400 and 800 cost meters were equivalent to approximately 60, 110 and 270 meters in straight-line distance. The amount of wetland vegetation and the length of stream were chosen because these landscape elements were most likely to provide the moist, cool conditions frogs require for survival during the summer and fall. The amount of upland was estimated, because it represented potential overwinter habitat for both species (Spencer 1964; Regosin et al. 2003, 2005). For each covariate, we hypothesized a positive, linear relationship with occupancy. We also hypothesized that occupancy would increase to a threshold with increases in values of each covariate.

Broad scale

We assessed covariates at a broad scale (i.e., dispersal) to evaluate the hypothesis that wetlands near occupied wetlands have a higher probability of occupancy than isolated wetlands. We mapped the location of every wetland where breeding by wood frogs and chorus frogs was detected from 2004 to 2006 during the occupancy surveys and other fieldwork in the KV. We detected breeding at 33 and 47 wetlands by breeding wood frogs and chorus frogs, respectively.

Dispersal in pond breeding amphibians differs from seasonal migration in two ways: it generally occurs over greater distances (Berven and Grudzien 1990; Baldwin et al. 2006; Semlitsch 2008), and juveniles are the primary dispersers (Berven and Grudzien 1990; Funk et al. 2005; but see Smith and Green 2006). We assumed juveniles would experience a higher cost of movement than adults through land cover types characterized by warm and dry conditions because of their smaller body size and greater surface area to volume ratio. Therefore, we used costs of movement relevant to juveniles when modeling the dispersal process (Table 1; Table S2 in the ESM).

For both species, we evaluated hypothesized relationships between occupancy and cost distance to the nearest occupied wetland (NEAREST), as well as the number of occupied wetlands within various cost distances (NUMOCC). We used cost distances of 1500, 3000, and 4500 cost meters for wood frogs. The latter two distances are

comparable to the minimum and maximum (930 and 1513 m straight-line distance) genetic neighborhood sizes estimated for wood frogs in Virginia (Berven and Grudzien 1990). Genetic neighborhood size is a measure of the spatial scale over which dispersal is sufficiently frequent to prevent genetic divergence among local populations. The 1500 m cost distance represents the level of connectivity that may be required for high rates of dispersal to occur between wetlands and, thus, maintain high occupancy. We used cost distances of 1000, 2000 and 3000 cost meters for chorus frogs. These maximum cost distances are comparable to maximum straight-line distances of 210, 350, and 630 m, thus they cover the range of distances moved by chorus frogs from a field study less than 20 km north of our study area (Spencer 1964). We hypothesized negative, linear and threshold relationships between occupancy and cost distance to the nearest occupied wetland and positive, linear and threshold relationships between occupancy and number of occupied wetlands within various cost distances.

Modeling procedure, model selection and goodness-of-fit

We developed models to make inference regarding the relative importance of covariates on occupancy of wetlands by breeding wood and chorus frogs. While we recognize that multiple factors affect the spatial distributions of species, we built single-covariate models only for p_{ij} and ψ_i . The rationale for single covariate models is that combining covariates in more complex models (either additively or interactively) would have resulted in an impractical number of models to evaluate.

We evaluated the models in two steps. First, we paired each model of detection probability, p_{ij} , with ψ_i , the model that represents the hypothesis that occupancy is invariant across wetlands. We used Δ AIC-values, Δ_i , and Akaike weights, w_i , to determine which model of p_{ij} was best supported by the data (due to evidence of overdispersion in the data, we used QAIC in the analysis for chorus frogs). Both Δ_i and w_i quantify the strength of evidence in support of a particular model as the best model in the set of models being evaluated (Burnham and Anderson 2002). As Δ_i increases, the strength of evidence for model i decreases. The Akaike weight, w_i , of a particular model can be interpreted as the probability that the model is the best model (of those models under consideration; Burnham and Anderson 2002). After selecting the best structure for p_{ij} , we paired each of the structures of ψ_i with the best structure for p_{ij} and used Δ_i and w_i to determine their strength of evidence. We conducted all analyses in Program PRESENCE (Hines 2006). We rescaled covariates between zero and one by dividing all the measurements for a particular covariate by a denominator that was greater than the maximum measurement.

We used the goodness-of-fit (GOF) test in Program PRESENCE to assess the fit of the most highly parameterized model to the data. The GOF test in Program PRESENCE compares the test statistic ($\chi^2/\text{degrees of freedom}$) from the observed data to the distribution of the test statistic from a collection of bootstrapped datasets (MacKenzie and Bailey 2004). If the GOF test indicated poor fit of the model to the data, we derived an estimate of the overdispersion parameter, \hat{c} , by dividing the test statistic from the field data by the average value of the test statistic across all bootstrapped datasets.

Results

We conducted surveys from 18 May to 29 June. Breeding by wood frogs was detected at 11 of 95 wetlands during at least one survey and by chorus frogs at 32 of 95 wetlands. We detected evidence of breeding by tiger salamanders at only two wetlands. Results of the GOF test for the wood frog data suggest adequate fit of the most highly parameterized model ($P = 0.96$). The GOF test for the chorus frog data, however, indicate poor fit ($P = 0.02$), and a \hat{c} of 2.62.

Wood frogs

The model selection results indicate that the best structure for detection probability, p_{ij} , is $p(\cdot)$ (i.e., no effect of covariates on p). Other models have $\Delta_i < 2$, but regression coefficients for the covariates included in these models are imprecisely estimated, and their 95 % confidence intervals overlap 0. Across the three surveys, wood frogs were detected at 9, 8 and 10 wetlands and were detected on all three surveys in 7 of the eleven wetlands at which they were observed. These results indicate a high detection probability that varies little between surveys. The estimate of detection probability from the top model is 0.82 (95 % CI from 0.64 to 0.92).

Regarding the models of occupancy probability, the model selection results provide the strongest support for a positive relationship between the occupancy probability at a wetland and the length of stream within 1000 cost meters of the wetland (intermediate scale; Table 2). The top two models include this covariate, and the combined w_i for the models is 0.70. The model selection results indicate nearly equivalent support for the linear and threshold forms of the relationship (Table 2). The estimated regression coefficient for STREAM1000 from the linear model is 5.78 (95 % CI from 2.01 to 9.55) and 2.27 (95 % CI from 0.47 to 4.08) from the threshold model. Estimates of occupancy across wetlands, $\hat{\psi}_i$, from the top model range from 0.01 (95 % CI from 0.002 to 0.08) to 0.74 (95 % CI from 0.30 to 0.95), and though estimates from the 2nd-ranked model are generally lower, the 95 % confidence intervals around the

Table 2 Model selection results for analysis of the occupancy data for wood frogs, *Lithobates sylvaticus*

Scale	Model	AIC	Δ_i	w_i	k	$-2L$
Intermediate	$\psi(\text{STREAM1000_LIN})$	93.0	0.0	0.41	3	87.0
Intermediate	$\psi(\text{STREAM1000_THRESH})$	93.7	0.7	0.29	3	87.7
Broad	$\psi(\text{NEAREST_THRESH})$	96.9	3.9	0.06	3	90.9
Intermediate	$\psi(\text{WETVEG400_LIN})$	97.8	4.8	0.04	3	91.8
Broad	$\psi(\text{NUMOCC3000_THRESH})$	98.4	5.4	0.03	3	92.4
Broad	$\psi(\text{NUMOCC4500_THRESH})$	98.8	5.8	0.02	3	92.8
Local	$\psi(\text{EMERGVEG 1, 2 = 3 = 4})$	103.2	10.2	<0.01	3	97.2
All	$\psi(.)$	103.3	10.3	<0.01	2	99.3

All models with $\Delta_i < 6$ are shown, as well as the two highest ranked models at each spatial scale. For all models in the table, the structure on detection probability is $p(.)$. Column k contains the number of parameters in each model and column $-2L$ is -2 times the value of the log likelihood function at its maximum. $\psi(.)$ is a null model and applies to all scales

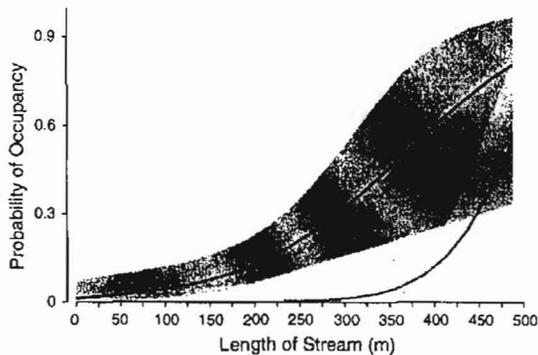


Fig. 3 The relationship between the probability of occupancy by breeding wood frogs and the length of stream within 1000 cost meters of a wetland from the top two models. The highest ranked model (black line; dark shaded area shows 95 % confidence interval) represents a linear relationship between the probability of occupancy and the length of stream (on the logit scale), and the 2nd-ranked model (gray line; light shaded area shows 95 % confidence interval) represents a threshold relationship

estimates from the two models overlap over much of the range of stream lengths (Fig. 3). Model selection results provide weak support for relationships between wetland occupancy and the cost distance to the nearest occupied wetland (broad scale), as well as the amount of wetland vegetation within 400 cost meters (intermediate scale; Table 2). The correlation between occupancy and the cost distance to the nearest occupied wetland is negative [$\hat{\beta}_{\text{NEAREST}}$, is -0.77 (95 % CI from -1.40 to -0.13)], and the correlation with the amount of wetland vegetation is positive [$\hat{\beta}_{\text{WETVEG400}}$, is 4.55 (95 % CI from 1.08 to 8.02)]. Covariates measured at the local scale have the weakest support in the data. The w_i of the models that include covariates at this scale have w_i near 0 (Table 2).

Chorus frogs

Model selection results provide strongest support for $p(\text{SAMPTIME_THRESH})$ as the best structure on p_{ij} . Parameter estimates from this model indicate that detection probability increases with the amount of time a wetland is surveyed but reaches an asymptote. The estimates of p_{ij} from the top model range from 0.13 (95 % CI from 0.04 to 0.35) to 0.96 (95 % CI from 0.85 to 0.99).

High model selection uncertainty precludes strong inference regarding causes of spatial variation in the probability of occupancy in chorus frogs. Four models have $\Delta_i < 2$, and more than 30 models have $\Delta_i < 3$. Models that represented hypotheses from all spatial scales are among these models (Table 3). Estimates of regression coefficients from three of the four highest ranked models consistently indicate that occupancy for a wetland increases as the number of occupied neighboring wetlands increases (broad scale). Estimates of ψ_i from the top-ranked model range from 0.27 (95 % CI from 0.16 to 0.43) for a wetland with no occupied wetlands within 1000 cost meters to 0.74 (95 % CI from 0.45 to 0.91) for a wetland with four occupied wetlands within 1000 cost meters. Estimated regression coefficients from the highest ranked models with covariates measured at the intermediate scale provide weak evidence of a positive relationship between occupancy and the amount of wetland vegetation adjacent to a wetland (Table 3). We found little to no support for covariates measured at the local scale.

Discussion

Investigations into the environmental factors correlated with occupancy patterns in plant and animal populations

Table 3 Model selection results for analysis of the occupancy data for boreal chorus frogs, *Pseudacris maculata*

Scale	Model	QAIC	Δ_i	w_i	k	$-2L$
Broad	$\psi(\text{NUMOCC1000_LIN})$	90.7	0.0	0.09	4	216.7
All	$\psi(\cdot)$	91.5	0.8	0.06	3	224.1
Broad	$\psi(\text{NUMOCC1000_THRESH})$	92.1	1.4	0.05	4	220.4
Broad	$\psi(\text{NUMOCC2000_LIN})$	92.2	1.5	0.04	4	220.6
Intermediate	$\psi(\text{WETVEG400_LIN})$	92.8	2.1	0.03	4	222.2
Intermediate	$\psi(\text{WETVEG800_LIN})$	92.9	2.1	0.03	4	222.3
Local	$\psi(\text{AREA_LIN})$	93.1	2.4	0.03	4	222.9

All models with $\Delta_i < 2$ are shown, as well as the two highest ranked models at each spatial scale. For all models in the table, the structure on detection probability is $p(\text{SAMPTIME_THRESH})$. Column k contains the number of parameters in each model and column $-2L$ is -2 times the value of the log likelihood function at its maximum. $\psi(\cdot)$ is a null model and applies to all scales

have traditionally focused on attributes at relatively fine spatial scales (i.e., the scale of the sampling unit; Ricklefs 1987; Dunning et al. 1992). However, more recent work has demonstrated the importance of processes that operate at larger spatial scales (Knapp et al. 2003; Boscolo and Metzger 2011). In this study, we found that occupancy of wetlands by two species of pond-breeding amphibian was correlated with attributes of the landscape measured beyond the scale of the individual wetland. Occupancy by breeding wood frogs was most strongly correlated with environmental covariates measured at intermediate (scale of seasonal migration) and broad (scale of dispersal) spatial scales. For example, we found that as the length of stream within 1000 cost meters of a wetland increases, the probability of occupancy by breeding wood frogs increases (Table 2; Fig. 3). In addition, our results provide weak support for a positive relationship between occupancy and the amount of wetland vegetation within 400 cost meters. After breeding, wood frogs migrate to moist, cool areas to spend the drier portions of the year (summer and early fall; Vasconcelos and Calhoun 2004; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007b). Streamside locations and areas with wetland vegetation may provide wood frogs with these more suitable environmental conditions, particularly in relatively arid areas like the western United States (Baldwin et al. 2006). At the broadest spatial scale examined, there was weak support for higher occupancy by breeding wood frogs at wetlands with lower cost distances to nearby occupied wetlands (Table 2). Dispersal among wetlands that are near one another may lead to higher occupancy as adjacent unoccupied wetlands are more likely to be colonized, populations at neighboring wetlands are more likely to be rescued, and the deleterious effects of inbreeding depression are less likely to occur (Green 2003). Our data suggest that hydrologic changes in the study area that reduce the probability of successful dispersal among local populations and between occupied and unoccupied wetlands may lower the persistence probability of wood frogs (*sensu* Funk et al. 2005).

Models including either a linear or threshold relationship between the probability of occupancy by breeding wood frogs and the length of stream within 1000 cost meters received similar support (Table 2; Fig. 3). Parameter estimates from the threshold model indicate that a minimum of 300 m of adjacent stream length is required for a wetland to be occupied by breeding wood frogs, and the rate of increase in the probability of occupancy is much greater for lengths beyond 300 m (Fig. 3). Similar thresholds have been observed in simulation and empirical studies for a variety of taxa [Lamberson et al. 1992 (owl); Alados et al. 2009 (woody plants); Jones et al. 2011 (passerine bird)]. For example, Rhodes et al. (2008) found that threshold models tended to be more strongly supported than linear models in occupancy studies of the koala, *Phascolarctos cinereus*.

Insights into the environmental factors and spatial scale of processes that affect occupancy of wetlands by breeding chorus frogs were much weaker. The highest ranked model of occupancy indicated a positive relationship between occupancy at a wetland and the number of occupied wetlands within 1000 cost meters (Table 3). On average, 1000 cost meters for a chorus frog in the study area is equivalent to a maximum straight-line distance of approximately 210 m, which is consistent with the spatial scale over which dispersal affected occupancy patterns of western chorus frogs in Michigan (Werner et al. 2009). Though models that included other covariates had similar support, the estimated regression coefficients from these models were imprecise, and their 95 % confidence intervals overlapped zero. In contrast to the wood frog, little information is available on movement and habitat use in chorus frogs. As a consequence, we had less information on which to base hypothesized relationships between occupancy and environmental covariates and to parameterize cost surfaces. In addition, wood frog breeding sites in the KV were better known and this information was used to estimate the number of occupied wetlands within the various cost buffers. This relative dearth of information probably

contributed to the lack of strong inferences regarding factors influencing patterns of occupancy in chorus frogs.

Previous studies of spatial distribution and patterns of abundance in wood frogs and other amphibians have reported a strong influence of covariates measured at the local scale. For example, these studies have found evidence for the importance of wetland depth (Knapp et al. 2003), wetland vegetation structure (Mazerolle et al. 2005), wetland hydroperiod (Van Buskirk 2005), and predator densities (Van Buskirk 2005). In our study, models that included covariates measured at the local scale were not among the highest ranked models but estimates from these models were consistent with earlier work and our prior predictions, indicating that wood frogs breed in ponds with moderate to high cover from emergent vegetation and short to moderate hydroperiod (Egan and Paton 2004; Cunningham et al. 2007; Hartel et al. 2009). We were unable to evaluate the importance of predation at the local scale, because our data suggested that the detection probability of fish was much less than 1. Of the 25 wetlands at which fish were detected, we detected fish on 1 of 3 surveys at 11 wetlands, 2 of 3 surveys at 8 wetlands, and 3 of 3 surveys at 6 wetlands. Therefore, we were concerned about potential biases caused by false absences (fish were not detected but were actually present) in the data. Most of the wetlands that contained fish were connected to adjacent streams, and we suspect that a primary cause of the low detectability of fish was their transient use of wetlands.

A key insight gained in this study was the role of landscape-scale environmental factors in explaining patterns of amphibian occupancy. These findings do not diminish the significance of local scale attributes of individual wetlands. Factors such as water depth, hydroperiod, and the structure and composition of the vegetation are essential attributes of suitable breeding sites. These factors clearly influence site selection and partly explain spatial difference in occupancy across wetlands. However, substantial components of spatial variation in occupancy may remain unexplained.

When the temporal frame of reference for occupancy studies is extended to include life history dynamics and seasonal environmental relationships, the importance of environmental factors within the larger landscape that surrounds the breeding sites becomes more apparent. One reason is the landscape conditions that promote high probabilities of successful local migration and long-distance dispersal, and thus occupancy, may be largely distinct from the factors associated with breeding site selection. It should not be surprising that the environmental factors that limit the distribution and abundance of a species vary temporally as well as spatially. Consideration of factors that influence long-term occupancy patterns and abundance, informed by considering a species' annual life

cycle requirements, may be essential for the long-term management and conservation of many amphibian species.

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