

Wetlands as habitat in urbanizing landscapes: Patterns of bird abundance and occupancy

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ARTICLE INFO

Article history:

Received 27 July 2010

Received in revised form

19 November 2010

Accepted 20 November 2010

Available online 26 January 2011

Keywords:

Urbanization

Avian diversity

Isolated wetland

New England

Occupancy modeling

ABSTRACT

Wetlands in urban landscapes provide nesting opportunities for wetland breeding birds as well as enhanced food resources that may be utilized by opportunistic species and those that can tolerate human activity. We investigated the degree to which birds utilize urban wetlands by examining breeding bird communities in urban and rural wetlands and nearby uplands in the northeast US. From mid-May through June in 2008, we conducted 10-min, 50 m radius point counts at 99 randomly chosen sites along a gradient of watershed urbanization. Bird abundance and species richness was significantly higher in wetlands versus uplands, and at urban wetlands versus urban uplands, but not at rural wetlands versus rural uplands. Overall, more species were present at wetland versus upland sites, but the difference between wetland and upland was less for human-tolerant species. While the amount of natural vegetation within a 50 m buffer of a site was significantly negatively correlated with the amount of urban land within 1 km, bird abundance and species richness increased. Species-specific habitat models using general vegetation classes showed differences in bird habitat associations as watersheds became more urbanized. Our findings demonstrate the importance of wetland habitats for birds, and add to the body of evidence that supports the protection and restoration of wetlands as a means towards maintaining or enhancing habitat heterogeneity and biodiversity in urban landscapes.

Published by Elsevier B.V.

1. Introduction

Interest in the effects of urbanization on wildlife habitat has been growing in response to continued expansion of urban areas into adjacent rural landscapes. Several studies have focused on birds, possibly because they are highly visible species whose habitat requirements are well documented (Chace and Walsh, 2006; Evans et al., 2009). A majority of these studies have examined changes in bird communities as a result of urbanization and human-induced alteration of habitats. Generally, avian species richness has been shown to peak at intermediate levels of urbanization, whereas abundance peaks at high urbanization as a result of high densities of a few synanthropic or human-tolerant species (Blair, 1996; Marzluff, 2001; Tratalos et al., 2007). It has been proposed that synanthropic birds dominate highly urbanized areas in response to both bottom-up (enhanced resources) and top-down (relaxed predation) forces (Faeth et al., 2005; Rodewald and Shustack, 2008). Under these conditions, a few species of synanthropic birds

are often able to out-compete endemic species, leading to structural homogenization of bird communities (Devictor et al., 2008; Ortega-Alvarez and MacGregor-Fors, 2009). Indeed, the presence of endemic species has been shown to decrease at sites with increasing surrounding urban land, and conversely increase in the presence of natural vegetation and increasing vegetative structural complexity (Aurora et al., 2009; Evans et al., 2009; Suarez-Rubio and Thomlinson, 2009). A conservation strategy geared towards maximizing avian species diversity, and in particular conserving endemic species that have been displaced in urban landscapes, should therefore consider maintaining or enhancing natural habitat heterogeneity at multiple scales.

Several studies have demonstrated that natural habitat heterogeneity within urban landscapes can enhance avian species richness. Gifford et al. (2010) showed that even highly fragmented urban pine barren habitats can provide breeding habitat and may aid in the conservation of early-successional shrubland birds. Urban forest fragments in Australia were found to provide suitable habitat for ecological specialists and species otherwise found in low density in urban settings (Platt and Lill, 2006). Other habitat types such as desert scrub, grasslands, and coastal sage shrublands have been shown to potentially ameliorate urban impacts on native bird community assemblages (Chace and Walsh, 2006). Wetlands may

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also help mitigate urbanization effects on bird species richness by providing enhanced habitat and resources as a result of mesic conditions and enhanced productivity relative to nearby upland areas (Mitsch and Gosselink, 2000). This may be particularly true when wetland obligate species are endemic to an area impacted by increasing urbanization. However, few studies have examined bird communities associated with wetlands in urban landscapes. In the northeastern US, seasonal pool wetlands were found to support higher avian diversity and abundance than nearby upland areas (McKinney and Paton, 2009). In contrast, several landscape-scale studies have demonstrated reduced avian diversity in wetlands subject to higher levels of human disturbance (DeLuca et al., 2004; Whited et al., 2000). Therefore, as a first step in understanding the role of urban wetlands in maintaining avian species diversity, we need a better understanding of wetland bird community composition in urban settings.

In this study we investigated breeding birds associated with wetlands throughout urban and rural areas in the urbanizing northeast US. We tested the hypothesis that urban wetlands support a greater richness and abundance of birds than upland (i.e., non-wetland) areas by assessing abundance, species richness, and community composition at a series of wetlands and adjacent upland sites. We also classified vegetative structure at our sites to identify habitat characteristics that may be influencing bird occurrence in wetlands, and used occupancy modeling to examine whether proximity to urban areas influences avian abundance or community composition near wetlands. Results from our study will provide information about the habitat value of urban wetlands to help inform regulatory and resource management agencies in evaluating protection and restoration strategies.

2. Methods

2.1. Study sites

We randomly selected 50 small wetlands from a larger set of sites identified for a concurrent study of amphibian breeding habitats (Curtis, 2009), and also from an ongoing study examining the effects of development strategies on habitat quality in a series of cluster developments (i.e., residential developments that seek to preserve contiguous areas of natural habitat). The sites were located within Providence, Kent, and Washington counties in Rhode Island ($41^{\circ}40'00''N$, $71^{\circ}30'00''W$). Wetland size ranged from 0.01 to 1.39 ha, with a mean (± 1 SE) area of 0.17 ± 0.04 ha.

2.2. Bird surveys

We established point count stations at the edge of wetlands using a randomly oriented transect radiating outward from the center of wetlands, and conducted 10-min point counts at each station from mid May to the end of June 2008. A subset of 17 stations was sampled during mid May and of June 2009. All birds seen or heard within a 50-m radius were recorded using a dependent-observer approach. In this approach, survey teams consisted of a primary observer who noted bird species and abundance, and a secondary observer who recorded data and noted any individuals missed by the primary observer (Forcey et al., 2006; Nichols et al., 2000). We also conducted point counts at upland stations, which were placed at the end point of a randomly oriented line radiating 150 m from each wetland's point count station. Although we recognize there may be some bias resulting from subjective inclusion of birds that could occur outside of the 50-m radius, we were consistent in our survey effort at both wetland and upland sites, such that any tendency to overestimate bird abundance should be equal across all sites. During each site visit, we conducted one point count survey at

both the wetland and upland stations within 20 min of each other. All point counts were conducted between 0600 and 1000 h.

We also collected data on four survey-specific covariates for use in occupancy modeling (developing best-fit regression models to assess habitat characteristics that influence the occurrence of birds at sites): sample day (days from May 17), time of day (minutes from 06:00 h), estimated percent cloud cover, and air temperature ($^{\circ}$ C) at the time of the point count (Ralph and Scott, 1981; Selmi and Boulinier, 2003). We used these survey covariates to model detection probability, or the probability of detecting a species when it is actually present during a single visit (MacKenzie et al., 2002).

2.3. Habitat characterization

To assess vegetative structure at our sites, we used a modification of the Habitat Structure Assessment (HSA) Protocol established for the Monitoring Avian Productivity and Survivorship program (Nott et al., 2003). In this protocol, vegetation was classified using vegetation formations described in the National Vegetation Classification Standard (NVCS, 1997). We classified vegetation within a 50 m radius around each site using a formation code that included class (e.g., forest, shrubland), subclass (e.g., deciduous forest, evergreen shrubland), group (e.g., cold-deciduous forest) and formation (e.g., temporarily flooded cold-deciduous forest). True-color 2003–2004 digital aerial photos (RIGIS, 2010) were heads-up digitized to determine the areal percent of each formation within the 50 m circular buffer (0.79 ha) around each site. In addition to aerial photo interpretation, vegetation at twenty randomly selected sites was assessed during a site visit using the same classification protocol as a check on the photo interpretation method. Twenty-two vegetation formations were identified across all sites which were condensed into ten broad vegetation categories prior to occupancy modeling. We used the 2003–2004 digital aerial photos to estimate the percent wetland within a 50-m radius of each point count station by digitizing the amount of open water and extent of wetland vegetation. Each wetland site was also assigned to a wetland class using a modification of the Cowardin et al. (1979) national wetlands classification system developed by the Rhode Island Geographic Information System Data Repository.

Additional habitat and land-use characteristics were quantified using Geographic Information System (GIS) topographic databases. We obtained GIS data (land use and land cover) from Rhode Island Geographic Information System (RIGIS, 2010) and processed data using Environmental Systems Research Institute ARC GIS software (Redlands, CA). Land use and land cover data were summarized from 1995 aerial photography (1:24,000 scale) coded to Anderson modified level 3 (Anderson et al., 1976) to 0.1 ha minimum polygon resolution. We used this information to calculate the percent impervious surface, percent urban land (residential, commercial, institutional, transportation infrastructure, and industrial land), and percent maintained open land (vacant and recreational land) within a 1 km buffer around the each point count station. As an operational definition, we classified sites with >40% urban land as urban based on a natural break (i.e., distinct decrease in values; Fig. 2a) in the proportion of natural lands (i.e., forest, shrub, grassland, wetland) in the 50 m buffer around the sites. Using this criterion 17 of the wetland sites were classified as urban.

2.4. Occupancy modeling

We used a likelihood-based method to develop models to predict site occupancy when species detection probabilities were less than one (MacKenzie et al., 2002). Species occurrence data from the 50 wetland and upland sites were used to estimate detection probabilities for all species observed using the program Presence (Hines, 2006). We then used a two-step process to compare a pri-

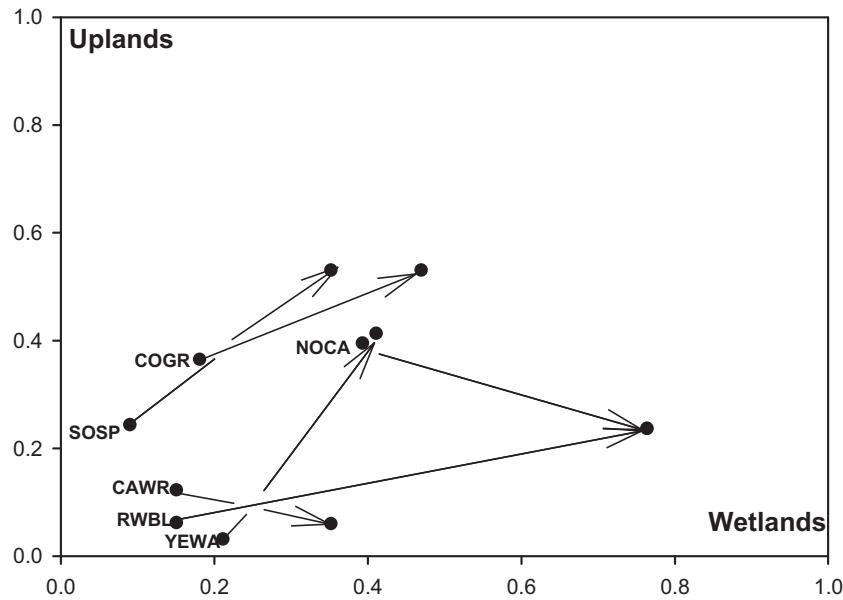


Fig. 1. Plot of the fraction of sites at which species were observed in urban and rural wetlands versus urban and rural uplands for 6 species whose percent detection increased in urban wetlands at sample sites in the Rhode Island, USA study area. Labeled circles indicate the fraction occurrence of the species at rural sites, circles at arrowheads indicate the fraction occurrence of the species at urban sites. Arrow lines indicate magnitude of increased presence at urban sites; a more horizontal orientation indicates greater relative presence in wetlands, while a more vertical orientation indicates greater relative presence in uplands. Species abbreviations are described in Table 1.

ori multiple regression models for 14 species that had detection probabilities greater than 0.30. We focused on species with detection probabilities greater than 0.30 because these species generally had sufficient detections to result in robust occupancy models. First, we determined a single best-fit regression model using small-sample size Akaike Information Criteria (AIC_c) in Presence for each species to evaluate candidate models constructed from the 4 survey-specific covariates (sample day, time of day, cloud cover, air temperature). With this model as a starting point, we then chose habitat characteristics to include in each species' regression models based on life history accounts published by Ehrlich et al. (1988). For example, we considered characteristics such as preferred nest location (e.g., ground versus shrub versus tree), diet preference, and preferred foraging technique, among others. In this way we were able to construct a series of parsimonious models for each species that took into account sampling covariates that may influence both detection and a species' habitat requirements.

Regression models were ranked according to AIC_c values (Burnham and Anderson, 2002). We then used model averaging to estimate parameter values for each habitat characteristic that occurred in the best fit models ($\Delta AIC_c < 2$; Burnham and Anderson, 2002).

2.5. Statistical analysis

Point count data were used to calculate detection probabilities, the abundance of individuals, and species richness at each site. To avoid bias from unequal sampling effort, we only used data collected in 2008 for these calculations and in occupancy modeling. We used the Shapiro-Wilk test to assess normality of residuals; all data were normally distributed (Sokal and Rohlf, 1995). We tested for differences in mean abundance and species richness between wetland and upland sites using paired t -tests, and for differences among habitat characteristics at the sites using two-tailed t -tests. Linear regression analysis was used to compare the extent of urbanization with bird abundance and species richness. Descriptive statistics were reported as means \pm 1 standard error (SE). Statistical analyses other than the likelihood-based modeling were performed with SAS for Windows ver. 6.12 (SAS Institute, Inc., Carey, NC, USA).

3. Results

3.1. Bird abundance and species richness

We detected 55 bird species across all point count stations (Appendix A), of which 50 were recorded at wetlands and 33 at uplands. A total of 28 species were recorded at both wetlands and uplands, while 10 species were observed exclusively at urban sites and 19 species were observed only at rural sites. Five wetland obligate species (Ehrlich et al., 1988) were observed across all wetland sites, with an average abundance of 0.26 birds per site and average species richness of 0.02 species per site. A total of 10 species were observed exclusively at urban sites, while 19 species were observed exclusively at rural sites. American robins (*Turdus migratorius*), gray catbirds (*Dumetella carolinensis*), Northern cardinals (*Cardinalis cardinalis*), common grackles (*Quiscalus quiscula*), and song sparrows (*Melospiza melodia*) were most abundant across all sites. American robins, gray catbirds, and red-winged blackbirds (*Agelaius phoeniceus*) were the species most often detected at wetland sites, while American robins, gray catbirds, and common grackles were most often detected at upland sites. More species were consistently observed at wetland versus upland sites, but more commonly observed species (i.e., those observed at a higher percentage of sites), are more likely to be observed equally at wetland versus upland sites (Table 1a). Six of fourteen species with detection probabilities greater than 0.30 were more frequently observed at urban wetlands versus rural wetlands (Fig. 1). Of these, red-winged blackbirds and Northern cardinals showed the greatest increase in percent occurrence at wetland sites when comparing rural versus urban sites (Table 2 and Fig. 1).

Mean abundance ($t=1.80, p=0.04$) and species richness ($t=1.90, p=0.03$) of all birds were significantly higher at wetlands than uplands across all sites (Table 3). For all birds, mean abundance at urban wetlands was 1.8 times greater than at urban uplands ($t=3.86, p<0.001$), and 2.2 times greater than at rural wetlands ($t=5.09, p<0.001$). Species richness at urban wetlands was also significantly greater than at urban uplands ($t=3.26, p=0.002$) and rural wetlands ($t=4.68, p<0.001$). Wetland area was not significantly correlated with abundance or diversity at either urban or

Table 1

Bird species richness and frequency of species observed at sample sites in the Rhode Island, USA study area. Frequency refers to number of occurrences within the various categories of sites; for example, 20 species were observed at more than 10% of the wetland sites (i.e., more than 5 sites), while only 3 species were observed at more than 50% of the wetland sites (i.e., more than 27 sites). Urban sites are those with greater than 40% urban land within a 1 km buffer of point count locations.

Frequency	All sites	Wetlands	Uplands	Urban wetlands	Urban uplands	Rural wetlands	Rural uplands
At least 1 site	55	50	33	32	20	39	29
>10% of sites	20	20	21	20	13	21	20
>20% of sites	10	11	7	13	9	9	14
>50% of sites	2	3	1	4	3	2	1

Table 2

Detection probabilities and percentage of sites at which the species were observed for 13 species with detection probabilities greater than 0.3 at sample sites in the Rhode Island, USA study area.

Species ^a	Detection probability	All sites	Wetlands	Uplands	Urban wetlands	Urban uplands	Rural wetlands	Rural uplands
AMRO	0.74	71.7	72.0	72.0	76.5	88.2	66.7	63.6
CAWR	0.34	16.2	22.0	10.0	35.3	5.9	15.2	12.1
COGR	0.61	36.4	30.0	42.0	47.1	52.9	18.2	36.4
COYE	0.32	5.1	10.0	0	5.9	0	12.1	0
GRCA	0.58	55.6	68.0	44.0	64.7	47.1	52.9	18.2
HOSP	0.69	12.1	4.0	20.0	5.9	41.2	3.0	9.1
MODO	0.32	16.2	12.0	20.0	17.6	17.6	9.1	21.2
NOCA	0.58	44.4	54.0	34.0	76.5	23.5	39.4	39.4
OVEN	0.60	18.2	24.0	12.0	0.0	0.0	39.4	18.2
RWBL	0.67	24.2	36.0	12.0	76.5	23.5	15.2	6.1
SOSP	0.63	26.3	18.0	34.0	35.3	52.9	9.1	24.2
TUTI	0.36	25.3	32.0	18.0	23.5	0.0	36.4	27.3
VEER	0.57	9.1	14.0	4.0	0.0	0.0	21.2	6.1
YEWA	0.31	22.2	28.0	16.0	41.2	41.2	21.2	3.0

^a AMRO: American robin (*Turdus migratorius*); CAWR: carolina wren (*Thryothorus ludovicianus*); COGR: common grackle (*Quiscalus quiscula*); COYE: common yellowthroat (*Geothlypis trichas*); GRCA: gray catbird (*Dumetella carolinensis*); HOSP: house sparrow (*Passer domesticus*); MODO: mourning dove (*Zenaidura macroura*); NOCA: northern cardinal (*Cardinalis cardinalis*); OVEN: ovenbird *Seiurus aurocapillus*; RWBL: red-winged blackbird (*Agelaius phoeniceus*); SOSP: song sparrow (*Melospiza melodia*); TUTI: tufted titmouse (*Baeolophus bicolor*); VEER: veery (*Catharus fuscescens*); YEWA: yellow warbler (*Dendroica petechia*).

rural sites. We saw no significant difference in bird abundance ($t=2.12$, $p=0.13$) or species richness ($t=2.08$, $p=0.10$) between visits at sites sampled multiple years.

3.2. Site vegetation and land use characteristics

Across all sites the predominant vegetation class was broad-leaved deciduous forest, followed by maintained open land and mixed forest (Table 4a). Urban sites were predominantly main-

tained open land, followed by broad-leaved forest and wetland. Urban wetlands had a higher percentage of wetland vegetation and maintained open land, and a lower percentage of forested land, than rural wetlands. The amount of natural vegetation within a 50 m buffer of a site was significantly negatively correlated with the amount of urban land within 1 km ($r=-0.71$, $F=100.2$, $p<0.001$). A plot of the percent natural vegetation within a 50 m buffer of a site versus urban land within 1 km showed a threshold at about 40% urban land, above which the amount of natural vegetation around a site decreased (Fig. 2a). Overall, at wetland sites the percent of forested wetlands was nearly double that of shrub wetlands, whereas at urban wetlands there was an equal percentage of forested and shrub wetlands (Table 4b). Bird abundance ($r=0.35$, $F=13.4$, $p<0.001$; Fig. 2b) and species richness ($r=0.33$, $F=11.7$, $p=0.001$) increased across all sites with increasing amounts of urban land within 1 km of a site. Of the five most abundant species across all sites, American robins ($r=0.29$, $F=8.81$, $p=0.004$), common grackles ($r=0.37$, $F=15.4$, $p<0.001$), and song sparrows ($r=0.41$, $F=19.7$, $p<0.001$) increased in abundance with increasing urban land within 1 km within 1 km of a site, while gray catbirds ($r=0.04$, $F=0.15$, $p=0.70$), and northern cardinals ($r=0.02$, $F=0.03$, $p=0.85$) were not significantly correlated.

3.3. Occupancy modeling

Five vegetation classes entered into best occupancy models across all 14 species (Table 5). The amount of wetland within 50 m of a site entered into best regression occupancy models of 10 of the 14 species detected at rural sites (Table 5a), and 8 of the 12 species detected at urban sites (Table 5b). Fraction wetland, along with fraction maintained open land, significantly entered into the most occupancy models. Considering only correlation coefficients greater than zero (i.e., mean – SE > 0), the occupancy of three species (gray catbirds, song sparrows, and yellow) warblers (*Dendroica petechia*) was significantly positively correlated with

Table 3

(a) Mean (\pm SE) abundance and (b) mean (\pm SE) species richness of breeding birds at wetland and upland sites, and results of paired *t*-tests between wetland and upland types in the Rhode Island, USA study area. Only comparisons that resulted in a significant difference were reported. Urban sites are those with greater than 40% urban land within a 1 km buffer of point count locations.

Habitat	Mean abundance	Significantly differs from	df	t	p
(a)					
All wetlands	8.74 \pm 0.81	All uplands	98	1.80	0.04
All uplands	6.79 \pm 0.65				
Urban wetlands	13.7 \pm 1.33	Urban uplands	31	3.86	<0.001
		Rural wetlands	25	5.09	<0.001
Urban uplands	7.56 \pm 0.89				
Rural wetlands	6.21 \pm 0.68				
Rural uplands	6.33 \pm 0.85				
Habitat	Mean abundance	Significantly differs from	df	t	p
(b)					
All wetlands	5.36 \pm 0.40	All uplands	98	1.90	0.03
All uplands	4.25 \pm 0.36				
Urban wetlands	7.59 \pm 0.56	Urban uplands	16	3.26	0.002
		Rural wetlands	25	4.68	<0.001
Urban uplands	4.89 \pm 0.55				
Rural wetlands	4.21 \pm 0.42				
Rural uplands	3.87 \pm 0.44				

Table 4

(a) Mean (\pm SE) percent of nine vegetation classes and maintained open land measured in a 50 m radius buffer, and land-use characteristics within a 1 km radius buffer, around sample sites in the Rhode Island, USA study area. (b) Percent of all wetland sites and urban wetland sites classified as one of five wetland classes. Wetland classes were developed for the Rhode Island Geographic Information System wetlands data layer (RIGIS, 2010) based on the Cowardin et al. (1979) national wetland classification system.

Vegetation class ^a	All sites	All wetlands	Urban sites	Urban wetlands	Rural wetlands
(a)					
BLDF	38.5 \pm 3.53	47.6 \pm 5.05	24.2 \pm 4.35	33.3 \pm 6.87	55.8 \pm 6.54
BLDS	2.37 \pm 1.16	1.94 \pm 1.61	4.57 \pm 2.43	1.04 \pm 1.04	2.47 \pm 2.44
BRYO	0.05 \pm 0.05	0.11 \pm 0.11	0.00 \pm 0.00	0.00 \pm 0.00	0.17 \pm 0.17
EVGF	2.82 \pm 0.86	3.20 \pm 1.33	2.77 \pm 1.37	2.76 \pm 2.04	3.54 \pm 1.77
EVGS	0.29 \pm 0.21	0.36 \pm 0.63	0.53 \pm 0.35	1.07 \pm 0.77	0.00 \pm 0.00
GRAS	0.29 \pm 0.19	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
MOPN	20.9 \pm 0.19	9.81 \pm 0.00	31.5 \pm 0.00	18.3 \pm 0.00	5.26 \pm 1.68
MXDF	18.9 \pm 3.20	11.3 \pm 3.80	7.20 \pm 2.84	0.62 \pm 0.62	17.0 \pm 5.63
MXDS	0.35 \pm 0.21	0.34 \pm 0.24	0.51 \pm 0.51	0.00 \pm 0.00	15.3 \pm 0.37
WETL	10.1 \pm 1.59	19.9 \pm 2.48	13.8 \pm 3.36	27.6 \pm 4.78	15.3 \pm 2.58
Urban	25.8 \pm 2.45	22.5 \pm 2.83	48.4 \pm 4.35	36.7 \pm 5.60	14.6 \pm 2.32
Agr	2.00 \pm 0.50	1.73 \pm 0.57	0.04 \pm 0.03	0.06 \pm 0.05	2.52 \pm 0.84
Natural	72.2 \pm 2.43	75.8 \pm 2.89	51.7 \pm 4.37	63.5 \pm 5.61	82.8 \pm 2.72
Wetland Class ^b					
(b)					
EEM	2.0	0.0			
EMA	8.0	17.6			
FOA	4.0	0.0			
FOB	56.0	41.2			
SSA	30.0	41.2			

^a BLDF: broad-leaf deciduous forest, BLDS: broad-leaf deciduous shrub, BRYO: bryophyte, EVGF: evergreen forest, EVGS: evergreen shrub, GRAS: grassland, MOPN: maintained open land (impervious surface and residential or recreational lawn with < 50% shrubs and trees), MXDF: mixed forest, MXDS: mixed shrub, WETL: wetland; Urban: urban land (residential, commercial, industrial, transportation, recreation, institutional, mixed urban) within 1 km, Agr: agricultural land (cropland, pasture, orchards, confined feeding operations) within 1 km, Natl: natural land (forest, shrubland, grassland, wetland, barren land, open water) within 1 km.

^b EEM: estuarine emergent wetland, EMA: emergent marsh or wet meadow, FOA: coniferous forested wetland, FOB: deciduous forested wetland, SSA: shrub swamp.

fraction wetland within 50 m of a site at rural sites. The occupancy of four species (Carolina wrens, common yellowthroats (*Geothlypis trichas*), red-winged blackbirds, and tufted titmice (*Baeolophus bicolor*) was significantly positively correlated with fraction wetland at urban sites).

4. Discussion

We observed a greater abundance and species richness of breeding birds at wetland than upland sites in our study area, and the

difference was more pronounced in urban areas. This result is consistent with results reported for breeding birds at seasonal pond wetlands in Tennessee and in Rhode Island (McKinney and Paton, 2009; Scheffers et al., 2006). Increased bird abundances and species richness observed at wetland sites may result in part from the increased availability of food and water in and around pools compared to surrounding uplands. Water is available when wetlands are flooded (generally in early spring to mid-summer) and may be an important, although little studied, determinant of habitat use. Insectivores, such as the yellow warblers and gray catbirds, may

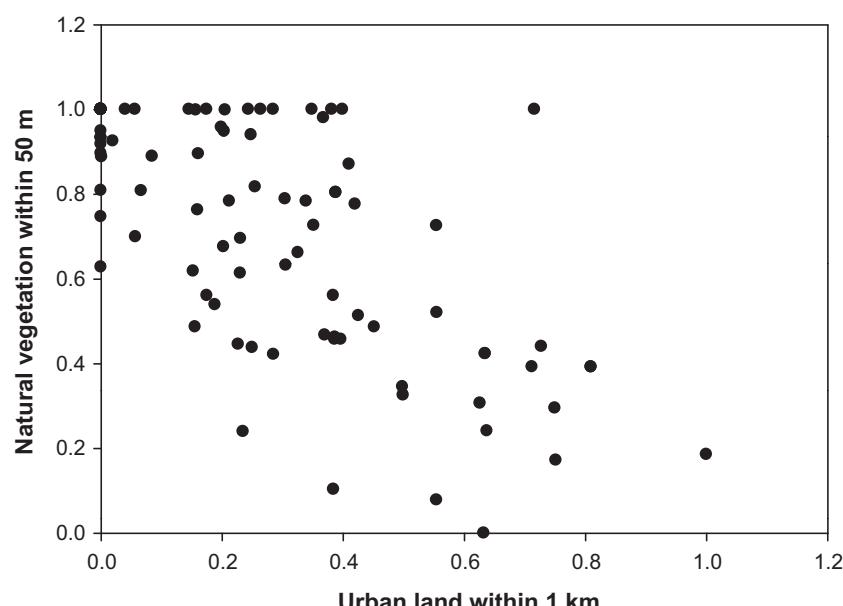


Fig. 2. (a) Proportion of natural land within a 50 m buffer around point count sites versus urban land within 1 km at sample sites in the Rhode Island, USA study area. (b) Breeding bird abundance at point count sites versus urban land within 1 km at sample sites in the Rhode Island, USA study area.

Table 5

Model averaged parameter estimates and unconditional standard errors for best-fit occupancy models ($\Delta AIC_c < 2.0$) of bird species with detection probabilities greater than 0.30 in (a) rural and (b) urban sites in the Rhode Island, USA study area. Model averages were based on an assessment of a priori parsimonious multiple regression models that incorporated linear combinations of vegetation classes identified using species life histories. Models are of the form: species occupancy: psi + parameter average (fraction vegetation class); for example, American robin occupancy (rural sites): $2.78 \pm 1.14 + 1.50 \pm 0.65(\text{fraction broad-leaved deciduous forest}) - 1.37 \pm 1.03(\text{fraction evergreen forest}) + 4.25 \pm 4.83(\text{fraction maintained open land})$. The vegetation classes mixed forest, evergreen shrubs, grassland, and bryophytes were not included because they did not enter into the best-fit model.

Species ^a	psi	WETL	BLDF	EVGF	BLDS	MOPN
(a) Rural sites						
AMRO	2.78 ± 1.14		1.50 ± 0.65	-1.37 ± 1.03		4.25 ± 4.83
CAWR	1.71 ± 3.20	-0.19 ± 0.89	2.07 ± 1.73			
COGR	20.1 ± 1.50	0.02 ± 0.61	0.82 ± 1.08			
COYE	-1.11 ± 1.55					
GRCA	-0.71 ± 0.71	2.47 ± 1.09				1.96 ± 0.84
HOSP	-3.28 ± 1.40					1.88 ± 0.89
MODO	1.62 ± 2.65	-0.64 ± 0.60	-0.10 ± 1.67			1.74 ± 2.67
NOCA	-0.17 ± 0.45	0.32 ± 0.31				2.22 ± 1.22
OVEN	-0.69 ± 1.17	2.65 ± 3.40	-1.69 ± 1.19			
RWBL	-1.27 ± 0.68	0.33 ± 0.44				0.01 ± 0.41
SOSP	-1.63 ± 0.47	0.57 ± 0.41				1.36 ± 0.44
TUTI	-1.70 ± 0.90					1.85 ± 0.76
VEER	-1.36 ± 0.43		-0.35 ± 0.38			-1.44 ± 0.88
YEWA	-1.53 ± 0.66	1.55 ± 0.71	0.13 ± 0.51			0.61 ± 0.57
(b) Urban sites						
AMRO	0.65 ± 0.42	-0.95 ± 1.66	-1.27 ± 1.49	0.45 ± 0.80		2.33 ± 2.23
CAWR	-0.19 ± 1.18	1.72 ± 0.84				-0.23 ± 0.55
COGR	9.07 ± 8.78	4.84 ± 7.00				2.11 ± 1.85
COYE	-2.38 ± 1.04	2.10 ± 0.91				
GRCA	0.66 ± 0.41		0.17 ± 0.42			
HOSP	-0.06 ± 0.12					
MODO	-1.43 ± 0.67				-1.97 ± 2.08	7.18 ± 1.63
NOCA	-1.05 ± 1.02	0.34 ± 0.68				-0.61 ± 0.51
OVEN	No birds detected					
RWBL	1.82 ± 1.23	5.01 ± 2.47				1.08 ± 0.08
SOSP	0.92 ± 2.27					1.36 ± 0.44
TUTI	-0.84 ± 0.99	6.54 ± 3.97				
VEER	No birds detected					
YEWA	0.77 ± 0.80	0.30 ± 0.60	-0.61 ± 0.56			0.52 ± 0.62

^a Species abbreviations are described in Table 2.

^b Abbreviations for vegetation classes are described in Table 4.

take advantage of increased densities of flying insects shown to be episodically associated with wetlands (Scheffers et al., 2006). Urban wetlands in our study area were surrounded by a higher density of shrubs than rural wetlands or upland sites, which could provide fruits and seeds. In addition, dense shrub vegetation may provide a degree of shelter or protection from predators. Some shrub and tree species provide potential nest sites for cup or platform nesting species (Ehrlich et al., 1988), such as red-winged blackbirds or Northern cardinals, both of which had higher abundances in wetlands. It is important to note that based on our study design, randomly chosen upland control sites in urban areas in some cases consisted of urban habitats including maintained land such as mowed fields or landscaped areas. This may have biased our results to some extent in that areas of natural vegetation within and immediately surrounding pools were compared to areas devoid of natural vegetation. Based on the number of sites in our sample population, we were unable to control for type of urban upland in our experimental design. However we felt that comparing pools to randomly chosen upland areas, especially in urban landscapes, gave a better representation of their habitat value to birds. Also, we believe that the lack of observed differences in abundance and species richness at sites sampled multiple years suggests that, although from a single sampling season, our data may reflect broader temporal patterns at the sites.

Bird abundance and species richness was greater at urban versus rural wetlands in our study area. This is consistent with previ-

ous studies of bird use of urban habitats, which generally report increased abundance, but contrary to previous reports of reduced diversity in urban landscapes (Cam et al., 2000; Chace and Walsh, 2006; Kluza et al., 2000). One proposed mechanism for the observation of increased abundance but reduced diversity is that as urbanization progresses, existing natural areas become increasingly fragmented and resulting patches are smaller with greater relative edge habitat. This may in turn result in a relative increase in new habitat for human-tolerant species that can take advantage of increased resources in these areas (Blair, 1996; Chace and Walsh, 2006). In our study area, these same processes could be in place, but increases in species richness at our urban sites may result from the regional community composition of birds (Cam et al., 2000). In the highly urbanized northeast, bird community composition may be skewed towards human tolerant species that are more apt to readily take advantage of increased availability of resources at urban wetlands. For example, several synanthropic species, including American robins, northern cardinals, gray catbirds, and red-winged blackbirds, were more abundant at urban wetlands, suggesting that these birds may be taking advantage of enhanced resources in the absence of competition from non-tolerant species. This finding also agrees with other studies suggesting that remaining areas of natural habitat that provide additional resources (i.e., food, water, shelter) may become increasingly valuable for birds inhabiting urban landscapes (Hanowski et al., 2006). Interestingly, we observed relatively few obligate wetland breeding birds at our sites, and this reinforces

that urban wetlands in our study area are providing resources by species not normally associated with wetlands but that can opportunistically take advantage of enhanced resources associated with these mesic habitats.

As the percent of urban land in a 1 km buffer around our sites increased above about 40%, the amount of natural land in our point count radii decreased precipitously. This suggested a possible threshold of urbanization that may have consequences for the occurrence of birds at a site. However, while overall bird abundance and species richness increased with increasing urbanization in the 1 km buffer, there was no evidence of a threshold for either of these metrics. This suggests that overall, and for synanthropic species such as American robins and common grackles, the enhanced resources available in urban settings, and their ability to take advantage of these resources, may be outweighing any loss in natural vegetation. We also saw that while the abundance of three of the five most common birds increased with increasing urbanization, that of Northern cardinals and gray catbirds did not. This may result from the enhanced reliance of these two species on wetland habitats in urban settings, and the relative lack of available wetland habitat in urban versus rural settings.

We observed greater bird abundance and species richness at urban wetlands versus uplands, and this coupled with the lack of significant difference in abundance and species richness between rural wetlands and uplands suggests that wetlands may have enhanced value to birds in urban settings. Wetlands, along with other remnant natural habitats, may be providing necessary resources such as food and shelter that facilitates the presence of birds in urban areas (Caula et al., 2008, 2010; Murgui, 2009). In this study we saw the presence of six facultative wetland species, in particular northern cardinals, Carolina wrens, and red-winged blackbirds, increase at our urban wetland sites relative to rural wetlands, providing further evidence of the role of wetlands in supporting avian abundance and diversity in urban settings. Also, we observed more species at wetland versus upland sites, but the difference between wetland and upland was less for human-tolerant species. This suggests that urban wetlands may to some extent be supporting less ubiquitous or human intolerant birds that are often targets for conservation. Although none were observed at our study sites, wetlands in urban habitats may also support obligate marsh-nesting birds such as Virginia rails (*Rallus limicola*), sora (*Porzana carolina*), swamp sparrows (*Melospiza georgiana*), and marsh wrens (*Cistothorus palustris*) (Smith and Chow-Fraser, 2010).

In interpreting our results, it is important to note that increased abundance may not be a good indicator of habitat quality. For example, increased abundance in a given habitat, such as an urban seasonal pool, may result from intra- and inter-specific competition in which competitive dominants displace individuals to sub-optimal habitat (Van Horne, 1983). In cases such as this, sites with increased abundances may in fact be functioning as sink habitats and may have limited value in sustaining populations (Morrison et al., 1998).

Occupancy estimates at our study sites were positively correlated with the proportion of wetland within 50 m at both rural and urban sites, which suggests that wetlands may be providing resources that can be used by a variety of bird species. Species that showed a relatively strong positive relationship with wetlands in occupancy models (tufted titmice, yellow warblers, common yellowthroats, gray catbirds, and red-winged blackbirds) are known either to be dependent on wetlands for some part of their life history or to readily take advantage of wetland resources (e.g., increased insect abundance or availability of nest sites; Ehrlich et al., 1988). For example, both common yellowthroats and gray catbirds prefer dense, early-successional shrub habitat for nesting and both are primarily insectivores (Ehrlich et al., 1988). These species

may therefore be taking advantage of increased vegetation density and food resources associated with wetlands. Red-winged blackbirds are an insectivore and nest in wetland habitats, preferring the dense vegetation associated with wetlands as roost sites during breeding (Yasukawa and Searcy, 1995). They also defend small territories (approximately 0.2 ha; Weatherhead and Robertson, 1977), which may account for their relatively high abundance at our wetland sites.

Occupancy models also showed differences in bird-habitat associations as watersheds became more urbanized. In particular, several species that were not positively associated with wetlands at rural sites (e.g., Carolina wrens, common yellowthroat, and tufted titmice) showed a positive association with wetlands in more urbanized landscapes. This suggests that changes in the extent of urbanization may impact bird use of remnant natural habitats to the extent that wetlands may be inordinately beneficial to maintaining populations of some species in human-dominated landscapes.

5. Conclusions and implications for management

Our results confirm previous studies that suggest a number of bird species are associated with wetland habitats. We found that bird associations were independent of size, suggesting that even small wetlands may be providing valuable habitat and resources. Increasing biodiversity is a goal of habitat conservation, and arguably can take on more urgency in urban and human-dominated habitats. Several studies have demonstrated the link between intact and functioning ecosystems and species composition or diversity (Daily, 2001; Tilman et al., 1996). Therefore wetland habitats may play a role in helping maintain intact ecosystems in urban landscapes. Unfortunately many of these smaller isolated wetlands are under constant threat of loss or fragmentation through urbanization. For example, a study of isolated wetlands in the northeast US found that as the extent of urbanization increased, wetland size and extent decreased (McKinney and Charpentier, 2009). Our results and those of others demonstrate that in spite of their decreased size, these areas continue to provide habitat for many birds and may in fact even have greater importance as a result of the resources they provide to remaining species. Our study results argue for the continued protection and restoration of isolated wetlands in urbanizing landscapes, and could be used as a rationale by both state and local land use planners for including or maintaining these habitats in local and watershed-level development plans. For example, the State of Rhode Island Department of Environmental Management encourages local communities to implement the principles of conservation development, a land use technique that accommodates growth while protecting a significant proportion of a development parcel as open space, in land use planning (Flinker, 2003). Studies such as ours that examine the value of specific habitats can help inform the debate on the optimal types of open space to be conserved under development plans, if maintaining biodiversity is a goal.

Further studies should focus on both the effect of local vegetation and landscape setting on the quality of habitat provided by wetlands in urban areas. For example, sites in our study area exhibited a threshold of surrounding urban land below which the amount of natural land surrounding a wetland precipitously declined. In light of this, more information is needed to determine both the composition of remaining vegetation and its role in determining habitat quality on a local scale. Landscape setting, including connectivity and proximity to other natural habitats (e.g., Bierwagen, 2008; Walter et al., 2009) has been shown to influence habitat value, and should also be further investigated with regard to urban wetland fragments.

Appendix A. Mean (\pm SE) abundance across all wetlands and uplands ($n=50$), urban uplands and wetlands ($n=18$), and rural uplands and wetlands ($n=33$) of birds species recorded at sites in the Rhode Island, USA study area.

Common name	Scientific name	All wetlands	All uplands	Urban wetlands	Urban uplands	Rural wetlands	Rural uplands
Great blue heron	<i>Ardea Herodias</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Green heron	<i>Butorides virescens</i>	0.04 ± 0.03	0	0.11 ± 0.08	0	0	0
Canada goose	<i>Branta Canadensis</i>	0	0.06 ± 0.06	0	0.17 ± 0.17	0	0
Mallard	<i>Anas platyrhynchos</i>	0.10 ± 0.04	0	0.17 ± 0.09	0	0.06 ± 0.04	0
Herring gull	<i>Larus argentatus</i>	0.04 ± 0.04	0.02 ± 0.02	0.11 ± 0.11	0.06 ± 0.06	0	0
Mourning dove	<i>Zenaidura macroura</i>	0.08 ± 0.05	0.19 ± 0.07	0.22 ± 0.13	0.11 ± 0.08	0	0.21 ± 0.09
Ruby-throated hummingbird	<i>Archilochus colubris</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Chimney swift	<i>Chaetura pelasgica</i>	0.02 ± 0.02	0	0.06 ± 0.06	0	0	0
Red-headed woodpecker	<i>Melanerpes erythrocephalus</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Red-bellied woodpecker	<i>Melanerpes carolinus</i>	0.04 ± 0.03	0.06 ± 0.03	0	0.06 ± 0.06	0.06 ± 0.04	0.06 ± 0.04
Downy woodpecker	<i>Picoides pubescens</i>	0.04 ± 0.03	0	0	0	0.06 ± 0.04	0
Hairy woodpecker	<i>Picoides villosus</i>	0	0.02 ± 0.02	0	0	0	0.03 ± 0.03
Eastern wood-peewee	<i>Contopus virens</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Eastern phoebe	<i>Sayornis phoebe</i>	0.04 ± 0.04	0	0	0	0.06 ± 0.06	0
Great crested flycatcher	<i>Myiarchus crinitus</i>	0.12 ± 0.05	0	0.06 ± 0.06	0	0.15 ± 0.08	0
Red-eyed vireo	<i>Vireo olivaceus</i>	0.08 ± 0.04	0.02 ± 0.02	0.06 ± 0.06	0	0.09 ± 0.05	0.03 ± 0.03
Blue jay	<i>Cyanocitta cristata</i>	0.27 ± 0.09	0.13 ± 0.05	0.28 ± 0.14	0.06 ± 0.06	0.27 ± 0.12	0.15 ± 0.06
American crow	<i>Corvus brachyrhynchos</i>	0.06 ± 0.04	0.04 ± 0.03	0.11 ± 0.11	0.06 ± 0.06	0.03 ± 0.03	0.03 ± 0.03
Tufted titmouse	<i>Baeolophus bicolor</i>	0.49 ± 0.15	0.06 ± 0.03	0.28 ± 0.14	0	0.61 ± 0.21	0.09 ± 0.05
Barn swallow	<i>Hirundo rustica</i>	0.02 ± 0.02	0	0.06 ± 0.06	0	0	0
Black-capped chickadee	<i>Poecile atricapilla</i>	0.25 ± 0.09	0.15 ± 0.06	0.44 ± 0.22	0	0.15 ± 0.08	0.21 ± 0.08
White-breasted nuthatch	<i>Sitta carolinensis</i>	0.02 ± 0.02	0	0.06 ± 0.06	0	0	0
Carolina wren	<i>Thryothorus ludovicianus</i>	0.24 ± 0.08	0.04 ± 0.03	0.33 ± 0.11	0.06 ± 0.06	0.18 ± 0.10	0.06 ± 0.04
House wren	<i>Troglodytes aedon</i>	0.04 ± 0.04	0.17 ± 0.09	0.11 ± 0.11	0	0	0.24 ± 0.13
Marsh wren	<i>Cistothorus palustris</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
American robin	<i>Turdus migratorius</i>	1.10 ± 0.18	1.58 ± 0.22	1.61 ± 0.37	1.94 ± 0.36	0.82 ± 0.19	1.61 ± 0.31
Wood thrush	<i>Hylocichla mustelina</i>	0.08 ± 0.04	0.04 ± 0.03	0.06 ± 0.06	0.11 ± 0.08	0.09 ± 0.05	0.06 ± 0.04
Veery	<i>Cathartes fuscescens</i>	0.08 ± 0.05	0.04 ± 0.03	0	0	0.12 ± 0.07	0.06 ± 0.04
Gray catbird	<i>Dumetella carolinensis</i>	0.90 ± 0.16	0.42 ± 0.10	1.22 ± 0.34	0.50 ± 0.12	0.73 ± 0.17	0.39 ± 0.14
Northern mockingbird	<i>Mimus polyglottos</i>	0.06 ± 0.06	0	0.17 ± 0.17	0	0	0
European starling	<i>Sturnus vulgaris</i>	0.02 ± 0.02	0.06 ± 0.03	0.06 ± 0.06	0.17 ± 0.09	0	0
Northern parula	<i>Parula Americana</i>	0.02 ± 0.02	0	0.06 ± 0.06	0	0	0
Cedar waxwing	<i>Bombycilla cedrorum</i>	0.31 ± 0.22	0	0.89 ± 0.68	0	0	0
Yellow warbler	<i>Dendroica petechia</i>	0.25 ± 0.08	0.15 ± 0.05	0.56 ± 0.18	0.39 ± 0.12	0.09 ± 0.05	0
Yellow-rumped warbler	<i>Dendroica coronata</i>	0.04 ± 0.08	0	0	0	0.06 ± 0.04	0
Black-throated green warbler	<i>Dendroica virens</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Prairie warbler	<i>Dendroica discolor</i>	0	0.02 ± 0.02	0	0	0	0.03 ± 0.03
Pine warbler	<i>Dendroica pinus</i>	0	0.02 ± 0.02	0	0	0	0.03 ± 0.03
American redstart	<i>Setophaga ruticilla</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Ovenbird	<i>Seiurus aurocapillus</i>	0.25 ± 0.08	0.23 ± 0.09	0	0	0.39 ± 0.11	0.33 ± 0.14
Common yellowthroat	<i>Geothlypis trichas</i>	0.14 ± 0.08	0	0.06 ± 0.06	0	0.18 ± 0.13	0
Scarlet tanager	<i>Piranga olivacea</i>	0.02 ± 0.02	0.04 ± 0.04	0	0	0.03 ± 0.03	0.06 ± 0.06
Eastern towhee	<i>Pipilo erythrrophthalmus</i>	0.04 ± 0.03	0.08 ± 0.04	00	0	0.06 ± 0.04	0.12 ± 0.06
Northern cardinal	<i>Cardinalis cardinalis</i>	0.65 ± 0.12	0.31 ± 0.07	1.06 ± 0.22	0.28 ± 0.14	0.42 ± 0.13	0.30 ± 0.08
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
Chipping sparrow	<i>Spizella passerina</i>	0.14 ± 0.06	0.19 ± 0.08	0.06 ± 0.06	0	0.18 ± 0.09	0.27 ± 0.12
Song sparrow	<i>Melospiza melodia</i>	0.22 ± 0.08	0.25 ± 0.06	0.44 ± 0.17	0.50 ± 0.12	0.09 ± 0.07	0.15 ± 0.06
Brown-headed cowbird	<i>Molothrus ater</i>	0.02 ± 0.02	0.23 ± 0.10	0	0	0.03 ± 0.03	0.33 ± 0.16
Red-winged blackbird	<i>Agelaius phoeniceus</i>	0.82 ± 0.22	0.13 ± 0.06	1.78 ± 0.50	0.33 ± 0.16	0.30 ± 0.16	0.15 ± 0.09
Common grackle	<i>Quiscalus quiscula</i>	0.71 ± 0.21	1.19 ± 0.37	1.56 ± 0.51	1.78 ± 0.62	0.24 ± 0.12	0.91 ± 0.44
Baltimore oriole	<i>Icterus galbula</i>	0.06 ± 0.03	0.04 ± 0.03	0.11 ± 0.08	0.06 ± 0.06	0.03 ± 0.03	0.03 ± 0.03
House finch	<i>Carpodacus mexicanus</i>	0	0.04 ± 0.03	0.11 ± 0.08	0.06 ± 0.06	0.03 ± 0.03	0.03 ± 0.03
Purple finch	<i>Carpodacus purpureus</i>	0.02 ± 0.02	0	0	0	0.03 ± 0.03	0
American goldfinch	<i>Carduelis tristis</i>	0.10 ± 0.06	0.21 ± 0.11	0.17 ± 0.12	0.06 ± 0.06	0.06 ± 0.06	0.27 ± 0.16
House sparrow	<i>Passer domesticus</i>	0.08 ± 0.05	0.23 ± 0.07	0.17 ± 0.12	0.50 ± 0.17	0.03 ± 0.03	0.12 ± 0.06

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