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THE ROLES OF SPATIAL CONFIGURATION AND SCALE IN EXPLAINING ANIMAL DISTRIBUTIONS IN DISTURBED LANDSCAPES: A CASE STUDY USING POND-BREEDING ANURANS

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ABSTRACT. — Scale is fundamental to ecological studies as patterns exist at multiple levels of organisation. Scale is critically important when assessing a species' distribution, and it can influence the results of complex landscape analyses. If ignored, conservation and management decisions may be inappropriate. In this study, we assessed an often overlooked element in landscape analyses, spatial configuration, to uncover patterns of species distribution. Specifically, we evaluated cover by native vegetation within an urban landscape using a non-nested approach based on discrete consecutive rings (e.g., 0–50 m, 50–100 m, etc.) and a traditional nested approach based on concentric circles (e.g., 0–50 m, 0–100 m, etc.) to determine whether these approaches differ in their effectiveness in uncovering relationships between land cover and animal occurrence in a disturbed, urban landscape. We performed spatial configuration analyses using two anuran amphibian species (wood frog, *Lithobates sylvaticus*; and boreal chorus frog, *Pseudacris maculate*) sampled via call surveys at 75 wetlands (of constructed stormwater sites [n=58] and natural wetlands [n=17]) located within the city of Edmonton, Alberta, Canada. Furthermore, we evaluated the relationship between proportion of native vegetation and species occurrence at three grain sizes (10 m, 50 m, and 100 m) based on analyses of non-nested concentric zones. The nested and non-nested approaches differed in their predictions regarding the occurrence of the frog species. The nested approach explained a higher percentage of deviance when predicting wood frog occurrence than did the non-nested analyses whereas the non-nested approach explained a higher percentage of deviance when predicting boreal chorus frog occurrence. We identified locations surrounding wetlands that predicted occurrence using the non-nested approach that were not detected by the nested approach, suggesting that non-nested analyses may represent an overlooked tool for habitat assessment. Top models for predicting occurrence varied among the three grain sizes, suggesting that our ability to detect environmental heterogeneity is scale-dependent. Incorporating spatial configuration (non-nested and nested designs) and multiple grain sizes in analyses may provide better resolution of landscape patterns and help uncover causes behind species' distributions.

KEY WORDS. — landscape ecology, conservation, urbanisation, spatial grain size, spatial analyses

INTRODUCTION

Landscape ecology addresses how elements or patches are configured in relation to one another within a heterogenous mosaic and how landscape structure influences ecological patterns and processes (Turner, 1989; Wiens & Milne, 1989). Landscape ecology is central to conservation science as habitat loss and disturbance are the most important drivers of species extinctions globally and are predicted to affect biodiversity negatively more than other threats such as climate change and invasive species (Sala et al., 2000; Brooks et al., 2002; Bradshaw et al., 2008). Thus, it is essential to examine the spatial patterns of animal occurrence in human-modified landscapes and the processes that drive these patterns.

Scale is a fundamental consideration in ecological and conservation studies (Levin, 1992; Sodhi et al., 2011). Patterns exist at multiple levels of organisation (e.g., from a stand of trees to a forested landscape), thus the scale of sampling is critically important in analyses of a species' distribution (Liew et al., 2008). Scale can influence results obtained from complex landscape analyses, and if its fundamental role is ignored, management decisions may be inappropriate (Wiens, 1989). Thus, examining how species occurrence relates to land cover sampled at varying scales is imperative for informed conservation practice. The effect of scale has been widely examined across a variety of taxonomic groups (e.g., American redstart, *Setophaga ruticilla*, by Sodhi et al., 1999; grizzly bear, *Ursus arctos*, by Ciarniello et al., 2007), and habitats (e.g., streams, Cooper et al., 1998; marine ecosystems, Mora et al., 2008).

According to Wiens (1989), scale has two components: extent, the spatial area defined as a landscape; and grain (or resolution), the smallest area which a study can characterise based on data collected. Previous research on animal populations have examined the influence of different land cover types within various nested distances (e.g., 0–100 m, 0–200 m, etc., within an extent of 0–1000 m) surrounding a specified area. For example, to determine effects of land cover on response metrics (e.g., species abundance or occurrence obtained from the transects or point counts), researchers conduct field transects or point counts from a particular location and relate these data to surrounding land cover; yet few studies have examined how the grain size and spatial configuration (e.g., nested vs. non-nested arrangements; Fig. 1) used in sampling land cover affects analyses of species occurrence.

In this study, we explore a new methodology to incorporate spatial configuration in deriving relationships between land cover attributes and species occurrence. To our knowledge, this is the first direct comparison of a non-nested approach based on a series of same-sized concentric rings (e.g., 0–100 m, 100–200 m, etc.) to the traditional nested approach based on concentric circles varying in size (e.g., 0–100 m, 0–200 m, etc. as used by Egan & Paton, 2008) to determine whether the two approaches yield different relationships between land cover and animal occurrence. We further evaluate the relationship between land cover, sampled at different grain sizes, and species occurrence using only non-nested analyses. Our non-nested approach is novel because 1) it identifies specific ranges at which a landscape feature may affect species distribution (an interval does not overlap those preceding or following it), and 2) it recognises that the relationship between land cover and species occurrence may vary depending on the grain size used to sample land cover. For example, the importance of small areas of natural vegetation located immediately adjacent to a species' breeding habitat (e.g., within 10 m) may be lost if the finest grain used to examine the surrounding landscape integrates cover from 0 to 100 m. Testing the effect of grain size on analyses that use land cover as a predictor of species occurrence may help refine analytical techniques used to guide conservation in spatially-heterogeneous landscapes.

To examine the relationship between species occurrence, scale, grain size, and spatial configuration, we used natural vegetation (forest and shrubland) sampled at three grain sizes (10 m, 50 m, and 100 m) within a nested and non-nested framework to predict the occurrence of adult boreal chorus frog (*Pseudacris maculata*) and wood frog (*Lithobates sylvaticus*) at two types of natural wetlands and at constructed stormwater wetlands located in the urban landscape of Edmonton, Alberta, Canada. We chose these two anurans to test our methodology as both species require multiple habitats to persist (i.e., biphasic life cycles). Adults breed at centralised locations (i.e., wetlands) and produce aquatic larvae that metamorphose within three months. Both juveniles and adults use terrestrial habitat for foraging and overwintering (Semlitsch, 1998). Thus, adult occurrence sampled at a central location is biologically tied to attributes of the surrounding landscape making these two species well suited for examining the relationship between occurrence and surrounding land cover and for comparing analytical approaches.

Assessing differences in land cover under two sampling criteria (nested vs. non-nested) requires a heterogenous landscape. Among various human-induced disturbances that result in habitat loss and land cover change, urbanisation represents an especially inhospitable landscape transformation (Cushman, 2006) known to affect many amphibian species globally (Hamer & McDonnell, 2008; Scheffers & Paszkowski, 2012). We therefore saw urban environments as an appropriate setting for considering the roles of grain and spatial configuration in explaining species distributions.

METHODS

We sampled 75 urban wetlands (consisting of three types: constructed stormwater sites [n=58], natural river-valley wetlands [n=5], and natural upland wetlands [n=12]). The City of Edmonton exists at an ecotone between the Aspen Parkland and the Boreal Mixed-wood Forest (Royer & Dickinson, 2007). The dominant native trees are *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera*, interspersed with patches of *Picea mariana*, *Picea glauca*, and grasslands. Geospatial analyses were completed using the ArcGIS 9.2x software package (Environmental Systems Research Institute, Redlands, CA). We mapped all native vegetation (mixed-wood forest and shrubland [areas of tall grass mixed with shrubs]) using aerial photo interpretation (1:20,000 scale) from 0.25-m resolution black and white digital orthophotos (leaf-off) from Apr/May 2007 (produced by Land Data Technologies Inc. for the City of Edmonton Regional Joint Ortho Initiative). All areas that represented a contiguous surface of vegetation were mapped. If land cover was ambiguous, we used high-resolution colour imagery from Google Earth images to aid in classification (Google Earth v4.3; http://earth.google.com). We created an error matrix to assess the accuracy of mapping. We generated one randomly placed point post hoc per 1 km² for all land-use types. A second round of classification was conducted at each point to determine the accuracy of original mapping classifications; overall accuracy was 94%.

Native vegetation was mapped within a 1000 m radius of each wetland as 1000 m represents a working approximation of dispersal and migration distances for many pond-breeding amphibians in North America (Berven & Grudzien, 1990; Semlitsch, 1998; Smith & Green 2005). We first sampled natural vegetation at a 50 m grain size for both nested and non-nested concentric buffers within 1000 m (extent) surrounding each wetland (Fig. 1). Second, to identify the grain size that best predicted frog occurrence, we generated non-nested concentric buffers based on 10 m, 50 m, and 100 m grain size within a 1000 m radius (extent) surrounding each wetland (Fig. 1). The smallest grain size of 10 m was chosen because many, but not all, stormwater wetlands in the study had narrow riparian buffers (mostly consisting of tall grass) between 5–25 m in width (Scheffers, unpublished data). Larger grain sizes of 50 and 100 m were chosen to sample intermediate-sized and landscape areas, respectively (Pellet et al., 2004; Regosin et al., 2005; Rittenhouse & Semlitsch, 2007).

Our response variable is species occurrence (presence/absence) which was collected via breeding call surveys conducted at a central breeding location (i.e., wetlands). Specifically, in 2008, breeding call surveys for anurans began at ice-off and were conducted within a 3-hour period starting 30 minutes after sunset (2100–2300 hrs). Call surveys occurred from 29 Apr – 15 May and each wetland was surveyed once. An initial survey point was established in an area with calling anurans, or at a random point if no males were heard calling. Point counts were conducted every 100 m for a maximum of four points per wetland. At each point we conducted a 180° point count for 5 minutes to record all anurans heard within 50 m. (See Scheffers, 2010 for more details on call surveys).

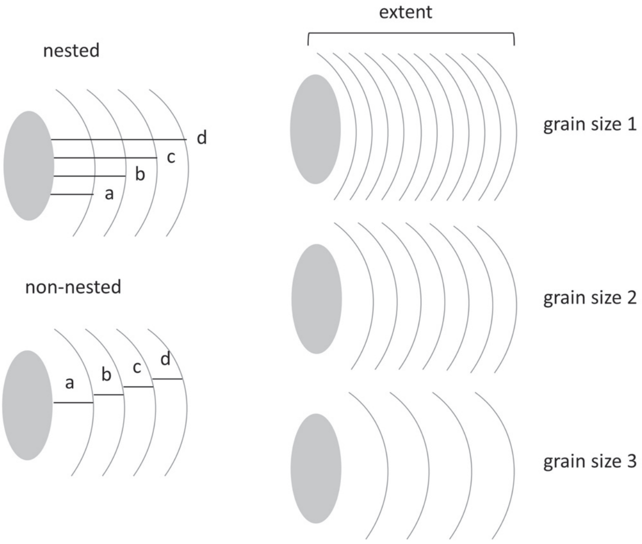

Fig. 1. Sampling of land cover traditionally follows a nested approach based on concentric buffers (top left). In our study, natural vegetation was also sampled using a non-nested approach with buffers as rings (bottom left) at three different grain sizes (10 m, 50 m, and 100 m) (right). Extent represents the spatial area defined as a landscape. In our study, extent is represented by the area between 0–1000 m surrounding breeding wetlands. Grey circles represent a hypothetical wetland and partial rings (a–d) represent the area in which land cover was sampled. Land cover sampled under scenario **a** is equivalent for both sampling approaches whereas land cover sampled under scenario **c** of the nested approach contains land cover from both **a** and **b**, whereas land cover sampled under scenario **c** of the non-nested approach is a confined zone, independent of **a** and **b**.

Generalised linear models (GLM) with a binomially distributed error term and a logit link function in R 2.12.2 were used to relate the presence of calling frogs at the study wetlands in Spring 2008 to the proportion of a circle 1000 m in radius covered by native terrestrial vegetation. We first compared the success of sets of nested versus non-nested buffers in predicting relationships between species occurrence and land cover. Our analyses compared wood frog occurrence across all 75 wetlands to native terrestrial vegetation sampled at a 50 m grain size within nested concentric buffers and non-nested concentric buffers. We then compared the effect of grain size on predicting species' occurrence for non-nested buffers only. We ran a single regression for wood frog and boreal chorus frog occurrence for each grain size (10 m, 50 m, and 100 m) resulting in 130 regressions in total for each species (100 regressions for 10 m intervals, 20 regressions for 50 m intervals, and 10 regressions for 100 m intervals). We ran GLMs for all 75 wetlands combined (across all wetland types) and then a second set of GLMs for the 58 stormwater wetlands as distinct patterns of surrounding vegetation cover and occurrence of anurans (nearly 100%) at natural sites might have strongly affected overall results. We used a single land cover type as the predictor of species occurrence in this study. We recognise that the entire habitat matrix (with various land cover types) influences the distribution and occurrence of amphibian populations. However, a multivariate approach that combines many land cover types with various scales and grain sizes would unnecessarily complicate our analyses and interfere with our assessment of grain size and spatial configuration on animal occurrence on a landscape.

Models were evaluated using Akaike's Information Criterion adjusted for small samples (AICc) to identify the distance that best predicted occurrence for each species (Burnham & Anderson, 2002). Relative likelihoods of candidate models were calculated using AICc weights, with weights varying from 0 (no support) to 1 (complete support) relative to the entire model set. Models with an importance weight >0.2 were considered substantial predictors of occurrence (Gahl & Calhoun, 2008). The amount of variance in the response variable captured by each model was assessed as the percent deviance explained (% DE). Lastly, to further explore the importance of different grain size on analysis, we plotted all univariate deviance that was explained in relation to each 10 m, 50 m, and 100 m grain size for the area 0–1000 m. All deviance values were evaluated relative to each other, thus models with high values were better predictors of frog occurrence than models with low values.

We used a permutation method to validate our models, which compared the effect of grain size on species' occurrence for non-nested buffers. This technique recalculated the explained deviance of each fitted model with 1000 random permutations of the response variable. In order to do this, we randomly generated occurrence, 0s and 1s [i.e., absence and presence], for each permutation in the same proportion as was observed for our real data set. GLMs were repeated 1000 times to create a bootstrapped distribution of explained deviance. We averaged across all 1000 simulations and plotted average explained deviance (with 95% confidence intervals) alongside the actual explained deviance generated by our models based on observed occurrence patterns. This analysis tested whether the observed deviance in species occurrence could be generated by inherent patterns in the independent variable, which might be unrelated to occupancy of wetlands, for example patterning of patches of natural vegetation in Edmonton owing to the North Saskatchewan River valley or main transportation corridors.

RESULTS

Natural wetlands (river valley and upland sites) had a higher proportion of native vegetation (31%, range: 10–59%) within the 0–1000 m zone, which was expected as many of these wetlands are located within protected parks. Land around stormwater wetlands supported lower proportions of native vegetation within 1000 m with an average of 10% (range: 0–39%).

Wood frogs were found at 47% of stormwater, 80% of river valley, and 92% of upland wetland sites in 2008. For wood frog, the nested approach resulted in higher explained deviance than the non-nested approach across all models. The local zone nearest the pond (0–50 m) was the best predictor of wood frog occurrence for both nested and non-nested analyses. However, percent explained deviance for nested analyses generally increased with distance away from wetlands. Percent explained deviance derived from the non-nested analyses was highly variable (many peaks and troughs) for buffer-rings situated farther away from wetlands (Fig. 2). The best supported models (based on wAICc) derived from the nested approach indicated that natural vegetation within 0–50 m and 0–1000 m best predicted wood frog occurrence. Models derived from non-nested analyses suggest that natural vegetation located at 0–50 m and 950–1000 m best predicted wood frog occurrence (Table 1). Although the top models were relatively similar, differences exist between the two approaches; the non-nested approach also indicated that natural vegetation located at intermediate distances (200–250 m and 250–300 m) from wetlands predicted wood frog occurrence (Table 1).

Boreal chorus frogs were found at 45% of stormwater, 60% of river valley, and 92% of upland wetland sites. Unlike patterns seen for wood frog occurrence, nested and non-nested approaches varied considerably in percent deviance explained across the 0–1000 m extent for boreal chorus frog. Notably, the non-nested approach outperformed the nested approach at numerous scales (Fig. 2). Besides for the most local zone (0–50 m), which was the best predictor of boreal chorus frog occurrence (Table 1), percent explained deviance for nested analyses generally increased with distance from wetlands. In contrast, percent explained deviance derived from non-nested analyses varied, displaying three major peaks (0–50 m, 450–500 m, and from 850–1000 m; Fig. 2). The best supported models (based on wAICc) derived from the nested approach suggest that natural vegetation within 0–50 m and 0–1000 m best predict boreal chorus frog occurrence. The best models derived from non-nested analyses suggest that natural vegetation located in rings ranging from 850–1000 m, as well as 0–50 m, best predicted boreal chorus frog occurrence (Table 1). Although the top models were relatively similar, differences existed between the two approaches; the non-nested approach also indicated natural vegetation located at intermediate distances (450–500 m) from wetlands predicted boreal chorus frog occurrence. Percent cover by natural vegetation at 100–300 m for all wetlands was especially poor at predicting boreal chorus frog occurrence, as the explained deviance derived from random permutations was greater than that based on observed vegetation patterns.

We used natural vegetation sampled at three different grain sizes to predict species occurrence across all wetlands combined. Based on non-nested buffers, our analyses suggest

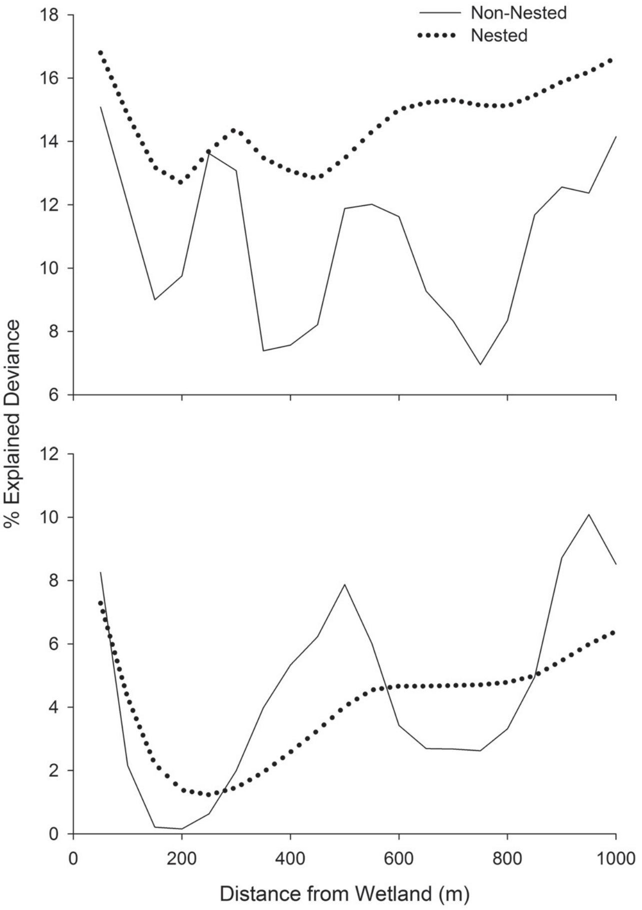

Fig. 2. A comparison between nested and non-nested analyses. Differences in percent explained deviance suggest that nested and non-nested designs yield variable results when analysing species occurrence. Explained deviance for models of occurrence of wood frog (top) and boreal chorus frog (bottom) is based on the proportion of area covered by native vegetation sampled every 50 m within a 1000 m radius surrounding 75 urban wetlands (stormwater and natural wetlands). The solid black line represents the non-nested analyses and the dotted line represents the nested analysis.

Table 1. A comparison among models, based on the proportion of native terrestrial vegetation in nested and non-nested buffers (50 m grain size) surrounding wetlands, in predicting occurrence of wood frogs and boreal chorus frogs at 75 urban wetlands. The top five models for each model set are reported. All models with a ωi > 0.2 were considered substantial predictors of occurrence.

					AICc Comparison			
	Nested vs. Non-Nested	Rank	Model (m)	LL	AICc	ΔAICc	wAICc	%DE
Wood Frog	Nested	1	0–50	–42.00	87.99	0	0.12	16.80
		2	0–1000	–42.07	88.14	0.15	0.11	16.65
		3	0–950	–42.30	88.61	0.62	0.09	16.19
		4	0–900	–42.46	88.92	0.93	0.08	15.88
		5	0–850	–42.68	89.50	1.36	0.08	15.45
	Non-Nested	1	0–50	–42.86	89.72	0	0.23	15.08
		2	950–1000	–43.33	90.67	0.94	0.14	14.15
		3	200–250	–43.60	91.20	1.48	0.11	13.62
		4	250–300	–43.88	91.75	2.03	0.08	13.08
		5	850–900	–44.14	92.27	2.55	0.07	12.56
Boreal Chorus Frog	Nested	1	0–50	–47.45	98.89	0	0.19	7.29
		2	0–1000	–47.90	99.81	0.91	0.12	6.40
		3	0–950	–48.11	100.22	1.33	0.10	5.99
		4	0–900	–48.38	100.75	1.86	0.07	5.47
		5	0–850	–48.62	101.24	2.35	0.06	4.99
	Non-Nested	1	900–950	–46.02	96.03	0	0.30	10.08
		2	850–900	–46.72	97.43	1.40	0.15	8.72
		3	950–1000	–46.82	97.63	1.60	0.13	8.52
		4	0–50	–46.95	97.90	1.87	0.12	8.26
		5	450–500	–47.15	98.29	2.26	0.10	7.87

that the occurrence of adult wood frogs was best predicted by the amount of natural vegetation within the most local zone examined for each grain size (Table 2), i.e., intervals of 0–10 m, 0–50 m, and 0–100 m. Boreal chorus frog occurrence, however, was best predicted by both the very local, fine grain at 0–10 m, and landscape scales of 900–950 m and 900–1000 m for the two coarser grains (Table 2).

For stormwater wetlands only, natural vegetation became increasingly more important as a predictor of occurrence for both species with increasing distance from wetland edge (Fig. 3). Compared to model sets for all wetlands combined, the decrease in the predictive power of natural vegetation (as measured by wAICc) in models for stormwater wetlands only, suggests that other environmental parameters (not included in our analyses) may influence the occurrence of the two frog species at these constructed sites. Cover by natural vegetation occurring from 150–400 m from stormwater wetlands also poorly predicted occurrence for both frog species as our random permutations explained greater deviance than our actual models.

In general, relative support of models (as measured by wAICc) increased with increasing grain size. This trend of increasing model support with grain size was most pronounced for analyses of stormwater wetlands (Table 3). Characteristics of top models varied with grain size. For example, for all wetlands combined, natural vegetation within buffer rings nearest wetlands, 0–10 m for 10 m grain size and 0–50 m for 50 m grain size, best predicted the occurrence of boreal chorus frog, whereas natural vegetation within the nearest buffer, 0–100 m, did not for the 100 m grain size. Similarly, at stormwater wetlands only, natural vegetation within the nearest buffer, 0–10 m (10 m grain) was a relatively effective predictor of wood frog occurrence whereas the adjacent natural vegetation within 0–50 (50 m grain) and 0–100 m (100 m grain) intervals were not (Table 3; Fig. 3).

DISCUSSION

We present a novel approach for investigating animal distributions in heterogeneous landscapes that allows identification of the specific spatial ranges at which landscape features affect species' distributions. Hence, we endorse configuration as an important refinement of the two components of scale (i.e., extent and grain) in Wien (1989). In particular, non-nested sampling offers a useful tool in landscape ecology; however, our analyses suggest that the application of this approach is species- and grain size- dependent.

In predicting the occurrence of boreal chorus frog, novel, non-nested models generally yielded higher percent explained deviance than nested models, whereas for wood frog, the widely used nested-design produced higher percent explained deviance. In addition, non-nested analyses displayed many peaks and troughs across the spatial extent for both species, whereas percent explained deviance was relatively consistent for traditional nested analyses. Possibly, the nested approach

Table 2. A comparison among models that differed in grain size and evaluated the performance of the proportion of native terrestrial vegetation in non-nested buffers for predicting occurrence of wood frogs and boreal chorus frogs at 75 urban wetlands. A total of 130 regressions were performed in total for each species based on three grain sizes, intervals of 10, 50, or 100m. The top five models for each grain size are reported. All models with a wi > 0.2 were considered substantial predictors of occurrence.

				AICc Scale Comparison				
	Grain Size	Rank	Model (m)	LL	AICc	ΔAICc	wAICc	%DE
Wood Frog	10 m	1	0–10	–39.06	82.12	0	0.71	22.61
		2	990–1000	–42.95	89.89	7.77	0.01	14.91
		3	250–260	–42.98	89.97	7.84	0.01	14.84
		4	240–250	–43.06	90.12	7.99	0.01	14.69
		5	260–270	–43.12	90.24	8.12	0.01	14.57
	50 m	1	0–50	–42.86	89.72	0	0.23	15.08
		2	950–1000	–43.33	90.67	0.94	0.14	14.15
		3	200–250	–43.60	91.20	1.48	0.11	13.62
		4	250–300	–43.88	91.75	2.03	0.08	13.08
		5	850–900	–44.14	92.27	2.55	0.07	12.56
	100 m	1	0–100	–42.98	89.97	0	0.35	14.84
		2	200–300	–43.57	91.14	1.17	0.19	13.68
		3	900–1000	–43.65	91.29	1.32	0.18	13.43
		4	800–900	–44.18	92.37	2.40	0.10	12.46
		5	500–600	–44.39	92.78	2.82	0.08	12.05
Boreal Chorus Frog	10 m	1	0–10	–45.05	94.10	0	0.14	11.97
		2	900–910	–45.80	95.61	1.51	0.06	10.49
		3	920–930	–45.93	95.85	1.76	0.06	10.26
		4	910–920	–45.96	95.92	1.82	0.06	10.20
		5	890–900	–46.06	96.11	2.01	0.06	10.00
	50 m	1	900–950	–46.02	96.03	0	0.30	10.08
		2	850–900	–46.72	97.43	1.40	0.15	8.72
		3	950–1000	–46.82	97.63	1.60	0.13	8.52
		4	0–50	–46.95	97.90	1.87	0.12	8.26
		5	450–500	–47.15	98.29	2.26	0.10	7.87
	100 m	1	900–1000	–46.37	96.73	0	0.51	9.40
		2	400–500	–47.47	98.93	2.20	0.17	7.25
		3	800–900	–47.67	99.35	2.61	0.14	6.85
		4	300–400	–48.74	101.48	4.74	0.05	4.76
		5	500–600	–48.79	101.58	4.85	0.05	4.66

overestimates the importance of habitat factors at each scale as explanatory power is carried over from one buffer zone to the next. For example, 0–100 m may be a top supported model in a nested analysis primarily because of land cover located at 0–50 m which does represent over half the buffer area. However, this nested design may also inappropriately yield 0–200 m as a top supported model as essential habitat within 50 m of a wetland is nested within this extent as well. Thus, the major advantage gained by the use of non-nested designs is *increased* independence between scales.

The scale at which research is conducted, particularly grain size, must be linked with the scale of processes under consideration (Mac Nally & Quinn, 1998). On the basis of our non-nested analyses, the relative importance of the chosen landscape features (natural vegetation) in predicting species occurrence varied among the three grain sizes and the distance away from breeding wetlands. It is generally agreed that there is no single inherently “superior” extent or grain size at which to analyse landscape patterns of species occurrence (Wiens, 1989; Kotliar & Wiens, 1990; Levin, 1992; Mac Nally & Quinn, 1998). Therefore, grain size and spatial configuration must be carefully tailored to characteristics of the study area and the species under consideration. Including multiple grain sizes in analyses likely avoids the omission of important landscape features that may be “hidden” by adopting coarser grain sizes. For example, the importance of pond-side area in predicting occurrence would have been missed if we had not employed small grain size in our study. The greater the area sampled, the greater potential landscape heterogeneity. Therefore, land cover sampled at small grain sizes may yield high proportions of a single, critical land cover type that may be obscured when sampling occurs at larger grain sizes. Ultimately, incorporating multiple spatial grain sizes may be used to uncover patterns that are either consistent across grains (patterns are scale-independent) or inconsistent across grains (patterns are scale-dependent). Lastly, multiple grain sizes could be used in analyses to identify patterns that operate at different spatial scales (see Forman, 1995 for information on grain and scale). For example, analyses of animal distributions may be improved if they combine small grains to identify features associated with small-scale habitat suitability (e.g., foraging sites, hibernating sites) with large grains to identify occupancy patterns associated with large-scale phenomenon such as dispersal.

Our non-nested series of buffer rings may help uncover distant habitat patches or landscape features of importance to populations that are not identified using overlapping, nested designs. Combining our non-overlapping approach with spatially explicit models (e.g., see Baldwin et al., 2006), may help pinpoint for conservation locally important habitat elements that are specific to individual taxa or are scattered throughout highly heterogeneous landscapes (such as urban environments where undeveloped land is both limited and expensive). Analyses based on non-nested buffers may be applied in a variety of scenarios to examine the relationship between land cover at specific distances surrounding a centralised location (such as survey transects, point counts, or study plots). Our random permutations explained more deviance than actual models based on natural vegetation cover for distances 150–400 m from study sites for all wetlands combined (boreal chorus frog) and stormwater wetlands (both species). This may be due to the nature of the landscape that comprised our study area. Stormwater wetlands are generally located within housing or commercial developments, but builders typically allow natural vegetation to grow in the immediate vicinity of wetlands (e.g., 0–15 m). Thus, outside of this riparian zone, the nearest natural vegetation may be present a few hundred meters distance from wetlands (i.e., beyond the development). Additionally, the contrasting increase in explained deviance at about 500 m appears to coincide with the distance between wetlands (i.e., 500 m) in our study area, which is an important landscape predictor of frog occurrence (Scheffers, 2010).

When natural wetlands were removed from our analyses, the percent explained deviance dropped across all models, particularly for predicting wood frog occurrence. This suggests that other parameters (not accounted for in this study, such as proximity of other wetlands or road density) are likely influencing the occurrence of anurans at constructed sites. Alternatively, model performance decreased as coverage by natural vegetation at some spatial scales did not vary

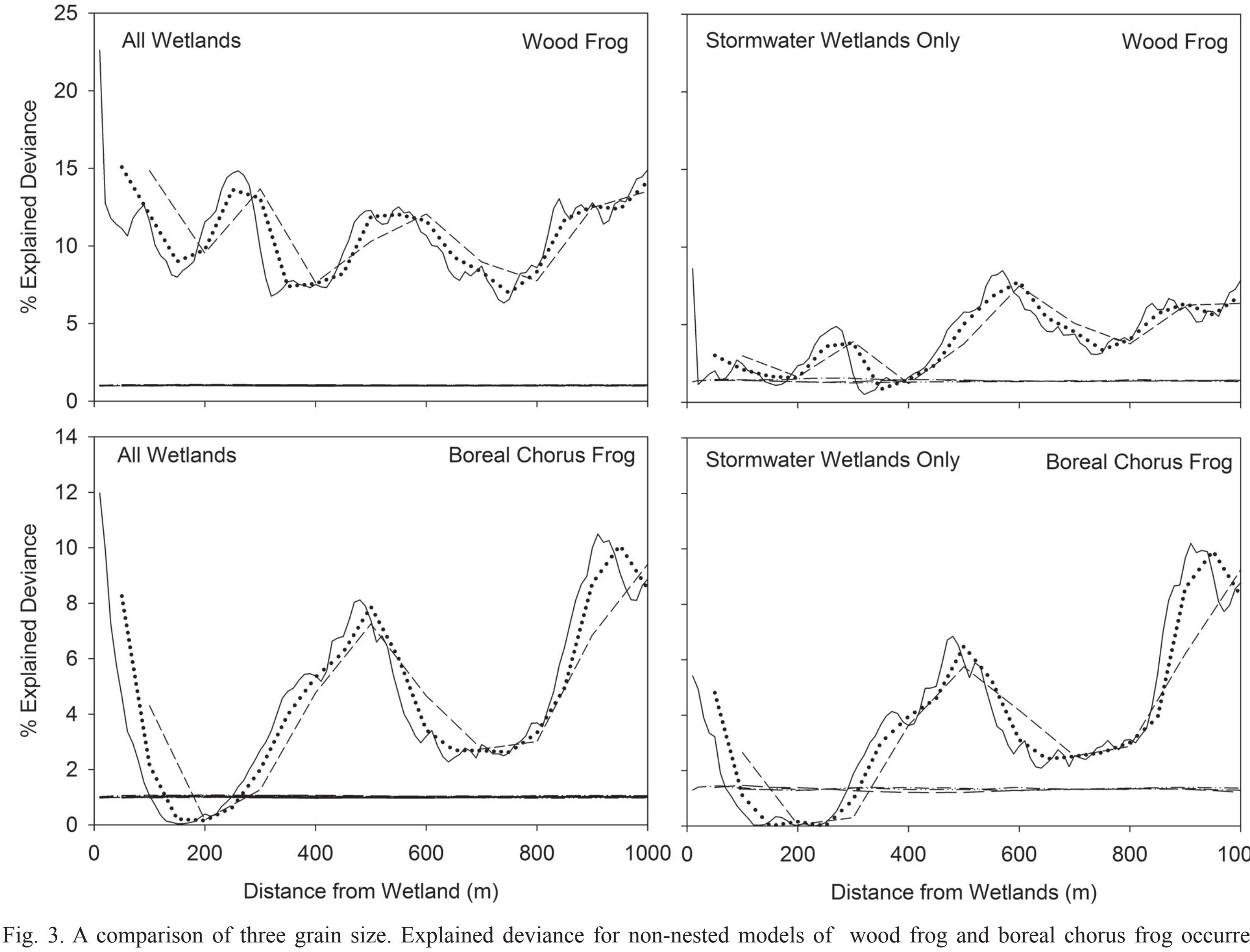

Fig. 3. A comparison of three grain size. Explained deviance for non-nested models of wood frog and boreal chorus frog occurrence based on proportion of native vegetation within buffer rings 10 m, 50 m, and 100 m within a circle 1000 m in radius surrounding 75 urban wetlands (stormwater and natural sites combined) and 58 stormwater wetlands. The solid black lines represent 10 m grain size, dotted lines represent 50 m grain size, and dashed lines represent 100 m grain size. The straight black lines represent the explained deviance based on 1000 random simulations for each of the three grain sizes.

Table 3. A comparison among models that differed in grain size and evaluated the performance of the proportion of native terrestrial vegetation in non-nested buffers for predicting occurrence of wood frogs and boreal chorus frogs at 58 urban stormwater wetlands. A total of 130 regressions were performed in total for each species based on three grain sizes, intervals of 10, 50, or 100 m. The top five models for each grain size are reported. All models with a ωi > 0.2 were considered substantial predictors of occurrence.

					AICc Scale Comparison			
	Grain Size	Rank	Model (m)	LL	AICc	ΔAICc	wAICc	%DE
Wood Frog	10 m	1	0–10	–36.71	77.42	0	0.04	8.61
		2	560–570	–36.76	77.52	0.10	0.04	8.48
		3	550–560	–36.87	77.74	0.32	0.04	8.21
		4	540–550	–36.90	77,80	0.38	0.04	8.13
		5	570–580	–37.00	77.99	0.56	0.03	7.90
	50 m	1	550–600	–37.04	78.09	0	0.16	7.78
		2	950–1000	–37.41	78.81	0.72	0.11	6.87
		3	500–550	–37.44	78.88	0.79	0.11	6.80
		4	850–900	–36.62	79.23	1.14	0.09	6.36
		5	800–850	–37.88	79.75	1.66	0.07	5.71
	100 m	1	500–600	–37.16	78.32	0	0.26	7.48
		2	900–1000	–37.61	79.22	0.90	0.17	6.37
		3	800–900	–37.66	79.32	0.99	0.16	6.25
		4	600–700	–38.13	80.26	1.93	0.10	5.08
		5	200–300	–38.60	81.20	2.88	0.06	3.90
Boreal Chorus Frog	10 m	1	900–910	–36.07	76.14	0	0.07	10.20
		2	920–930	–36.17	76.35	0.21	0.06	9.94
		3	930–940	–36.19	76.38	0.24	0.06	9.90
		4	910–920	–36.21	76.41	0.27	0.06	9.86
		5	890–900	–36.28	76.57	0.42	0.05	9.67
	50 m	1	900–950	–36.18	76.36	0	0.29	9.93
		2	850–900	–36.72	77.44	1.08	0.17	8.58
		3	950–1000	–36.83	77.66	1.30	0.15	8.31
		4	450–500	–37.56	79.13	2.76	0.07	6.49
		5	500–550	–38.05	80.11	3.74	0.04	5.27
	100 m	1	900–1000	–36.46	76.92	0	0.47	9.24
		2	800–900	–37.67	79.35	2.43	0.14	6.21
		3	400–500	–37.86	79.72	2.80	0.12	5.75
		4	500–600	–38.49	80.98	4.07	0.06	4.17
		5	300–400	–38.71	81.42	4.50	0.05	3.64

sufficiently to generate patterns based on this single land cover feature.

Our analytical design was directed at uncovering scale-related patterns rather than uncovering the biological significance of native vegetation as a predictor of frog occurrence. Nevertheless, we acknowledge that observed patterns are linked to the biology of the two study species. Amount of natural vegetation immediately adjacent to wetlands best predicted wood frog occurrence, whereas boreal chorus frog occurrence was best predicted by natural vegetation located at both small and large distances from wetlands. Habitat at distances >250 m away from breeding wetlands may play a role in maintaining wood frog and boreal chorus frog populations even if areas located between these distant habitats and wetlands are degraded. The importance of natural vegetation across grain size and extent corresponds to typical post-breeding movements of both study species examined (Spencer, 1964; Berven & Grudzien, 1990; Regosin et al., 2005; Baldwin et al., 2006) and of many amphibians in North America and Europe (Smith & Green, 2005; Rittenhouse & Semlitsch, 2007; Semlitsch, 2008). Our ability to predict occurrence for the two frog species differed by grain size as well as the range at which vegetation was sampled. Wood frogs are a long-lived, large bodied, and highly philopatric species: most individuals use the same breeding wetland and surrounding terrestrial habitat throughout their entire lives (AmphibiaWeb, 2012). Thus, this species is likely to respond to small scale patterns of vegetation surrounding breeding wetlands as well as the nature of the within-wetland environment (Browne et al., 2009). However, our results also indicate the potential of metapopulations or source populations existing within the 1000 m extent, reflected by the peaks and troughs in percent deviance explained between 0 and 1000 m. Conversely, boreal chorus frogs are small bodied and suspected to be short lived and highly dependent on regional populations to maintain occurrence especially within disturbed landscapes . Boreal chorus frogs are generalists in their selection of breeding habitat (ranging from permanent ponds to flooded roadside ditches). This species is quick to colonise and recolonise wetlands and thus the distribution of the boreal chorus frog reflects characteristics of the wider landscape (Browne et al., 2009; Werner et al., 2009).

CONCLUSIONS

We compared traditional nested designs to non-nested designs and found that the success of these two approaches in a disturbed landscape differed with species. The performance of the non-nested approach at identifying vegetated areas for predicting frog occurrence, which were not detected by the nested approach, suggests that non-nested analyses may represent useful tools for studies investigating patterns of species occurrence. Patterns also differed with grain size. Notably, analyses of smaller grains identified areas of the landscape that strongly predicted frog occurrence that were not identified as influential at the largest grain size. Our ability to detect environmental heterogeneity and the ability of organisms to respond to such patchiness is scale dependent (Wiens, 1989); thus, implementing spatial analyses with non-nested and nested designs at multiple grain sizes promises to provide better resolution of distribution patterns and their causes, and to illuminate interrelationships among scales.

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