

Bird and mammal use of vernal pools along an urban development gradient

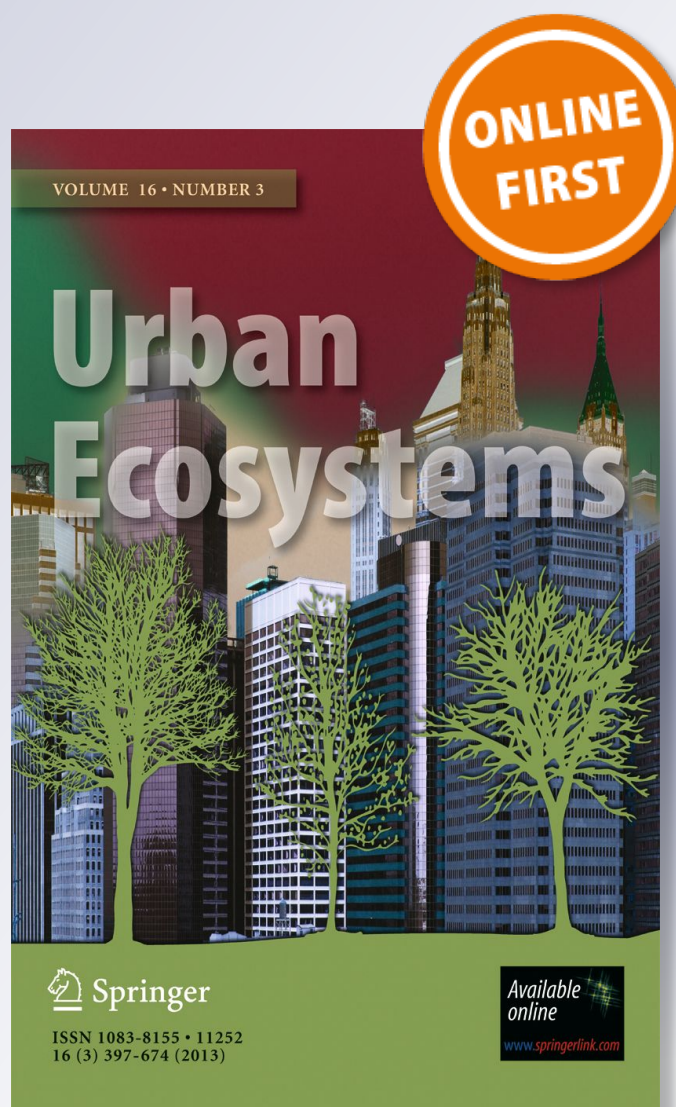
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Bird and mammal use of vernal pools along an urban development gradient

Carly J. Eakin¹ · Malcolm L. Hunter Jr¹ · Aram J. K. Calhoun¹

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Abstract

Vernal pools in the northeastern US are of conservation concern primarily because of their role as habitat for specialized pool-breeding amphibians, but their use by birds and mammals may also be of interest, especially from the perspective of the impact of urbanization. We describe camera-trapped wildlife (CTW) at 38 vernal pools along an urban development gradient in greater Bangor, Maine, USA. We detected 20 mammal and 39 bird taxa (29 contacted pool water; 39 detected at >1 site). Land cover type within 1000 m (%), within-pool vegetation (%), and amphibian egg mass numbers explained a substantial portion of the variance (40.8%) in CTW assemblage composition. Submerged vegetation within pools and cover by water and impervious surfaces within 1000 m of pools were key site characteristics defining assemblages. We scored the urban-affiliation of taxa and modeled the relationship between weighted assemblage scores for each site and impervious cover. Impervious cover within 1000 m of pools was positively ($p < 0.01$) related to site urban-affiliation scores. Use probability for red fox increased and snowshoe hare decreased with impervious cover at 1000 m. These results indicate that within-pool vegetation and land cover types at 1000 m influenced bird and mammal assemblages that used study pools and greater impervious cover at 100 and 1000 m was correlated with a shift in assemblages from being dominated by urban-avoider to urban-adapted species. We encourage land use planners and managers to consider the influence of land use practices within 1000 m of vernal pools on birds and mammals, especially near amphibian breeding pools.

Keywords Vernal pool · Camera trap · Urban gradient · Urban wildlife · Subsidized wildlife · Urban wetlands

Introduction

Vernal pools provide important seasonal sources of food or water for many species of birds and mammals (Silveira 1998; Colburn 2004; Mitchell et al. 2008), especially for those that prey on seasonally abundant pool-breeding amphibians or nutrient-rich aquatic vegetation early in spring

(Shurin et al. 2006). For example, gray jays (*Perisoreus canadensis*), wild turkeys (scientific names not listed in the text are in Table 1), and raccoons are known to eat amphibians (Childs 1953; Murray et al. 2005; A. Calhoun, personal communication, 13 June 2017). Although the ecological roles of birds and mammals in vernal pool ecosystems are poorly known, there is evidence that they facilitate ecological processes such as nutrient transport, seed and egg dispersal, and regulation of amphibian populations (Childs 1953; Zedler 1987; Black and Zedler 1992), thereby making vernal pool ecological functions disproportionately large compared to their area (Calhoun et al. 2017).

Vernal pool conservation is challenging; pools are typically small and seasonally inundated, poorly regulated, and difficult to inventory (Calhoun et al. 2017). Conflicts between conservation and urbanization are most acute where economic growth converts forest into residential, commercial, and/or industrial developments (Windmiller and Calhoun 2008). These conflicts will escalate as urban areas expand >12.2 million ha

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Table 1 Predictor variables used to evaluate use and detection probability of species detected by camera traps at 33 vernal pools across an urban development gradient in 2014–2016 in greater Bangor, Maine, USA

Parameter	Variable	Description
Detection	Emergent	Mean within-pool emergent vegetation cover (%)
	Shrub	Mean within-pool shrub cover (%)
	View	Mean pool basin* photographed (%)
Use	Imp100	Impervious cover within 100 m (%)
	Imp300	Impervious cover within 300 m (%)
	Imp600	Impervious cover within 600 m (%)
	Imp1000	Impervious cover within 1000 m (%)

*Basin refers to inundated area at spring high-water

throughout the US by 2051 (Lawler et al. 2014). As urban development replaces forest, habitat for forest-reliant wildlife is lost and fragmented (Fischer and Lindenmayer 2007); impervious surfaces alter hydrology and rapidly transport unfiltered anthropogenic chemicals into pools (Faulkner 2004); and novel threats to wildlife may increase, including human disturbance and predation from pets and subsidized predators (Hansen et al. 2005).

Shifts in bird and mammal assemblage composition in response to urban development have been well documented (Chace and Walsh 2006; McKinney 2008; Chupp et al. 2013). Urbanization typically involves a reduction in vegetation cover (McKinney 2006), a shift towards non-native plants (Aronson et al. 2014), and the addition of novel human structures and subsidies (e.g., food waste). Birds and mammals typically exhibit one of three responses to these changes (as coined by Blair 2001): avoidance, adaptation, or exploitation with these responses predominating in undeveloped/rural, suburban, and urban core areas, respectively (McKinney 2006). Examples of avoiders include area-sensitive birds (Friesen et al. 1995) and large predatory mammals that are persecuted by humans (Fischer et al. 2012). Examples of adapters include red squirrels, which thrive in areas where understory vegetation has been removed but trees remain (Racey and Euler 1982), and American robins, which benefit from increased forest edges (Minor and Urban 2010). Rock dove (*Columba livia*), house sparrows (*Passer domesticus*), and Norway rats (*Rattus norvegicus*) can exploit novel food and shelter in the urban core (Blair 1996, McKinney 2002).

Here we investigated bird and mammal assemblage composition and individual species use at vernal pools along an urban development gradient using motion-activated cameras. We used impervious cover to represent development intensity because it includes buildings and pavement and is thus linked to traffic and chemical, light, and noise pollution. Our

primary objectives were to describe the composition of assemblages and examine how they corresponded to pool conditions and land cover types near pools at various spatial scales across an urbanization gradient.

Methods

Study area

We conducted this study within a 25 km × 7 km area that included downtown Bangor (44° 48' 8" N, 68° 46' 13" W) where there is 80–100% impervious cover (Maine Land Cover Dataset, MELCD; <http://www.maine.gov/megis/catalog/>). In general, impervious cover decreases and cover by mid-successional mixed forest (oak, *Quercus* spp.; Eastern hemlock, cover *Tsuga Canadensis*; white pine, *Pinus strobus*; American beech, *Fagus grandifolia*; poplar, *Populus* spp.; birch, *Betula* spp.; maple, *Acer* spp.; balsam fir, *Abies balsamea*) increases with distance from Bangor. Each site consisted of a vernal pool and the area within 1000 m of its high-water mark. Sites were selected based on the presence of vernal pool-breeding amphibians and to represent the range of land cover types.

Camera trapping

We placed infrared, motion-activated cameras (Bushnell Trophy Cam HD, Overland Park, Kansas; 18 m maximum detection) at 38 sites with a subset of 27, 35, and 11 sites surveyed in 2014, 2015, and 2016, respectively. At each pool one camera was placed within 2 m of the ground and within 3 m from the pool's high-water mark to capture as much of the pool as possible. Each site had a camera functioning 12–622 d (*median* = 214, *IQR* = 79–338). We identified species, behavior, and whether the animal(s) contacted pool water in photographs. All animals were detected between 15 May 2014 and 22 September 2016. We conducted this study in compliance with [institution name removed for review process] Institutional Animal Care and Use Committee standards as no animals were handled.

For modeling, we used data from sites with >50 d of camera function between 14 May – 26 August 2014–2016 (33 sites; 63–293 d per site out of 315 total days, *median* = 139, *IQR* = 93–180). This “summer” season was selected to align with peak camera function among all sites (54.0% [4711/8725] of total camera days), to capture the most taxa (87.8% [52/58] of mammal and bird taxa), and to better meet assumptions of closure for occupancy modeling.

Site characteristics

We quantified surrounding land cover types, pool vegetation, and amphibian egg masses. Using ArcView GIS 10.2 and MELCD (2004 all land use; 2011 impervious cover) we quantified tree, open water and non-forested wetland, and impervious cover within 100, 300, 600, and 1000 m from pool high-water marks. Distances matched spatial scales relevant to pool-breeding amphibians (Homan et al. 2004; Rittenhouse and Semlitsch 2007). We edited cover types to correct misclassifications and to reflect more recent aerial photographs (World Imagery; 10 July 2015).

We surveyed spring and summer vegetation at 27, 31, and 9 pools in 2014, 2015, and 2016, respectively. Spring surveys were conducted when vernal pool-breeding amphibian eggs were present in May and June. We conducted summer surveys after typical summer dry down in July and August. We visually estimated shrub, emergent, and submerged vegetation cover and measured woody vegetation canopy over pools using a spherical convex densiometer. We conducted vernal pool-breeding amphibian egg mass counts following Crouch and Paton (2000; April and May). Inter-annual means were used as covariates in analyses.

Taxon sampling curves

All statistical analyses were conducted using R version 3.3.1 (R Core Team 2016). We used the ‘vegan’ package (Oksanen et al. 2017) to create sample-based taxon sampling curves with camera-day as the sampling unit. We created species accumulation curves for sites with >30 camera days (35 sites) by adding species in order of detection. We created rarefaction curves across these 35 sites by randomly sampling (1000 random permutations, sampling without replacement) all camera days and for the subset of days from the summer season (Gotelli and Colwell 2001).

Partial redundancy analysis (pRDA)

We conducted a pRDA and variance partitioning using the ‘vegan’ package (Oksanen et al. 2017) to identify how site characteristics correlate with dominant gradients of variation in camera trapped wildlife (CTW) assemblages among sites (Borcard et al. 2011). We conditioned the RDA on latitude and longitude to account for the portion of Curtis-Bray dissimilarity in assemblages attributed to spatial correlation (Spearman’s rank correlation = 0.143, $p < 0.01$).

We represented CTW assemblage composition with a matrix of detection frequencies (proportion of camera-days a taxon was observed) of taxa \times sites. We did not account for detection probabilities when examining

assemblages because sparse detections of many taxa may produce occupancy estimates more misleading than ignoring non-detection altogether (Welsh et al. 2013) and because multi-species models may not be appropriate within groups of species that select habitat features at dissimilar scales (Dorazio et al. 2006; Royle and Dorazio 2008). We used a square root ($y + 1$) transformation on detection frequencies to dampen the influence of rare and super-abundant species.

We selected variables to represent vegetation, amphibian abundance, and land cover types. Within each category, we examined multivariate normality of variables and transformed across all variables as needed. We centered and column-standardized all explanatory variables to account for differences in units and assessed variables’ categories for collinearity (pairwise Pearson product-moment bivariate correlations ≥ 0.7). When collinearity was detected, we used forward-step variable selection (Akaike Information Criterion [AIC]-based) to select three variables in each category with < 0.7 correlation (Pearson correlation ≤ 0.63 among the nine selected variables).

We conducted Monte Carlo global permutation tests to determine the significance of the ordination, the pRDA axes, and each constraining variable. Because constraining variables are assessed sequentially for significance, we tested each variable as the first term in the model. Upon determining significance of the ordination ($p = 0.001$), we compared the pRDA with an unconstrained, unconditioned principle component analysis to assess if extracted patterns in the pRDA likely represent actual dominant gradients (Legendre and Gallagher 2001). We similarly compared the “all species” pRDA ordination to pRDAs based on “limited species” data sets (i.e., removing species only observed at one site and/or the single most common species across all sites). Since all ordinations were similar, we assumed that the constraining variables in the pRDA are related to actual gradients of variation and that rare and abundant species were not highly influential in structuring the pRDA. We then calculated the proportion of variance explained by each axis and overlaid generalized additive model (GAM) fitted surfaces on the ordination to examine the linearity of variation of each vector.

Modeling urban-affiliation

We examined the relationship between urban development intensity, as indicated by impervious cover, and an index of assemblage urban-affiliation using linear modeling. We used AIC backward-step variable selection to select well-supported ($\Delta AIC < 2$) models from a global model that included predictor terms of impervious cover within 100, 300, 600, and 1000 m. To calculate an index of urban-affiliation, we scored each taxon on a scale of 1–4 with one for taxa that avoid and/or are greatly impaired by urbanization and four for taxa that benefit from urbanization. For each site, we

multiplied the detection frequency of each taxon by its urban-affiliation score and averaged the products of all detected species, yielding an urban-affiliation index value. We did not incorporate a spatial variance structure into the model because of a lack of evidence of spatial autocorrelation among sites (Spearman's rank correlation = 0.007, $p = 0.88$).

Single-species use probability modeling

We fit single-season occupancy models (MacKenzie et al. 2006) using package 'unmarked' (Fiske et al. 2017) to examine the relationship between species-specific probability of use (θ) of a vernal pool and impervious cover while accounting for detection probability (p ; MacKenzie, 2006). We were interested in use, as opposed to occupancy, because species occupancy (i.e., home range) in an area containing a vernal pool does not necessitate their use of the pool. Following Trzcinski et al. (1999) we modeled species detected at >10% of sites (≥ 4 sites) during the summer season, using a 7-day camera function period as the sampling unit for detections to increase detectability and precision of use probability estimates. We truncated the number of sampling periods to reduce excessive missingness in the dataset and maintain ≥ 10 sites with data for all sampling periods (24 periods, 24% missingness). In using single-season models we assume that use (θ ; i.e., availability for detection) is constant across sampling units.

We identified three a priori detection covariates based on camera placement and the mean of interannual spring and summer within-pool vegetation and modeled four variables indicating intensity of urban development (impervious cover) within 1000 m (Table 1). We expected detection to decrease with thicker vegetation (Emergent, Shrub) and to increase with the percent of a pool's basin captured in a camera's view (View; which varied from 10 to 80% [$median = 60$, $IQR = 47-66$]). All detection covariates were centered and column-standardized to account for differences in distributions.

Because our small sample size (33 pools) negated a complex model including terms for spatial autocorrelation, we fit one-covariate models to estimate detection and then ranked models by AICc (AIC, adjusted for small sample size). When >1 model was $\leq 2 \Delta AICc$ we tested additive models that included all combinations of covariates ranked above the null model. We retained the detection parameter from the top ranked model and repeated the process with use covariates to determine the best use model for each species. For best-fitting models we tested goodness-of-fit (1000 bootstrap permutations; Mackenzie and Bailey 2004) and reassessed overdispersed models ($\hat{c} > 1$) using

quasi-AICc (QAICc) where \hat{c} is used as a variance inflation factor for comparing models for a more conservative model (Burnham and Anderson 2002). We calculated Nagelkerke's (1991) R-squared index to represent model improvement in comparison to the null model for selected models that had $\hat{c} \leq 4$ using. Measures of fit (i.e., $\Delta QAICc$, relative model weight, R^2_N) were not assessed for models with $\hat{c} > 4$ due to probable inadequate model structure (Burnham and Anderson 2002). To avoid overstating the potential influence of impervious cover, when the model containing a null θ covariate was $\leq 2 \Delta AICc$ (or $\Delta QAICc$) of the top model we considered the influence of θ covariates to be no different from the null and only reported model structure and parameter estimates for the null model.

Results

From 2014 to 2016 we detected 59 species (20 mammals, 39 birds) during 8725 camera days at 35 of 38 sites (Table 2). We detected 11 predatory mammals, one omnivorous mammal, seven predatory birds, and 31 insectivorous and omnivorous birds (Table 2). Thirty-nine taxa were observed at >1 site, and 29 taxa contacted pool water (Fig. 1). We observed CTW bathing, drinking, feeding on vegetation, foraging for aquatic prey, preening, swimming, standing, and walking in pools. Fifty-two species were included in assemblage analyses and occupancy modeling.

Among the 38 pools, 19 dried every year, 5 dried at least 1 year, and 14 dried down considerably but still had open water during each of the 3 years of our study (Table 3). Impervious cover was relatively low with $<10\%$ median cover across spatial scales and no site with $>40\%$ impervious cover at any spatial scale. Wood frog (*Lithobates sylvaticus*), spotted salamander (*Ambystoma maculatum*), and blue-spotted salamander (including the unisexual complex, *Ambystoma laterale - jeffersonianum*) egg masses were detected at 38, 31, and 23 sites, respectively. Among sites included in statistical analyses, the only site condition that clearly covaried with impervious cover was tree cover (negatively, Fig. 2).

Species accumulation curves (SAC) indicated that we detected only a subset of the full bird and mammal assemblage because for most sites (73%) with >30 camera-days SAC did not approach an asymptote; and neither did rarefaction curves (Fig. 3). However, rarefaction curves included an 'elbow', indicating that we captured the most rapid increase of species within the first 500 camera-days, followed by a slower increase (e.g.,

Table 2 Birds and mammals detected during a 2014–2016 camera trap survey at 38 vernal pools in Maine

Species	Camera-days swimming or wading in pool water / total camera-days detected	Sites detected (total, summer)	Only detected at sites with <10% or >20% impervious cover within 1000 m	Mean summer season detection frequency	Urban-affiliation score (1–4)
<i>Birds</i>					
wood duck (<i>Aix sponsa</i>)	82/87	10, 9	–	0.0235	1
mallard (<i>Anas platyrhynchos</i>)	188/207	17, 15	–	0.0415	3
Canada goose (<i>Branta canadensis</i>)	1/1	1, 1	<10%	0.0003	3
hooded merganser (<i>Lophodytes cucullatus</i>)	1/1	1, 1	<10%	0.0004	1
common merganser (<i>Mergus merganser</i>)	1/1	1, 1	<10%	0.0002	3
ruffed grouse (<i>Bonasa umbellus</i>)	1/7	6, 2	–	0.0007	1
wild turkey (<i>Meleagris gallopavo</i>)	3/51	10, 4	–	0.0022	2
northern goshawk (<i>Accipiter gentilis</i>)	0/0	2, 2	<10%	0.0004	1
sharp-shinned hawk (<i>Accipiter striatus</i>)	5/7	2, 1	<10%	0.0002	2
broad-winged hawk (<i>Buteo platypterus</i>)	1/1	1, 1	<10%	0.0002	2
American woodcock (<i>Scolopax minor</i>)	1/3	2, 1	–	0.0002	1
mourning dove (<i>Zenaidura macroura</i>)	0/0	2, 1	<10%	0.0001	3
great horned owl (<i>Bubo virginianus</i>)	0/0	1, 1	<10%	0.0003	2
barred owl (<i>Strix varia</i>)	1/10	4, 3	<10%	0.0005	1
ruby-throated hummingbird (<i>Archilochus colubris</i>)	0/0	1, 1	<10%	0.0003	3
northern flicker (<i>Colaptes auratus</i>)	0/0	4, 2	<10%	0.0004	3
downy woodpecker (<i>Dryobates pubescens</i>)	0/0	1, 1	>20%	0.0005	3
pileated woodpecker (<i>Dryocopus pileatus</i>)	0/0	2, 2	–	0.0006	1
hairy woodpecker (<i>Picoides villosus</i>)	0/0	4, 4	–	0.0015	3
eastern phoebe (<i>Sayornis phoebe</i>)	0/0	2, 0	–	–	–
eastern kingbird (<i>Tyrannus tyrannus</i>)	0/0	1, 1	<10%	0.0004	3
American crow (<i>Corvus brachyrhynchos</i>)	5/111	18, 14	–	0.0134	3
blue jay (<i>Cyanocitta cristata</i>)	0/0	8, 4	–	0.0007	3
tufted titmouse (<i>Baeolophus bicolor</i>)	0/0	1, 1	>20%	0.0004	3
black-capped chickadee (<i>Poecile atricapillus</i>)	0/0	3, 1	>20%	0.0002	3
red-breasted nuthatch (<i>Sitta canadensis</i>)	0/0	1, 0	–	–	–
hermit thrush (<i>Catharus guttatus</i>)	0/0	5, 3	–	0.0013	1
Swainson's thrush (<i>Catharus ustulatus</i>)	0/0	1, 0	–	–	–
American robin (<i>Turdus migratorius</i>)	5/66	11, 8	–	0.0034	3
gray catbird (<i>Dumetella carolinensis</i>)	0/0	1, 1	–	0.0038	3
European starling (<i>Sturnus vulgaris</i>)	0/0	2, 2	>20%	0.0004	4
common yellowthroat (<i>Geothlypis trichas</i>)	0/0	1, 1	>20%	0.0002	3
black-and-white warbler (<i>Mniotilta varia</i>)	0/0	1, 1	>20%	0.0005	1
yellow warbler (<i>Setophaga petechia</i>)	0/0	1, 1	>20%	0.0002	3
northern cardinal (<i>Cardinalis cardinalis</i>)	0/0	1, 0	–	–	–
rose-breasted grosbeak (<i>Pheucticus ludovicianus</i>)	0/0	1, 0	–	–	–
common grackle (<i>Quiscalus quiscula</i>)	2/23	5, 2	>20%	0.0032	3
song sparrow (<i>Melospiza melodia</i>)	0/0	1, 1	–	0.0024	3
American goldfinch (<i>Spinus tristis</i>)	0/0	2, 2	–	0.0014	3
<i>Mammals</i>					
coyote (<i>Canis latrans</i>)	13/66	16, 8	–	0.0026	3
domestic dog (<i>Canis familiaris</i>)	47/143	11, 8	–	–	–
gray fox (<i>Urocyon cinereoargenteus</i>)	0/0	1, 1	>20%	0.0001	2
red fox (<i>Vulpes vulpes</i>)	7/97	17, 8	–	0.0087	3
domestic cat (<i>Felis catus</i>)	2/63	8, 4	–	0.0066	4
bobcat (<i>Lynx rufus</i>)	0/0	5, 3	–	0.0008	2
striped skunk (<i>Mephitis mephitis</i>)	0/0	5, 2	–	0.0034	3
fisher (<i>Martes pennanti</i>)	7/73	10, 5	–	0.0034	1
weasel (<i>Mustela</i> spp.)	5/18	4, 0	–	–	–
raccoon (<i>Procyon lotor</i>)	211/505	30, 29	–	0.0805	4

Table 2 (continued)

Species	Camera-days swimming or wading in pool water / total camera-days detected	Sites detected (total, summer)	Only detected at sites with <10% or >20% impervious cover within 1000 m	Mean summer season detection frequency	Urban-affiliation score (1–4)
black bear (<i>Ursus americanus</i>)	5/36	15, 14	–	0.0054	2
moose (<i>Alces alces</i>)	1/1	1, 1	<10%	0.0003	2
white-tailed deer (<i>Odocoileus virginianus</i>)	93/429	30, 24	–	0.0545	3
North American porcupine (<i>Erethizon dorsatum</i>)	2/47	13, 7	–	0.0028	2
muskkrat (<i>Ondatra zibethicus</i>)	1/2	2, 2	–	0.0009	3
woodchuck (<i>Marmota monax</i>)	0/0	3, 3	–	0.0045	3
eastern gray squirrel (<i>Sciurus carolinensis</i>)	35/1105	29, 23	–	0.1161	4
red squirrel (<i>Sciurus vulgaris</i>)	2/214	12, 9	–	0.0246	3
eastern chipmunk (<i>Tamias striatus</i>)	0/0	12, 10	–	0.0185	4
snowshoe hare (<i>Lepus americanus</i>)	11/117	10, 8	–	0.0080	2

Species detected during the summer season from 33 sites were used in an ordination and to quantify urban-affiliation of the bird and mammal assemblage at each site. Urban affiliation scores are: 1 = avoids suburban and urban areas, 2 = somewhat adaptable to suburban areas, 3 = very adaptable to suburban areas, 4 = adaptable to suburban and urban area; references for these are in Online Resource Table 1

between camera-days 2000 and 4000 < 10 species were added).

Site characteristics corresponding to wildlife assemblages

Site characteristics and spatial distribution of sites affected CTW assemblages. All modeled land cover types, summer canopy cover, spring submerged vegetation cover, and *A. maculatum* egg mass counts were significant predictors of CTW assemblages ($p < 0.05$). Summer shrub cover and *L. sylvaticus* egg mass counts were marginally significant predictors ($0.05 < p < 0.1$).

Considerable variation in CTW assemblages among sites was constrained by site characteristics and Euclidean distance (40.8 and 26.4% of the variance, respectively). Land cover types, pool vegetation, and egg mass count variables respectively accounted for 19.4, 10.0, and 6.8% of variation in CTW assemblages (47.5, 24.4, and 16.8%, respectively, of the constrained, non-spatial variance).

The first canonical axis ($p = 0.003$), which explains 23.1% of the variation among assemblages (56.6% of constrained variance), is primarily described by Water1000 ($r = 0.51$) and Imp1000 ($r = 0.36$), summer canopy density above a pool ($r = 0.40$), and cover of



Fig. 1 Examples of camera-trapped wildlife (CTW) in contact with vernal in greater Bangor, Maine: fisher (a), black bear (b), barred owl (c), wood duck (d), white-tailed deer (e), and raccoon (f)

Table 3 Site characteristics measured at 38 vernal pools during a 2014–2016 camera trap survey in Maine

Characteristic	Range (median)
Hydroperiod (drying date)	June 6 – did not dry during study (24 pools [63%] dried ≥ 1 year)
Pool area at high-water mark (m ²)	63–9978 (420)
Impervious surface (%)	
100 m radius	0.0–34.5 (2.7)
300 m radius	0.0–36.8 (6.2)
600 m radius	0.0–38.4 (8.1)
1000 m radius	0.3–37.9 (8.5)
Tree canopy density above pool (%)	
Spring	1.0–97.0 (40.8)
Summer	2.1–99.5 (51.6)
Shrub cover (%)	
Spring	0.0–77.5 (26.3)
Summer	0.0–80.0 (27.1)
Emergent vegetation cover (%)	
Spring	0.0–99.0 (11.3)
Summer	0.0–90.0 (37.1)
Submerged vegetation cover (%)	
Spring	0.0–60.0 (10.0)
Summer	0.0–90.0 (10.0)
Amphibian mean egg mass count	
Wood frog (<i>Lithobates sylvaticus</i>)	1.3–300.7 (30.8)
Spotted salamander (<i>Ambystoma maculatum</i>)	0.0–290.0 (16.2)
Blue-spotted salamander (<i>Ambystoma laterale</i>) ^a	0.0–2065.0 (3.8)

^a Includes the unisexual complex, *Ambystoma laterale* - *jeffersonianum*

spring submerged vegetation ($r = -0.39$; Fig. 4). The second pRDA axis ($p = 0.025$), which explains 9.2% of the variance among assemblages (22.6% of constrained variance), was positively correlated with spring submerged vegetation ($r = 0.72$) and to a lesser degree with summer shrub cover ($r = 0.29$) and amphibian egg mass counts ($r = 0.24$ – 0.27). All vectors varied roughly linearly in ordination space except Imp100 (Fig. 4).

Assemblage composition along an urban development gradient

The only significant covariate in both top models predicting urban-affiliation scores was Imp1000, which was positively related to urban-affiliation scores (Table 4, Fig. 5). Thirteen species were only detected at sites with <10% impervious cover within 1000 m, and nine species were only detected at sites with >20% impervious cover within 1000 m (Table 2).

However, there was also considerable overlap of species across the development gradient: 16/52 taxa (30.8%) were detected at sites with <10% and at sites with >20% impervious cover within 1000 m.

Detection and use models

We modeled pool use for 19 species using single-season occupancy models (Table 5). Detection decreased with shrub and/or emergent cover for raccoon, white-tailed deer, eastern gray squirrel, red fox, North American porcupine, and fisher, but detection probabilities of waterfowl and domestic cat were highest in areas with greater shrub cover (Table 6, Online Resource Fig. 1–2). Models with View as a detection covariate (Table 6) indicated increased detection as more pool basin (%) was captured in photos (Online Resource Fig. 3). Red fox and snowshoe hare were respectively more and less likely to use pools with greater impervious cover within 1000 m (Table 6, Online Resource Fig. 4).

Discussion

We observed 59 bird and mammal taxa during three years of camera-trapping, expanding insights into the composition of bird and mammal assemblages using vernal pools and how these assemblages may respond to site characteristics related to urbanization. Land cover types within 1000 m and within-pool vegetation conditions strongly influence the composition of birds and mammals that use vernal pools (Fig. 4). The abundance of pool-breeding amphibians may influence assemblages, but to a lesser degree.

Although our accumulation curves (Fig. 3) indicate that we did not capture all species, the steep initial slope is characteristic of a community with a high proportion of common species (Thompson and Withers 2003). Additionally, with sufficient effort (1000s of days) species undetected by camera traps are typically those considered rare (Tobler et al. 2008). Thus, we believe that we detected a high portion of the birds and mammals that regularly used studied pools (Table 2).

Land cover

Although we explored the less developed sector of the urban development gradient compared to similar studies (e.g., Blair 1996; Clergeau et al. 1998), we still detected wildlife responses to impervious cover within 1000 m of pools. CTW trends corresponding with increased impervious cover may also signal wildlife responses to

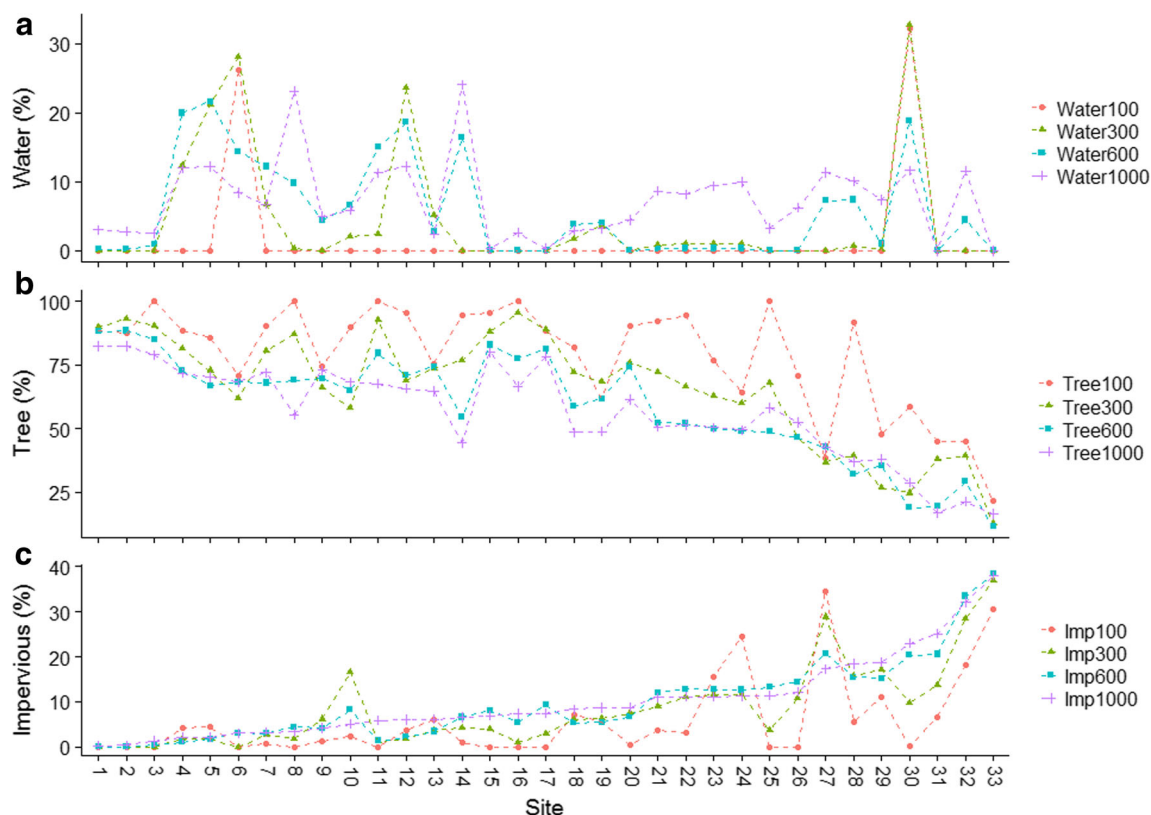


Fig. 2 Water (a), tree (b), and impervious (c) cover within 100, 300, 600, and 1000 m of 33 vernal pool sites with >50 days of camera function during a camera-trapped wildlife (CTW) survey during late spring and summer in greater Bangor, Maine in 2014–2016. Sites are arranged in

ascending order based on impervious cover within 1000 m and roughly indicate increased intensity of urbanization. Dashed lines connecting sites for each variable are for clarity in showing how all other variables change with urbanization intensity

deforestation and, more generally, to urban development, especially since the pre-disturbance matrix in our study area was dominated by forest, and impervious and tree cover are negatively correlated (Fig. 2). In our study, land cover types within 1000 m of pools explained more variation in CTW assemblages than within-pool vegetation or amphibian egg numbers aligning with the

idea that land cover types at broad spatial scales shape the set of species present at smaller scales (Johnson 1980) and/or limit resources that affect home range size (McLoughlin and Ferguson 2000). More specifically, our findings suggest little response of assemblages to small-scale (100 m) impervious cover when impervious cover is relatively high at large scales (1000 m; Fig. 4). However, assemblages at pools in relatively undisturbed larger landscapes (1000 m) are predicted to respond to impervious cover at small scales (100 m). Consequently, the influence of development up to 1000 m from pools may be dominant in determining the birds and mammals using pools even if areas directly adjacent to pools are undeveloped (Rodewald 2003; Hanowski et al. 2006).

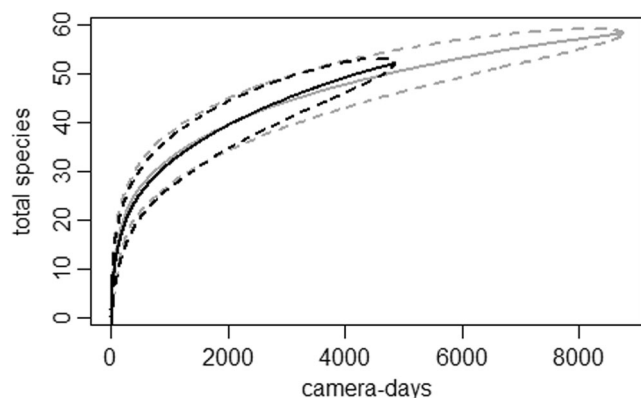


Fig. 3 Rarefaction curves of camera-trapped bird and mammal taxa at 38 vernal pools with year-round (gray) and summer season (black) observations in Maine during 2014–2016. Curves (solid lines) are based on 1000 random permutations, sampling without replacement. Dashed lines are standard deviations

The positive association we detected between impervious cover and urban-affiliation of CTW (Fig. 5) further supports the idea that development within 1000 m of pools may influence bird and mammal assemblages even in landscapes with relatively little urban development (e.g., 0.3–37.9% impervious cover within 1000 m; Table 3, Fig. 2). Although we detected a significant association between impervious cover and use probabilities only for red fox (positive) and snowshoe hare (negative), these use probabilities varied predictably

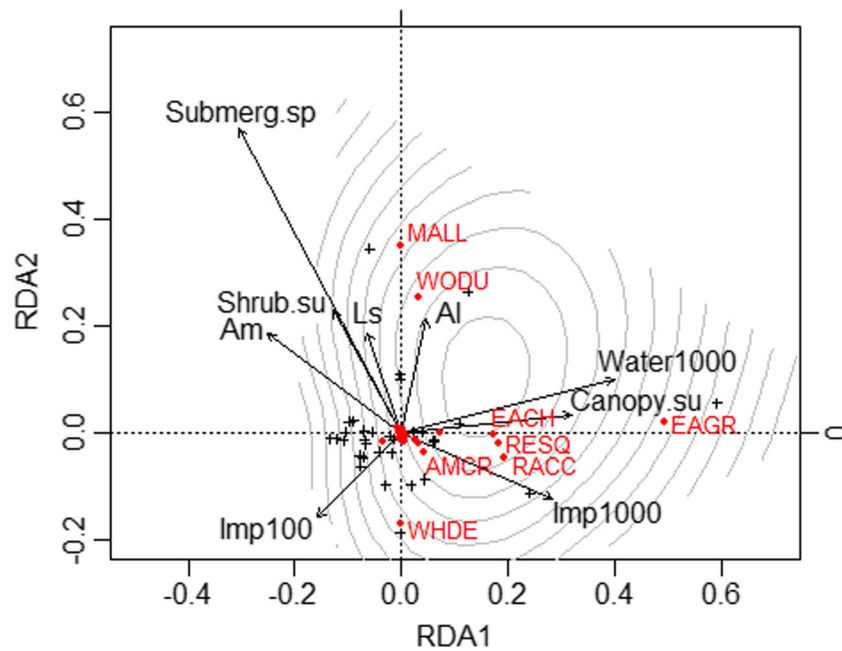


Fig. 4 Partial redundancy analysis (pRDA) ordination for observation frequencies of 52 camera-trapped bird and mammal taxa across 33 vernal pools in Maine during 2014–2016. Sites are black crosses, red dots are observed taxa, and vectors represent site characteristics. Labeled taxa are: MALL = mallard (*Anas platyrhynchos*), WODU = wood duck (*Aix sponsa*), AMCR = American crow (*Corvus brachyrhynchos*), WHDE = white-tailed deer (*Odocoileus virginianus*), RACC = raccoon (*Procyon lotor*), EAGR = eastern gray squirrel (*Sciurus carolinensis*), RESQ = red squirrel (*Sciurus vulgaris*), and EACH = eastern chipmunk (*Tamias*

striatus). Vector labels are: Canopy.su = mean density of summer tree canopy across years, Shrub.su = mean summer shrub cover, Submerg.sp. = mean spring submerged vegetation cover; AI, Am, and Ls = mean egg mass counts for *A. laterale*, *A. maculatum*, and *L. sylvaticus*, respectively; and Imp100, Imp1000, and Water1000 are the percent impervious or open water cover within 100 or 1000 m of pools. Variance explained: RDA1 = 56.6%; RDA2 = 22.6%. Contours (gray) represent change in impervious cover within 100 m across ordination space

relative to species' urban affiliations (Table 2). These relationships align with previous research on community composition response to human disturbance (Beissinger and Osborne 1982; Nilon and VanDruff 1986; Croonquist and Brooks 1991).

The abundance of several urban-adaptable species (e.g., raccoon, eastern gray squirrel, American robin, and white-tailed deer) across study sites also may explain why use probability was not associated with impervious cover for 17 of the 19 modeled species (Table 5); i.e., the mean urban-affiliation score was 3 or 4 for 12 of the 17 species for which use was modeled but no

response to impervious cover was detected (Tables 2 and 5). Because we only modeled data from frequently detected species (detected at >10% of sites), our analyses were biased towards urban adapters and away from those species that avoid human disturbance and would likely have a strong negative response to impervious

Table 4 Top ranked models predicting urban-affiliation scores of bird and mammal assemblages at vernal pools

Model	Covariates	β Estimate (p-value)	95% CI lower	95% CI upper	AIC	Δ AIC
1	Imp100	-0.004	-0.012	0.004	-119.06	1.01
	Imp1000	(0.347)	0.004	0.020		
2	Imp1000	0.009 (0.005)	0.003	0.016	-120.07	NA

The 52 modeled bird and mammal taxa were detected with camera-traps across 33 vernal pools in Maine during 2014–2016

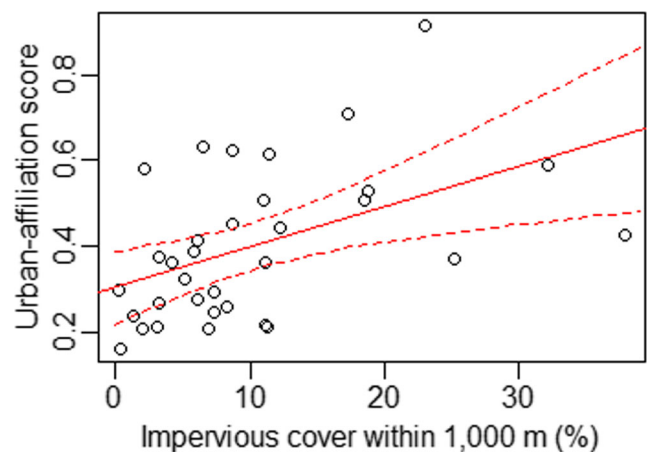


Fig. 5 Predicted and observed urban affiliation-scores of bird and mammal assemblages at vernal pools in Maine during late spring and summer 2014–2016. Open circles are observed values, the solid line represents predicted values, and dashed lines represent the 95% confidence interval

Table 5 Summary of the selected use models for 19 species at 33 vernal pools in Maine, USA, during summer 2014–2016

Species	Top model	K	p	\hat{c}	ΔAICc or QAICc	w	R^2_N
raccoon	$\theta(\cdot)\text{P}(\text{Shrub}+\text{Emergent})^{\text{a, b}}$	5	0.00	2.6	0.00	0.51	0.55
white-tailed deer	$\theta(\cdot)\text{P}(\text{Shrub})$	3	0.57	0.7	0.00	0.31	0.64
eastern gray squirrel	$\theta(\cdot)\text{P}(\text{Emergent})^{\text{a}}$	4	0.38	1.1	0.00	0.41	0.47
mallard	$\theta(\cdot)\text{P}(\text{Shrub})$	3	0.69	0.1	1.35	0.12	0.29
American crow	$\theta(\cdot)\text{P}(\cdot)$	3	0.00	4299.0	–	–	–
black bear	$\theta(\cdot)\text{P}(\cdot)$	2	0.11	0.0	0.00	0.32	0.00
eastern chipmunk	$\theta(\cdot)\text{P}(\cdot)$	3	0.00	378.1	–	–	–
red squirrel	$\theta(\cdot)\text{P}(\text{View})$	3	0.96	0.0	1.83	0.22	0.63
wood duck	$\theta(\cdot)\text{P}(\text{Emergent})$	3	0.87	0.1	0.00	0.39	0.58
red fox	$\theta(\text{Imp1000})\text{P}(\text{Shrub})^{\text{b}}$	4	0.81	0.1	0.00	0.80	0.48
snowshoe hare	$\theta(\text{Imp1000})\text{P}(\cdot)$	3	0.18	0.5	0.00	0.23	0.21
American robin	$\theta(\cdot)\text{P}(\cdot)$	3	0.00	197.3	–	–	–
coyote	$\theta(\cdot)\text{P}(\cdot)$	2	0.08	0.8	0.06	0.35	0.00
North American porcupine	$\theta(\cdot)\text{P}(\text{Shrub})$	3	0.16	0.6	0.00	0.35	0.15
fisher	$\theta(\cdot)\text{P}(\text{View}+\text{Emergent})$	4	0.43	0.3	0.00	0.47	0.35
domestic cat	$\theta(\cdot)\text{P}(\text{Shrub})$	3	0.48	0.1	1.84	0.09	0.54
wild turkey	$\theta(\cdot)\text{P}(\cdot)^{\text{b}}$	3	0.00	1014.8	–	–	–
hairy woodpecker	$\theta(\cdot)\text{P}(\text{View})$	3	0.55	0.0	1.71	0.09	0.32
blue jay	$\theta(\cdot)\text{P}(\cdot)$	2	0.18	0.7	0.74	0.23	0.00

Model terms in parentheses represent detection (P) and use (θ). Model appropriateness and fit were assessed via an estimated overdispersion parameter (\hat{c}) and the Chi-squared goodness-of-fit test p -value (p), rank (ΔAICc or QAICc), relative model weight (w), and Nagelkerke's R-square value (R^2_N). Delta AICc or QAICc, w , and R^2_N were not assessed for models with $\hat{c} > 4$ due to probable inadequate model structure (Burnham and Anderson 2002). Model covariate descriptions are in Table 1

^a QAICc was used to assess model rank

^b All other models were $> 2 \Delta\text{AICc}$ or ΔQAICc

cover. Alternatively, we may not have detected use differences for species that respond to facets of urbanization other than impervious cover (e.g., vegetation composition, landscape fragmentation; Boren et al. 1999). Additionally, aiming cameras at pools may have biased detections towards urban adapters as small animals and especially canopy species, most of which are urban avoiders (e.g., Beissinger and Osborne 1982), were less likely to be detected (Tobler et al. 2008; Rowcliffe et al. 2011).

Within-pool vegetation

Within-pool vegetation was the second-most important category of predictors (% variance explained). Our observations of white-tailed deer and moose foraging in pools suggest vegetation may be an attractant for some species. The negative effect of emergent and shrub cover on the detection probabilities for raccoon, eastern gray squirrel, red fox, white-tailed deer, and North American porcupine (Table 6, Online Resource Fig. 1–2) likely demonstrates that lower-strata vegetation within pools can provide cover for mammals such as these

(Chamberlain et al. 2002; Fuller and Destefano 2003). Positive associations between vegetation and detection are difficult to interpret but may indicate that detection and use are confounded for species that respond to lower-strata vegetation via changes in abundance or frequency of use (Welsh et al. 2013).

Aquatic amphibians

The associations between CTW and vernal pool-breeding amphibian egg numbers support the idea that amphibians provide food for birds and mammals (Fig. 4). More specifically, spotted salamander and wood frog egg numbers were significant predictors of CTW and all three amphibian species had a similar direction of effect (Fig. 4). Additionally, raccoon, mallard, and wood duck displayed behaviors commonly associated with foraging and may have preyed upon embryonic or larval amphibians and/or insects within-pools. Other studies have also documented birds and mammals consuming pool-breeding amphibians (Berven 1990) and aquatic invertebrates (Cox et al. 1998). Even if these suspected predator-prey interactions do not significantly shape bird and mammal assemblages they may be important for prey population

Table 6 Estimated parameters (β) and standard error (S.E.) for use (θ) and detection (P) parameters of the top ranked occupancy models predicting species use for species detected at ≥ 4 sites

Species	Parameter	Variable	β	S.E.
raccoon	θ	Intercept	2.26	0.66
	P	Intercept	-0.73	0.10
	P	Shrub	-0.38	0.12
	P	Emergent	-0.36	0.11
white-tailed deer	θ	Intercept	1.50	0.53
	P	Intercept	-1.28	0.13
	P	Shrub	-0.86	0.15
eastern gray squirrel	θ	Intercept	0.86	0.39
	P	Intercept	-0.49	0.10
	P	Emergent	-0.48	0.12
mallard	θ	Intercept	-0.06	0.37
	P	Intercept	-1.50	0.17
	P	Shrub	0.55	0.16
black bear	θ	Intercept	0.66	0.76
	P	Intercept	-2.81	0.33
red squirrel	θ	Intercept	-0.94	0.42
	P	Intercept	-1.32	0.24
	P	View	1.66	0.36
wood duck	θ	Intercept	-0.54	0.44
	P	Intercept	-1.21	0.21
	P	Emergent	3.16	0.63
red fox	θ	Intercept	-1.78	0.65
	θ	Imp1000	2.01	0.77
	P	Intercept	-1.32	0.24
	P	Shrub	-0.60	0.25
snowshoe hare	θ	Intercept	-2.66	1.08
	θ	Imp1000	-2.86	1.49
	P	Intercept	-1.84	0.29
coyote	θ	Intercept	-0.80	0.70
	P	Intercept	-2.96	0.55
North American porcupine	θ	Intercept	-0.88	0.55
	P	Intercept	-2.98	0.46
	P	Shrub	-1.02	0.46
fisher	θ	Intercept	-0.78	0.74
	P	Intercept	-4.61	1.30
	P	View	1.07	0.49
	P	Emergent	-2.49	1.33
domestic cat	θ	Intercept	-1.29	0.65
	P	Intercept	-2.83	0.60
	P	Shrub	1.51	0.35
hairy woodpecker	θ	Intercept	0.46	1.11
	P	Intercept	-6.54	1.64
	P	View	3.31	1.34
blue jay	θ	Intercept	5.96	45.5
	P	Intercept	-5.29	0.59

Parameters were not estimated for grossly overdispersed models ($\hat{c} > 4$)

dynamics. For example, Childs (1953) observed that in a single night a raccoon consumed all tadpoles in a pool. Additionally, diseases that can threaten amphibian populations, such as chytridiomycosis (Wake and Vredenburg 2008) and ranavirus, could be introduced by birds and mammals that move among pools (Gray et al. 2009).

Conclusions

Our results support commonly observed trends in bird and mammal assemblage composition along urban gradients, primarily an increase in species that can adapt to or even exploit human-altered landscapes. This occurs even with relatively low intensity development at spatial scales encompassing land quite distant from pools (e.g., 0.3–37.9% impervious cover within 1000 m). Birds and mammals are likely important components of pool ecosystems and should be considered in management decisions even though they are not pool specialists. These animals can be thought of as surrogates that indicate natural system function (Hunter et al., 2016), and changes in their occupancy and assemblage composition with urbanization are likely to parallel degradation of pool-breeding amphibian populations and other vernal pool ecosystem functions. We encourage land use planners and managers to consider bird and mammal responses to zoning and land use practices within 1000 m of pools and to select pools embedded in landscapes that are relatively undisturbed (i.e., fully functioning) within 1000 m to implement vernal pool mitigation or conservation planning (Calhoun et al. 2017). We also encourage preferential conservation of pools that have sizable populations of breeding amphibians as they may provide important food for birds and mammals.

Because our primary aim was to document birds and mammals using vernal pools we did not compare use between vernal pool and non-vernal pool sites. Further study of such paired sites could help disentangle the effects of pool presence on bird and mammal assemblages from land cover type and local vegetation cover as well as identify possible bird and mammal community response to pool destruction. Comparing assemblages between pairs of pools with and without pool-breeding amphibian eggs and/or larvae could further elucidate the role of amphibians in influencing use of pools by birds and mammals, and predation experiments could substantiate to what extent birds and mammals can prey on amphibian eggs and larvae. We also suggest that future research also address influences of pool hydrology (e.g., pool area, hydroperiod, depth) on birds and mammals as area, hydroperiod, and depth of vernal pools can differ dramatically among pools and these differences may be exacerbated by hydrological alterations in urbanizing landscapes.

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