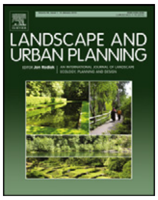
Landscape and Urban Planning 103 (2011) 64–73

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan



Effects of low-density housing development on shrubland birds in western Massachusetts

Scott Schlossberg[a,*], David I. King[a,b], Richard B. Chandler[a]

[a] *Department of Environmental Conservation, University of Massachusetts-Amherst, 204 Holdsworth Hall, Amherst, MA 01003, USA*
[b] *USDA Forest Service, Northern Research Station, University of Massachusetts-Amherst, 204 Holdsworth Hall, Amherst, MA 01003, USA*

ARTICLE INFO

Article history:
Received 11 August 2010
Received in revised form 22 April 2011
Accepted 8 June 2011
Available online 4 August 2011

Keywords:
Exurban development
Housing
Shrubland birds
Massachusetts
Nest predation
Urbanization

ABSTRACT

Housing development in rural areas is the fastest-growing type of land use in the U.S. For birds, development near natural habitats is a problem because it can reduce abundances and nesting success and increase brood parasitism by brown-headed cowbirds (*Molothrus ater*). In southern New England, populations of shrubland birds are declining rapidly while exurban development is widespread and increasing. We studied effects of landscape-scale low-density housing development on abundance and nesting success of birds in western Massachusetts shrublands. Study sites included beaver wetlands, utility rights-of-way managed as shrublands, regenerating clearcuts, and mechanically treated old fields. Of 14 focal bird species, four increased with development within 1 km of study sites whereas white-throated sparrow (*Zonotrichia albicollis*) decreased. Abundances of avian nest predators increased slightly with development, and abundances of brown-headed cowbirds decreased with development. Prairie warblers (*Dendroica discolor*) had lower nest success in more developed areas, but for seven bird other species and the community as a whole, nest success did not change with development in the surrounding landscape. Brood parasitism by brown-headed cowbirds was higher on sites with more development. Overall, only white-throated sparrow and prairie warbler showed negative impacts of development, but both of these species are declining rapidly in New England. Housing development in the surrounding landscape should be a consideration in management of these species. For other shrubland birds, however, low-density housing development at the landscape scale appears to have more neutral or even positive effects.

1. Introduction

Urbanization poses a growing threat to biodiversity (Chace & Walsh, 2006; Marzluff, 2001; McKinney, 2002). Numerous studies have documented harmful effects of urban development on plants and animals, and the pace of urban development is increasing in many areas (Brown, Johnson, Loveland, & Theobald, 2005). In the U.S., for instance, the developed area is expected to grow by 80% between 1997 and 2025 (Alig, Kline, & Lichtenstein, 2004). Ecologists have given much attention to high-density urban development, which results in transformation of natural habitats to human uses and losses of many native species (Blair, 1996; McKinney, 2006; McKinney & Lockwood, 1999; Shochat, Stefanov, Whitehouse, & Faeth, 2004). In many respects, however, low-density rural or exurban development, with housing densities on the order of ~10 units/km^2, has the potential to have greater impacts on biodiversity (Fraterrigo & Wiens, 2005; Hansen et al., 2005; Maestas, Knight, & Gilgert, 2003). Highly developed urban areas tend to be distant from high-quality natural habitats. In contrast, rural housing development can impinge directly on protected areas, and the extent of low-density housing development is large and growing. Since 1950, exurban development has increased more rapidly than other category of land use in the U.S. (Brown et al., 2005). Today, roughly 9% of the country is considered "wildland–urban interface" where low-density housing intermingles with natural habitats (Radeloff et al., 2005).

Studies of exurban development show that low-density housing can harm bird populations. For instance, Odell and Knight (2001) found that densities of some birds are depressed within ~100 m of individual houses. In contrast, exotic and human-adapted animals, including many potential predators of birds' nests, often increase near rural housing (Hansen & Rotella, 2002; Maestas et al., 2003; Odell & Knight, 2001). Effects of exurban development on nest predation have been equivocal in past studies. For instance, Hansen and Rotella (2002) found no effect of development on nest success in American robins (*Turdus migratorius*) but negative effects in yellow warblers (*Dendroica petechia*). Brood parasitism by brown-headed cowbirds (*Molothrus ater*), however, often increases with housing density (Burhans & Thompson, 2006;

---

* Corresponding author. Tel.: +1 413 545 1655, fax: +1 413 545 1860.
E-mail addresses: srs@eco.umass.edu (S. Schlossberg), dking@fs.fed.us (D.I. King), rchandler@eco.umass.edu (R.B. Chandler).

0169-2046/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.landurbplan.2011.06.001

Rodewald & Shustack, 2008; Tewksbury, Hejl, & Martin, 1998). For some birds, cowbird parasitism can seriously reduce reproductive success (Hoover, 2003). Cowbirds may be attracted to exurban developments by foraging opportunities on lawns and cleared spaces (Brittingham & Temple, 1983; Fraterrigo & Wiens, 2005).

Most studies of urbanization effects on birds have taken place in forests (Marzluff, Bowman, & Donnelly, 2001). In the northeastern U.S., forests are the predominant habitat, and populations of forest birds are generally stable (Sauer, Hines, & Fallon, 2008). By contrast, shrubland birds have been declining for decades in this region, primarily because of habitat loss (Hunter, Buehler, Canterbury, Confer, & Hamel, 2001; Sauer et al., 2008; Schlossberg & King, 2007). Ecologists once believed that shrubland birds were edge specialists and should be insensitive to habitat fragmentation and other disturbances (Imbeau, Drapeau, & Mönkkönen, 2003). Recent findings, however, show that shrubland birds avoid edges and are area-sensitive (Chandler, King, & Chandler, 2009; Schlossberg & King, 2008). In the only previous study of urbanization effects in eastern shrublands, Burhans and Thompson (2006) found that urbanization had mixed effects on abundances of shrubland birds but led to increased brood parasitism by brown-headed cowbirds. Odell and Knight (2001) also reported negative effects of exurban development on several birds in a western shrubland community.

Compared to other parts of the U.S., rural areas in southern New England are heavily impacted by low-density housing development. Over 50% of the area in Massachusetts and Connecticut has been classified as wildland–urban interface, and much of the new housing being constructed in this region is at low densities (Radeloff et al., 2005; DeNormandie et al., 2009). As human populations and the rate of development increase, understanding how exurban development affects shrubland birds will be critical to their future conservation. The objective of our research was to examine effects of low-density housing on abundance and nesting success of shrubland birds in western Massachusetts.

2. Methods

2.1. Study sites

We analyzed effects of low-density development by combining data from three studies of shrubland birds in western Massachusetts (Fig. 1). These studies took place in regenerating clearcuts, managed old fields (wildlife openings), beaver ponds, and utility rights-of-way, representing the most common shrubland habitats in this region. We surveyed beaver-impounded wetlands in a 2800-km^2 study area in 2005 and 2006; we sampled all beaver ponds ($n = 35$) ≥ 1 ha in size that were <75% open water. We studied power line rights-of-way in Hampshire and Franklin Counties in 2002 and 2003. We randomly selected 15 1-km right-of-way segments from all sites in the region that contained shrubby habitat. Finally, we sampled birds in regenerating clearcuts ($n = 5$) and managed wildlife openings ($n = 6$) in Berkshire, Franklin, and Hampshire Counties from 2003 to 2005. Because suitable clearcuts and wildlife openings were scarce, we could not randomly select sites for this study. In all three studies, shrubland habitats were surrounded by mature forest.

2.2. Field methods

We surveyed breeding birds using 10-min point counts repeated 3 times during the breeding season, mid-May through early July. In the beaver pond and wildlife opening/clearcut studies, we sampled birds using 50-m-radius point counts. A few beaver ponds were irregularly shaped and could not accommodate a 50-m count circle. In such cases, we established a 0.785-ha plot, equivalent in area to a 50-m radius circle, with the aid of aerial photos. For the rights-of-way, we counted birds on 100-m long segments of the corridor, so plot area varied with corridor width. We accounted for plot size in our statistical models. During each point count, we counted all birds detected by sight or sound. We also recorded sightings of red (*Tamiasciurus hudsonicus*) and gray squirrels (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*), which are potential nest predators. All counts took place within the first 4 h after sunrise.

We defined a study site as a continuous area of shrubland habitat, or, in the case of managed wildlife openings, an individual management unit. The distribution of survey points within sites varied by study. For the beaver pond study, we placed points randomly with a minimum spacing of 200 m. For the rights-of-way, we choose a random starting point and then established 5 points spaced 250 m apart along the corridor's central axis. For the wildlife opening study, we placed study plots non-randomly, with the goal of maximizing coverage of each site. All points in the beaver pond and wildlife opening studies were at least 50 m from forest edges to avoid edge effects (Schlossberg & King, 2008).

On each point-count plot, we sampled vegetation at 20 random locations. At each of the 20 locations, we recorded the vegetation height and the plant species making up the canopy. If there was no vegetation, we recorded a height of 0 and the ground substrate. Past research has shown that this technique effectively summarizes vegetation structure in shrublands (King, Chandler, Schlossberg, & Chandler, 2009b).

On the rights-of-way and wildlife openings/clearcuts, we searched for birds' nests from early May to early August during the same years that we conducted point counts. We used standard searching techniques and monitored nests on ~3–4 day intervals until they were no longer active (Martin & Geupel, 1993). For nests that potentially fledged young, we searched nearby for adults with food or nestlings to confirm their success. Once each nest was no longer active, we measured its height above ground and the distance to the nearest forest edge. Because of funding constraints, we did not search for nests on the beaver ponds.

2.3. Landscape composition

Because few of our study sites were immediately adjacent to developed areas, we determined effects of development at the landscape scale. We used geographic information systems (GIS) to place a circular 1-km buffer around each point-count location and then merged the buffers by study site. We chose 1 km as our radius for landscape effects because landscape composition and configuration at this scale can affect abundances and nest success of shrubland birds (Askins, Zuckerberg, & Novak, 2007; Chandler, 2006; MacFaden & Capen, 2002).

To determine the extent of development in each landscape, we used data from the U.S. Census Bureau and the state of Massachusetts. Once each decade, the Census Bureau enumerates population and the number of households in the United States. At the smallest scale, these data are available for census blocks, irregularly shaped tracts that vary inversely in size with local population (U.S. Census Bureau, 2008). In our study area, census blocks from the 2000 census averaged 178 ha. For the 1-km landscape around each site, we calculated the overlap area of census blocks intersecting the landscape. To estimate population and housing density in our study landscapes, we assumed that the distribution of houses in each census block was uniform. Because housing densities were low in our study area, we believe that this assumption is justifiable (see Pidgeon et al., 2007). For each landscape, we then calculated the expected population size and number of houses and divided by landscape area to estimate densities.

To describe natural habitats on our study landscapes and to provide a second data source on development, we used the Land

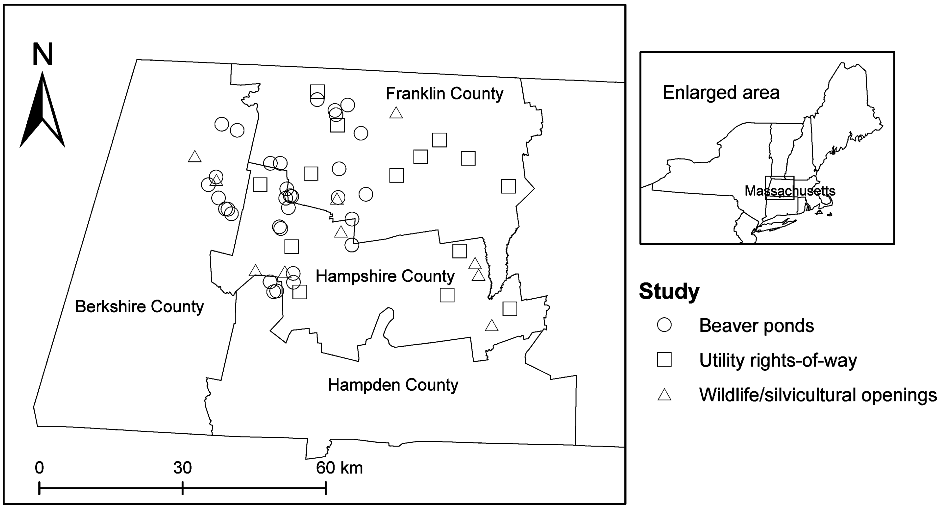


Fig. 1. Study sites in western Massachusetts.

Use 2005 GIS coverage from the state of Massachusetts (MassGIS, 2009). This data layer, based on 2005 aerial photography, divides the land area into 33 categories indicating type of development or natural habitat. To simplify analysis and eliminate sparse categories, we reclassified the MassGIS coverage into four categories: forest, agriculture, open land, and developed. “Open land” included shrublands, grasslands, marshes, and other non-forested natural habitats. “Developed” included all types of human-built categories. In our study landscapes, low- and medium-density housing (with typical lot sizes of 0.1–0.4 ha; density categories are based on spacing between houses) made up 84% of the developed category. Remaining developed areas included outdoor recreation sites, industrial/commercial sites, and transportation infrastructure. We used GIS to calculate the percent cover of the four reclassified categories in each 1-km landscape.

2.4. *Data analysis*

We examined effects of rural development on shrubland vegetation, avian abundances, and avian nesting success. We measured effects on vegetation because development can lead to introductions of exotic plants and other disturbances (Maestas et al., 2003), and these factors can affect bird populations.

2.4.1. *Landscape composition*

Categorical data on landscape composition are inevitably correlated, so we used principal components analysis (PCA) to simplify the data and extract underlying patterns of development and natural habitats. PCA also allowed us to simultaneously incorporate estimates of development from MassGIS and the Census Bureau. We ordinated percent cover (arcsine-square root transformed) of the four land cover categories from MassGIS along with housing and population density from U.S. Census Bureau.

We retained two principal component axes, which explained 82% of the variance in the original data (Table 1). The first axis, “DEV-PC,” had strong positive correlations with variables indicating development and housing density. We interpret DEV-PC as a measure of development in the landscape; this was our independent variable for examining effects of rural housing development. The second axis, “OPEN-PC,” had positive correlations with open land and indicated landscape openness. Both PCA axes were negatively correlated with forest cover and positively correlated with agriculture. These loadings were due to the fact that forest is the matrix habitat in our study landscapes, and agriculture is the dominant non-forest land-use category. We used one-way ANOVA to test whether the original landscape measures and the PCA scores differed between the three habitats we sampled.

2.4.2. *Vegetation*

We divided vegetation observations into categories based on canopy height and growth form: woody plants >3 m tall were “trees,” woody plants 1.5–3 m tall were “high shrubs,” and woody plants <1.5 m tall were “low shrubs.” We considered rock, bare soil, litter, and moss to be “bare ground.” We also had categories for forbs (including ferns) and grasses. For each vegetation category, we computed percent cover on each plot. For canopy height, we calculated the mean, CV, and maximum on each plot.

We used PCA to reduce the dimensionality of vegetation-structure data. We ordinated the mean, CV, and maximum of vegetation height and cover of trees, low shrubs (<1.5 m tall), high shrubs (≥1.5 m), forbs, and grasses. We retained 3 factors with eigenvalues >1 which accounted for 76% of variance in the original data. The first axis, “height,” had strong, positive correlations with all 3 height variables and tree cover. The second axis, “grass-lowshrub,” was positively correlated with grass cover and negatively correlated with low shrubs. Similarly, the third axis, “highshrub-forb” had a positive correlation for high shrub cover and a negative one for forbs.

We computed percent cover for each woody plant species on each study plot. Because individual species were generally rare, we grouped species by genus. We also grouped six exotic, invasive shrubs and vines: multiflora rose (*Rosa multiflora*), Japanese barberry (*Berberis thunbergii*), Japanese honeysuckle (*Lonicera japonica*), oriental bittersweet (*Celastrus orbiculatus*), common

Table 1
Factor loadings and variation explained for principal components analysis of housing and population density and landscape composition in 1-km-radius buffers around 61 shrubland sites in western Massachusetts. Important loadings (>0.5) are in bold.

Variable	DEV-PC	OPEN-PC
Population density	**0.91**	0.20
Housing density	**0.91**	0.18
% agriculture	0.**63**	0.48
% developed	**0.88**	0.00
% forest	−**0.69**	−**0.68**
% open	0.01	**0.94**
Eigenvalue	3.33	1.64
Variation explained	56%	27%

buckthorn (*Rhamnus cathartica*), and autumn olive (*Elaeagnus umbellata*).

We calculated Pearson correlation coefficients between DEV-PC and four variables describing vegetation structure: trees, highshrub-forb, grass-lowshrub, and cover of bare ground. In addition, we calculated correlations between DEV-PC and percent cover for the six exotic woody plants as a group and individually for the seven most common native plants. Our sample unit for these analyses was the study site. We averaged vegetation measures for all point-count plots on each site and then used the mean for analysis.

2.4.3. *Avian abundance models*

We determined effects of development on avian abundances with N-mixture models which estimate abundance for temporally replicated point counts (Royle, 2004). These models assume that there is an unknown number of birds present at each point, that the distribution of abundances across points has a Poisson or negative-binomial distribution (or zero-inflated version of either), and that there is a binomial probability of detecting each bird at each point. One can then use maximum likelihood to estimate the mean abundance and detectability of each species. The most useful feature of this model is that it allows one to model covariate effects on abundance and detectability. Thus, we could use the models to test for effects of development on avian abundances. For each species, we considered three possible sets of detection covariates, four sets of abundance covariates, and four distributions of abundance, for a total of 48 models. Our models were hierarchical in structure; we included covariates at the levels of point-count plot and study site.

For detectability, we considered a constant-only model, a model with a linear effect of date, and a model with linear and quadratic effects of date. For the abundance component of the models, we included DEV-PC, OPEN-PC, and plot size in all model runs. We included OPEN-PC to control for effects of landscape openness on abundances of birds. We included plot size because right-of-way survey plots were variable in size and smaller than the count circles in the other studies. Because abundances of shrubland birds are strongly influenced by local vegetation or habitat type, we considered two possible ways to control for these factors. First, we included four vegetation variables, bare ground cover and the three vegetation PCA axes described above, as covariates. Alternatively, we included habitat type (beaver pond, right-of-way, or wildlife/silvicultural opening) as a covariate. We did not include habitat type and vegetation variables simultaneously because they were correlated. We also included models with and without an effect of year on abundance. Thus, we had four sets of abundance covariates: habitat+year, habitat, vegetation+year, and vegetation.

For the distribution of abundances, we considered four possibilities: Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial (Wenger & Freeman, 2008). We estimated model parameters using PROC NLP in SAS (SAS Institute Inc., 2001). We computed Akaike's information criterion (AIC) for each model and used model averaging to estimate mean parameters and their unconditional standard errors (Burnham & Anderson, 2002). We used model averaging because there was not a clear best model for most species. Model averaging produces parameter estimates by averaging results across all models, with weights based on AIC. We restricted analysis to bird species that regularly breed in shrublands according to Schlossberg and King (2007) and had mean abundance $\geq$0.10 birds per count.

To determine effects of housing development on potential nest predators and brood parasites, we analyzed counts of brown-headed cowbird, American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), common grackle (*Quiscalus quiscala*), gray and red squirrels, and eastern chipmunk. Sample sizes for these species were too small for N-mixture models. Instead, for each point, we took the maximum count in each year for each species. Research suggests that the maximum of repeated counts can be a good index of population size (Toms, Schmiegelow, Hannon, Villard, & McDonald, 2009). Counts for most species were low, so summed the maximum counts for the three avian predators and for the three mammals on each count. We analyzed brown-headed cowbird separately. We used Poisson regression to estimate the effect of DEV-PC on counts of small mammals, avian predators, and cowbirds. We included habitat type (beaver pond, right-of-way, or wildlife opening/clearcut) as a covariate to account for differences in abundance across shrubland types. To determine the importance of development effects, we computed the Nagelkerke partial r^2 for development by subtracting the R^2 for a reduced model including only habitat type from the R^2 for the full model (Nagelkerke, 1991).

2.4.4. *Avian population trends*

Because housing development is the leading cause of habitat loss and modification in Massachusetts, we hypothesized that recent trends in bird populations may be related to how birds respond to development. To determine trends in bird populations, we used data from the North American Breeding Bird Survey (BBS; Sauer et al., 2008). The BBS is a volunteer-based program in which birds are counted on 39-km roadside routes each year. We calculated the correlation between each species' coefficient for DEV-PC from our N-mixture models and its reported population trend for 24 BBS routes in Massachusetts between 1980 and 2007.

2.4.5. *Avian nesting success*

We used the logistic-exposure model to determine how landscape-level development affected avian nest success (Shaffer, 2004). Because nesting success can be influenced by factors at the scale of the study site and the individual nest, we used hierarchical models. At the site level, we included DEV-PC and habitat type; the latter was necessary to account for consistent differences in nest success between rights-of-way and wildlife/silvicultural openings (King, Chandler, Collins, Petersen, & Lautzenheiser, 2009a; King et al., 2009b). At the nest level, we included three covariates that can affect nest success: day of year, distance to forest edge, and nest height (Burhans, Dearborn, Thompson, & Faaborg, 2002; Burhans & Thompson, 2006). We ran models for all species combined and for individual species with a sample of at least 20 nests. For the all-species analysis, exploratory analysis revealed no differences between ground and above-ground nesters, so we did not separate them. All nest failures in our sample were due to predation.

For cowbird parasitism, sample sizes for individual species were too small to compute site-specific parasitism levels. Instead, we restricted our sample to species that typically accept cowbird eggs (Appendix A) and computed the proportion of parasitized nests on each study site (Peer, Robinson, & Herkert, 2000; Schlossberg & King, 2007). We used linear regression to determine the effect of DEV-PC on the frequency of parasitism. Because the number of nests per site varied widely (range = 3–48 nests), we weighted the regression by the sample size for each site.

3. Results

Development occupied a mean of 3.9 ± SD of 4.2% of our study landscapes, and housing density averaged 0.8 ± 1.0 houses/km^2 (Table 2). These two measures of development were significantly correlated ($r_{61} = 0.59$, $p < 0.001$). Landscape measures of development varied by habitat type, but the explanatory power of habitat was low (all $r^2 \leq 0.20$; Table 2).

Of the four vegetation-structure variables, the highshrub-forb PCA axis and bare ground cover were correlated with landscape-scale development (Table 3). The result for highshrub-forb axis was likely driven by the positive relationship between DEV-PC and cover of forbs ($r_{61} = 0.41$, $p = 0.001$). We found no relationship

Table 2
Characteristics of shrubland study sites in western Massachusetts. Landscape measures are mean (minimum, maximum) for 1-km radius circles around each site. F, p, and R^2 values are for one-way ANOVA of habitat effects on landscape measures.

	Beaver ponds	Utility rights-of-way	Wildlife/silvic. openings	$F_{2,58}$	p	R^2
Number of study sites						
Point-count plots	35	15	11			
Landscape measures	83	75	48			
Agriculture (%)	6.1 (0.0, 26.4)	3.8 (0.0, 13.8)	10.7 (0.0, 37.1)	1.94	0.15	0.06
Developed (%)	3.2 (0.0, 16.4)	6.4 (0.0, 17.4)	2.5 (0.0, 6.6)	3.65	0.03	0.11
Forest (%)	85.1 (53.8, 99.3)	83.4 (70.1, 94.0)	77.6 (47.9, 93.7)	2.10	0.13	0.07
Open (%)	5.6 (0.7, 21.5)	6.4 (1.2, 22.3)	9.3 (3.4, 20.4)	2.85	0.07	0.09
House density (units/km2)	0.4 (0.0, 2.0)	1.7 (0.0, 4.2)	0.8 (0.0, 3.9)	7.12	0.002	0.20
DEV-PC	−0.24 (−1.71, 1.33)	0.64 (−1.85, 2.23)	−0.10 (−1.89, 1.73)	4.60	0.01	0.14
OPEN-PC	−0.11 (−1.78, 2.73)	−0.31 (−1.40, 1.90)	0.78 (−0.42, 2.97)	4.83	0.01	0.14

Table 3
Correlations between vegetation variables and DEV-PC for 61 shrubland sites in western Massachusetts. Significant results are in bold.

Variable	r	p
Trees	−0.18	0.17
Grass-lowshrub	−0.09	0.46
Highshrub-forb	**−0.29**	**0.02**
Bare ground cover	**0.25**	**0.05**
Spiraea spp.	−0.06	0.62
Salix spp.	−0.24	0.06
Alnus spp.	−0.13	0.31
Betula spp.	−0.05	0.69
Prunus spp.	0.05	0.70
Rubus spp.	0.06	0.62
Vaccinium spp.	−0.20	0.13
Nonnative woody plants	0.12	0.34

between development and cover of any plant genus or nonnative species (Table 3).

Fourteen bird species met our criteria for analysis with N-mixture models (Table 4 and Appendix B). Four species increased and one decreased with development in the landscape (Fig. 2 and Appendix C). We found a significant positive correlation between the development effect in our models and population trends on the BBS ($r_{14} = 0.62$, $p = 0.02$; Fig. 3). This result was clearly affected by white-throated sparrow (*Zonotrichia albicollis*), which had the most negative population trend and the most negative coefficient of development effects. After removing the sparrow, population trend was not significantly correlated with response to development ($r_{13} = 0.41$, $p = 0.15$).

Abundances of avian nest predators increased with development (coefficient = 0.18 ± 0.09, $\chi^2 = 4.4$, $p = 0.04$), but the partial r^2 for development was only 0.02 (Fig. 4). Similarly, abundance of brown-headed cowbirds decreased with development (coefficient = −0.43 ± 0.16, $\chi^2 = 3.16$, $p = 0.01$), with partial r^2 of 0.06.

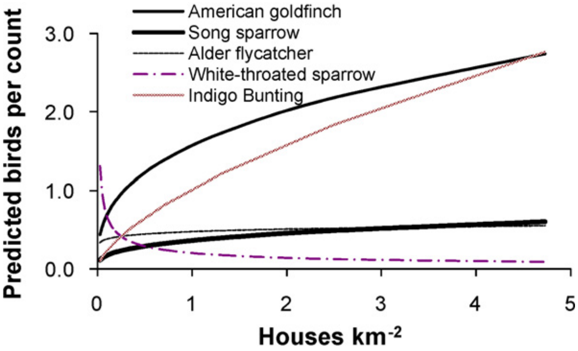


Fig. 2. Predicted avian abundances as a function of landscape-scale development in western Massachusetts shrublands. Values are based on N-mixture models of abundance.

Abundances of small mammals did not vary with development (coefficient = 0.05 ± 0.09, $\chi^2 = 0.3$, $p = 0.59$).

We analyzed nest success for eight bird species. Nest success of prairie warblers (*Dendroica discolor*) declined with increasing development (Table 5). For the other seven species and for all birds combined, we found no effect of development on nest success (see Appendix A for full list of species). Brood parasitism by brown-headed cowbirds increased with development ($r^2 = 0.24$, $F_{1,24} = 7.72$, $p = 0.01$; Fig. 5).

4. Discussion

We found variable effects of rural development on shrubland birds in Massachusetts. Development did not affect abundance for most species. Only one species decreased with development, and four increased. Still, we found an association between more negative effects of development on abundance and negative population trends in Massachusetts. Brood parasitism increased with development in the surrounding landscape, though cowbird abundance showed the opposite pattern. Both relationships, however, were relatively weak. One bird species had lower nest success in more developed landscapes, but we found no effect of housing development on nest success for seven other species or the bird community as a whole.

Our study was restricted to the rural end of the urbanization gradient. On our study landscapes, housing density was below what is considered "exurban" development, ~6–25 houses/km^2 (Hansen et al., 2005; Radeloff et al., 2005). Thus, our conclusions about development apply only to low-density housing in predominately undeveloped areas, and extrapolating our conclusions to more urbanized areas would not be justifiable. Throughout the discussion, we compare our results with those of the only other study of urbanization effects on eastern shrubland birds, by

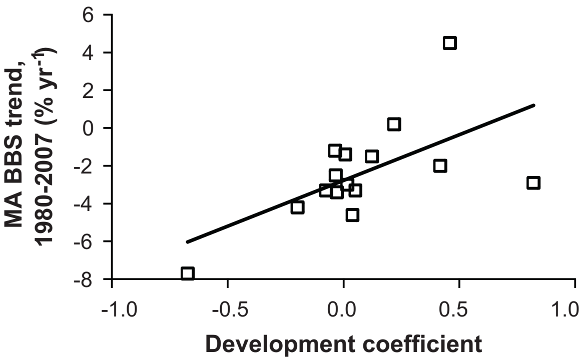


Fig. 3. Relationship between response to development, estimated from this study, and population trend on the North American Breeding Bird Survey (BBS) from 1980 to 2007 (see Sauer et al., 2008) for shrubland birds in Massachusetts. Least-squares regression line is shown.

Table 4
Effects of housing development on avian abundances via N-mixture models. Species with significant effects of development are in bold.

Species	DEV-PC coefficient	SE	*z*	*p*
Alder flycatcher (*Empidonax alnorum*)	**0.12**	**0.06**	**2.16**	**0.03**
Gray catbird (*Dumetella carolinensis*)	0.22	0.43	0.51	0.61
Cedar waxwing (*Bombycilla cedrorum*)	−0.03	0.06	−0.48	0.63
Yellow warbler (*Dendroica petechia*)	−0.04	0.05	−0.78	0.44
Chestnut-sided warbler (*Dendroica pensylvanica*)	−0.03	0.18	−0.18	0.85
Prairie Warbler (*Dendroica discolor*)	0.05	0.06	0.81	0.42
Black-and-white Warbler (*Mniotilta varia*)	−0.20	0.23	−0.86	0.39
Common yellowthroat (*Geothlypis trichas*)	0.02	0.08	0.21	0.84
Eastern towhee (*Pipilo erythrophthalmus*)	−0.07	0.20	−0.37	0.71
Field sparrow (*Spizella pusilla*)	0.04	0.24	0.16	0.87
Song sparrow (*Melospiza melodia*)	**0.42**	**0.07**	**5.88**	**<0.001**
White-throated sparrow (*Zonotrichia albicollis*)	**−0.67**	**0.23**	**−2.93**	**0.003**
Indigo bunting (*Passerina cyanea*)	**0.82**	**0.15**	**5.45**	**<0.001**
American goldfinch (*Spinus tristis*)	**0.46**	**0.11**	**4.31**	**<0.001**

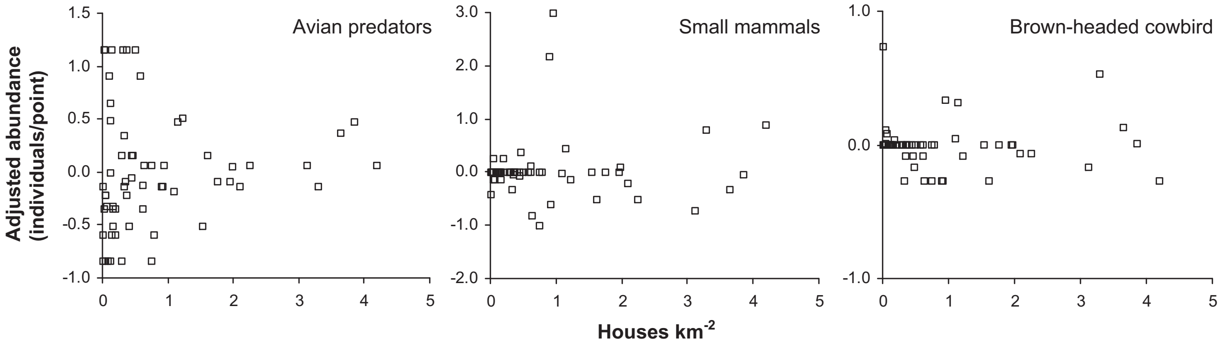


Fig. 4. Effects of development on abundances of avian predators, small mammals, and brown-headed cowbirds. Abundances have been standardized across habitats by subtracting the estimated abundance in each study based on Poisson regression models.

Table 5
Coefficients for effects of development and other covariates on avian nesting success in western Massachusetts shrublands (±1 SE). Significant effects ($p < 0.05$) are in bold.

Species	DEV-PC	Edge distance	Nest height	Day
American Robin ($n = 28$)	−0.01 ± 0.33	0.03 ± 0.02	1.00 ± 0.63	−0.01 ± 0.02
Common yellowthroat ($n = 47$)	0.27 ± 0.24	0.02 ± 0.02	−1.16 ± 1.19	0.04 ± 0.02
Chestnut-sided warbler ($n = 120$)	0.06 ± 0.17	0.01 ± 0.01	−0.08 ± 0.58	0.00 ± 0.01
Eastern Towhee ($n = 73$)	−0.01 ± 0.16	−0.02 ± 0.01	**1.52** ± **0.62**	**−0.02** ± **0.01**
Field Sparrow ($n = 34$)	−0.23 ± 0.38	0.01 ± 0.02	0.80 ± 0.94	−0.02 ± 0.01
Gray catbird ($n = 71$)	−0.19 ± 0.22	0.00 ± 0.01	0.51 ± 0.48	**0.05** ± **0.02**
Indigo bunting ($n = 23$)	1.45 ± 0.76	0.02 ± 0.02	5.76 ± 3.41	**−0.13** ± **0.06**
Prairie warbler ($n = 45$)	**−0.62** ± **0.21**	**0.03** ± **0.02**	0.74 ± 0.55	−0.01 ± 0.03
All birds ($n = 586$)	−0.04 ± 0.06	0.003 ± 0.003	**0.20** ± **0.09**	0.002 ± 0.004

Burhans and Thompson (2006). We note that the developed areas in their study (17% development in the surrounding landscape) were more urbanized than the sites in our study (average of 4% developed).

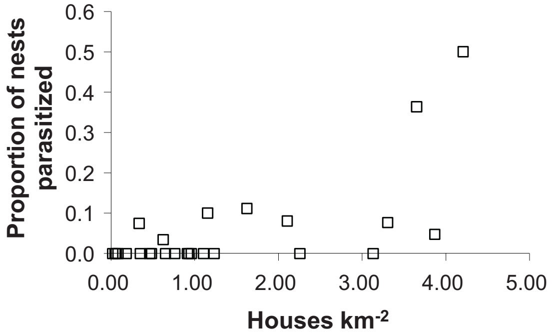


Fig. 5. Effects of landscape-level housing development on brood parasitism by brown-headed cowbirds in western Massachusetts shrublands.

Because our study was observational, our results may have been influenced by correlations between various landscape features. For instance, both of our landscape PCA axes had negative correlations with forest cover and positive correlations with agriculture. We do not believe, however, that these correlations affected our results. First, both forest and agriculture had roughly equal correlations with both the DEV-PC and OPEN-PC axes, but avian responses to those axes differed greatly. Alder flycatcher (*Empidonax alnorum*), American goldfinch (*Spinus tristis*), and white-throated sparrow showed significant effects of DEV-PC and OPEN-PC, but the signs of the coefficients were opposite. The two PC axes are distinguished by the influences of the development and open land categories. If birds had been responding to forest cover or agriculture, one would expect them to show similar responses to both DEV-PC and OPEN-PC.

4.1. Avian abundances

The four species that increased with housing density in our study fall into two categories: first, American goldfinch and song sparrow (*Melospiza melodia*) are short-distance migrants that often nest in yards and suburbs (Beissinger & Osborne, 1982; DeGraaf, 1989; Hooper, Smith, Crawford, McGinnes, & Walker, 1975; Middleton, 1979). Thus, our finding that these species are more abundant in more developed landscapes is consistent with past research. Second, alder flycatcher and indigo bunting (*Passerina cyanea*) are Neotropical migrants and generally occur in undeveloped areas (Beissinger & Osborne, 1982). In Missouri shrublands, indigo buntings were associated with lower housing densities (Burhans & Thompson, 2006). White-throated sparrow, the only species that decreased in abundance with housing development is declining rapidly in Massachusetts and is now uncommon in the state (Sauer et al., 2008).

What mechanisms would cause avian abundances to vary with housing density? Forb cover on our study sites increased with landscape-scale development. Herbaceous vegetation increases with disturbance frequency in eastern shrublands (Chandler et al., 2009; Zuckerberg & Vickery, 2006), so this result could indicate greater disturbance in more developed areas. Past research has shown that American goldfinch and indigo bunting increase with cover of herbaceous vegetation (Confer & Pascoe, 2003; Schlossberg, King, Chandler, & Mazzei, 2010; Thompson & Capen, 1988). As discussed below, nest predation and brood parasitism were only modestly affected by development, so these factors are unlikely to produce the patterns of avian abundances that we found. Research has shown that rural housing is not randomly distributed on the landscape, tending to favor lowlands and areas adjacent to water (Hansen & Rotella, 2002). If birds prefer the same features that attract housing development, then bird populations may covary with development. In our sample, alder flycatcher, a bird associated with wetlands, increased with development whereas white-throated sparrow, upland ground nesters, decreased (DeGraaf & Yamasaki, 2001). These results are consistent with the idea that the non-random distribution of housing influences avian responses to development. Unfortunately, the spatial resolution of our data on housing development was not sufficient to address this question directly. This would be a valuable area for future research.

In Massachusetts, the pace of suburban development has been increasing in recent years, and today, housing development is a leading cause of habitat loss and alteration (DeNormandie et al., 2009). Thus, we predicted that population changes in Massachusetts shrubland birds would be related to their responses to development. Nearly all shrubland birds are declining in Massachusetts (Schlossberg & King, 2007), so positive responses to development were related to less negative population trends rather than increases (Fig. 3). While this result was driven by the negative trend for white-throated sparrow, our findings still suggest that shrubland bird communities in Massachusetts may be shifting towards more development-tolerant species, as species that avoid developed areas decline more rapidly than adaptable species like American goldfinch. One caveat relating to this result is that the primary cause of population declines in New England's shrubland birds is habitat loss (Schlossberg & King, 2007). Thus, we are not claiming that rural development is the cause of population declines. Rather, our findings simply indicate that avoidance of rural development is correlated with population declines.

4.2. Avian nest success

In our sample, prairie warbler was the only species whose nesting success was affected by development. Why prairie warblers showed this unique response is not known, but prairie warblers are declining significantly in southern New England (Sauer et al., 2008). For other birds in our sample, nesting success was unaffected by landscape-scale development. Few other studies have examined effects of low-density housing on avian nest success, and results have been equivocal (Hansen & Rotella, 2002; Phillips, Nol, Burke, & Dunford, 2005). In Missouri, Burhans and Thompson (2006) found no effect of urbanization on nest predation. Though abundances of avian nest predators increased significantly with development in our study, development explained little variation in predator abundance.

Brood parasitism by brown-headed cowbirds increased with development on the landscape, but the explanatory power of development was relatively low ($r^2 = 0.24$). Moreover, this relationship appeared driven by a small number of heavily parasitized sites (Fig. 5). The tendency for cowbird parasitism to increase with housing development is one of the most consistent results in studies of rural housing and birds (Tewksbury et al., 1998; Phillips et al., 2005; Burhans & Thompson, 2006). On our sites, abundances of cowbirds actually showed the opposite effect, a slight decrease with development. Cowbirds are relatively uncommon in western Massachusetts, and research in the Northeast has shown that they are more likely to parasitize nests in forests than in open habitats (Hahn & Hatfield, 1995). Although parasitism rates increase with low-density development in Massachusetts shrublands, parasitism does not appear to pose the conservation threat that cowbirds do where they are more abundant.

4.3. Conclusion

For most birds in our study, effects of low-density development were neutral. We found negative effects of development on abundance of white-throated sparrows and nest success in prairie warblers. Both of these species are declining rapidly in Massachusetts, and maintaining their populations may require keeping development away from their shrubland habitats or creating new habitat in undeveloped areas. For other species, however, effects of rural housing were neutral or even positive in a few cases. For these species, low-density housing in the surrounding landscape, as exists in much of western Massachusetts and rural areas of the Northeast, does not appear to be a conservation threat. Development of new housing, however, could be problematic if it causes loss of early successional habitat. In addition, species such as song sparrow and American goldfinch may actually benefit from development. Our analysis focused only on landscape-scale development. Past research on exurban development has shown more negative effects of development immediately adjacent to natural habitats (Kluza, Griffin, & Degraaf, 2000; Odell & Knight, 2001; Phillips et al., 2005). Thus, our results do not preclude stronger local-scale effects near individual houses or developments.

Acknowledgements

Thanks to the National Resources Conservation Service, Resource Inventory and Assessment Division for providing financial support for S. S. Funding for fieldwork was provided by the Massachusetts Division of Fisheries and Wildlife. Thanks to four anonymous reviewers for constructive comments on the manuscript.

Appendix A.

Sample sizes for nests monitored in western Massachusetts shrublands. * indicates species used in the analysis of cowbird parasitism (see Table A1).

Table A1
Sample sizes for nests monitored in western Massachusetts shrublands. * indicates species used in the analysis of cowbird parasitism. The "forest openings" column includes wildlife and silvicultural openings.

Species	Number of nests			
	Forest openings	Rights-of-way	Total	Observation days
*Chestnut-sided warbler (*Dendroica pensylvanica*)	67	53	120	1479.5
*Eastern towhee (*Pipilo erythrophthalmus*)	19	55	74	679.5
Gray catbird (*Dumetella carolinensis*)	28	43	71	859
*Common Yellowthroat (*Geothlypis trichas*)	16	31	47	578
*Prairie warbler (*Dendroica discolor*)	6	39	45	508.5
*Field sparrow (*Spizella pusilla*)	9	25	34	282.5
American robin (*Turdus migratorius*)	12	16	28	262
*Indigo bunting (*Passerina cyanea*)	14	9	23	287
*Veery (*Catharus fuscescens*)	9	9	18	197.5
*Hermit thrush (*Catharus guttatus*)	1	16	17	210.5
Cedar waxwing (*Bombycilla cedrorum*)	13	3	16	248.5
*Song sparrow (*Melospiza melodia*)	10	3	13	114.5
Black-billed cuckoo (*Coccyzus erythropthalmus*)	11	0	11	91
*Alder flycatcher (*Empidonax alnorum*)	7	1	8	96.5
*Rose-breasted grosbeak (*Pheucticus ludovicianus*)	2	5	7	94
*Red-eyed vireo (*Vireo olivaceus*)	4	2	6	50.5
Blue jay (*Cyanocitta cristata*)	4	1	5	88.5
*Black-throated blue warbler (*Dendroica caerulescens*)	2	3	5	44.5
Mourning dove (*Zenaida macroura*)	5	0	5	78
*Yellow warbler (*Dendroica petechia*)	5	0	5	65
*American goldfinch (*Spinus tristis*)	3	1	4	47.5
*Northern cardinal (*Cardinalis cardinalis*)	1	2	3	5.5
*Ovenbird (*Seiurus aurocapilla*)	0	3	3	38
*Wood thrush (*Hylocichla mustelina*)	1	2	3	38
Brown thrasher (*Toxostoma rufum*)	0	2	2	38
*Blue-winged warbler (*Vermivora cyanoptera*)	0	2	2	28.5
*Chipping sparrow (*Spizella passerina*)	2	0	2	34
*Eastern phoebe (*Sayornis phoebe*)	2	0	2	35
*Magnolia warbler (*Dendroica magnolia*)	2	0	2	39.5
*White-throated sparrow (*Zonotrichia albicollis*)	2	0	2	9.5
*Red-winged blackbird (*Agelaius phoeniceus*)	1	0	1	14

Table B1
Mean abundance (birds per count ± SD) of shrubland birds on point counts in western Massachusetts by habitat type.

Species	Beaver ponds	Utility rights-of-way	Wildlife/silvic. openings
Alder flycatcher	0.61 ± 0.56	0.03 ± 0.15	0.20 ± 0.32
Gray catbird	0.27 ± 0.42	0.24 ± 0.32	0.52 ± 0.48
Cedar waxwing	0.25 ± 0.29	0.07 ± 0.18	0.28 ± 0.36
Yellow warbler	0.42 ± 0.65	0.01 ± 0.05	0.06 ± 0.25
Chestnut-sided warbler	0.24 ± 0.44	0.64 ± 0.51	1.19 ± 0.87
Prairie warbler	0.00 ± 0.00	0.38 ± 0.46	0.13 ± 0.28
Black-and-white warbler	0.06 ± 0.18	0.08 ± 0.18	0.21 ± 0.32
Common yellowthroat	1.33 ± 0.70	0.56 ± 0.46	1.07 ± 0.52
Eastern towhee	0.00 ± 0.03	0.38 ± 0.38	0.52 ± 0.59
Field sparrow	0.00 ± 0.00	0.18 ± 0.32	0.14 ± 0.30
Song sparrow	0.62 ± 0.61	0.06 ± 0.21	0.49 ± 0.68
White-throated sparrow	0.03 ± 0.12	0.01 ± 0.05	0.34 ± 0.68
Indigo bunting	0.01 ± 0.06	0.13 ± 0.26	0.28 ± 0.42
American goldfinch	0.21 ± 0.27	0.07 ± 0.17	0.18 ± 0.27

Appendix B.

Mean abundance (birds per count ± SE) of shrubland birds on point counts in western Massachusetts by habitat type (see Table B1).

Appendix C.

Model-averaged results (mean ± SE) for N-mixture models of abundance in western Massachusetts shrublands. All columns show actual parameters except "mean" under detectability, which shows actual estimated detectability (see Table C1).

Table C1
Model-averaged parameters (mean ± SE) for N-mixture models of avian abundance in western Massachusetts shrublands. All columns show actual parameters except "Detectability," which shows actual estimated detectability. "Beaver pond," "Rights-of-way," and "Forest openings" indicate effects of habitat type. "Trees," "Highshrub/forb," and "Grass/lowshrub" indicate vegetation effects.

Species	OPEN-PC	Beaver pond	Rights-of-way	Forest openings	Trees	Highshrub/forb	Grass/lowshrub	Detectability
Alder flycatcher	−0.18 ± 0.09	2.13 ± 0.29	0.39 ± 0.82	0.64 ± 0.65	0.02 ± 0.10	0.41 ± 0.07	0.01 ± 0.08	0.25 ± 0.02
Gray catbird	0.18 ± 0.10	−0.50 ± 1.29	−0.66 ± 0.55	−0.16 ± 0.86	0.24 ± 1.21	0.15 ± 3.79	−0.34 ± 1.62	0.12 ± 0.02
Cedar waxwing	0.20 ± 0.07	0.49 ± 0.21	−0.84 ± 0.48	0.12 ± 0.40	−0.17 ± 0.12	0.18 ± 0.09	−0.08 ± 0.09	0.18 ± 0.03
Yellow warbler	−0.10 ± 0.03	n/a	n/a	n/a	0.26 ± 0.12	0.80 ± 0.28	0.48 ± 0.39	0.15 ± 0.03
Chestnut-sided warbler	0.13 ± 0.15	−1.07 ± 0.29	0.29 ± 0.22	0.33 ± 0.24	0.17 ± 0.25	0.11 ± 0.46	−0.65 ± 0.13	0.33 ± 0.02

Table C1 (*Continued*)

Species	OPEN-PC	Beaver pond	Rights-of-way	Forest openings	Trees	Highshrub/forb	Grass/lowshrub	Detectability
Prairie Warbler	−0.07 ± 0.12	−8.21 ± 2.98	−0.35 ± 0.45	−1.85 ± 1.07	−0.13 ± 13.55	−0.26 ± 8.57	−0.46 ± 5.39	0.45 ± 0.04
Black-and-white warbler	−0.26 ± 0.24	−0.16 ± 0.57	0.29 ± 0.46	1.52 ± 0.69	0.39 ± 0.39	0.22 ± 0.20	−0.61 ± 0.32	0.45 ± 0.03
Common yellowthroat	−0.01 ± 0.09	0.29 ± 0.74	0.09 ± 1.58	0.03 ± 1.02	0.03 ± 0.14	0.14 ± 0.07	0.00 ± 0.07	0.38 ± 0.06
Eastern towhee	0.20 ± 0.15	−5.48 ± 0.67	−0.18 ± 0.49	−0.41 ± 1.00	0.30 ± 0.64	−0.07 ± 0.38	−0.61 ± 0.27	0.32 ± 0.03
Field Sparrow	0.11 ± 0.23	−8.43 ± 0.56	0.03 ± 0.38	−1.41 ± 0.77	−0.89 ± 0.61	−1.07 ± 0.44	−0.16 ± 0.23	0.27 ± 0.03
Song sparrow	−0.15 ± 0.09	1.74 ± 0.33	−0.02 ± 0.64	1.46 ± 0.54	0.01 ± 0.23	−0.20 ± 0.17	−0.03 ± 0.16	0.39 ± 0.04
White-throated sparrow	0.66 ± 0.22	0.44 ± 0.75	-0.07 ± 1.38	1.65 ± 1.22	−0.91 ± 0.50	−0.02 ± 0.23	−0.51 ± 0.16	0.52 ± 0.04
Indigo bunting	−0.16 ± 0.24	−2.47 ± 0.65	0.32 ± 0.34	0.57 ± 0.40	0.09 ± 0.38	−0.30 ± 0.31	−0.10 ± 0.23	0.37 ± 0.02
American goldfinch	−0.14 ± 0.09	0.51 ± 0.46	−0.01 ± 0.46	0.56 ± 0.51	−0.06 ± 0.17	0.11 ± 0.39	0.02 ± 0.45	0.19 ± 0.08

References

Alig, R. J., Kline, J. D., & Lichtenstein, M. (2004). Urbanization on the US landscape: Looking ahead in the 21st century. *Landscape and Urban Planning*, *69*, 219–234.

Askins, R. A., Zuckerberg, B., & Novak, L. (2007). Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland songbirds in southern New England? *Forest Ecology and Management*, *250*, 137–147.

Beissinger, S. R., & Osborne, D. R. (1982). Effects of urbanization on avian community organization. *Condor*, *84*, 75–83.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications*, *6*, 506–519.

Brittingham, M. C., & Temple, S. A. (1983). Have cowbirds caused forest songbirds to decline? *BioScience*, *33*, 31–35.

Brown, D. G., Johnson, K. M., Loveland, T. R., & Theobald, D. M. (2005). Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications*, *15*, 1851–1863.

Burhans, D. E., Dearborn, D., Thompson, F. R., III, & Faaborg, J. (2002). Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management*, *66*, 240–249.

Burhans, D. E., & Thompson, F. R. (2006). Songbird abundance and parasitism differ between urban and rural shrublands. *Ecological Applications*, 394–405.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference*. New York: Springer-Verlag, New York.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, *74*, 46–69.

Chandler, R. B. (2006). Early-successional bird abundance and nest success in managed shrublands on the White Mountain National Forest. Masters Thesis, University of Massachusetts, Amherst.

Chandler, R. B., King, D. I., & Chandler, C. C. (2009). Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. *Forest Ecology and Management*, *258*, 1669–1676.

Confer, J. L., & Pascoe, S. M. (2003). Avian communities on utility rights-of-ways and other managed shrublands in the northeastern United States. *Forest Ecology and Management*, *185*, 193–205.

DeGraaf, R. M. (1989). Territory sizes of song sparrows, Melospiza melodia, in rural and suburban habitats. *Canadian Field-Naturalist*, *103*, 43–47.

DeGraaf, R. M., & Yamasaki, M. (2001). *New England Wildlife: Habitat, Natural History, and Distribution*. Hanover, New Hampshire: University Press of New England.

DeNormandie, J., Corcoran, C., & Clarke, J. J. (2009). *Losing Ground: Beyond the Footprint*. Massachusetts: MassAudubon, Lincoln.

Fraterrigo, J. M., & Wiens, J. A. (2005). Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landscape and Urban Planning*, *71*, 263–275.

Hahn, D. C., & Hatfield, J. S. (1995). Parasitism at the landscape scale: Cowbirds prefer forests. *Conservation Biology*, *9*, 1415–1424.

Hansen, A. J., Knight, R. L., Marzluff, J. M., Powell, S., Brown, K., Gude, P. H., & Jones, K. E. (2005). Effects of exurban development on biodiversity: Patterns, mechanisms, and research needs. *Ecological Applications*, *15*, 1893–1905.

Hansen, A. J., & Rotella, J. J. (2002). Biophysical factors, land use, and species viability in and around nature reserves. *Conservation Biology*, *16*, 1112–1122.

Hooper, R. G., Smith, E. F., Crawford, H. S., McGinnes, B. S., & Walker, V. J. (1975). Nesting bird populations in a new town. *Wildlife Society Bulletin*, *3*, 111–118.

Hoover, J. P. (2003). Multiple effects of brood parasitism reduce the reproductive success of prothonotary warblers, *Protonotaria citrea*. *Animal Behaviour*, *65*, 923–934.

Hunter, W. C., Buehler, D. A., Canterbury, R. A., Confer, J. L., & Hamel, P. B. (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin*, *29*, 440–455.

Imbeau, L., Drapeau, P., & Mönkkönen, M. (2003). Are forest birds categorised as “edge species” strictly associated with edges? *Ecography*, *26*, 514–520.

King, D. I., Chandler, R. B., Collins, J. M., Petersen, W. R., & Lautzenheiser, T. E. (2009). Effects of width, edge and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. *Biological Conservation*, *142*, 2672–2680.

King, D. I., Chandler, R. B., Schlossberg, S., & Chandler, C. C. (2009). Habitat use and nest success of scrub-shrub birds in wildlife and silvicultural openings in western Massachusetts, USA. *Forest Ecology and Management*, *257*, 421–426.

Kluza, D. A., Griffin, C. R., & Degraaf, R. M. (2000). Housing developments in rural New England: Effects on forest birds. *Animal Conservation*, *3*, 15–26.

MacFaden, S. W., & Capen, D. E. (2002). Avian habitat relationships at multiple scales in a New England forest. *Forest Science*, *48*, 243–253.

Maestas, J. D., Knight, R. L., & Gilgert, W. C. (2003). Biodiversity across a rural land-use gradient. *Conservation Biology*, *17*, 1425–1434.

Martin, T. E., & Geupel, G. R. (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology*, *64*, 507–519.

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian ecology and conservation in an urbanizing world*. Norwell, Massachusetts: Kluwer Academic Publishers, pp. 19–47.

Marzluff, J. M., Bowman, R., & Donnelly, R. (2001). A historical perspective on urban bird research: Trends, terms, and approaches. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian ecology and conservation in an urbanizing world*. Norwell, Massachusetts: Kluwer Academic Publishers, pp. 1–17.

MassGIS (Massachusetts Office of Geographic and Environmental Information), 2009. Land Use (2005). <http://www.mass.gov/mgis/lus2005.htm>. [accessed 08.12.09].

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, *52*, 883–890.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*, 247–260.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*, 450–453.

Middleton, A. L. A. (1979). Influence of age and habitat on reproduction by the American Goldfinch. *Ecology*, *60*, 418–432.

Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, *78*, 691–692.

Odell, E. A., & Knight, R. L. (2001). Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology*, *15*, 1143–1150.

Peer, B. D., Robinson, S. K., & Herkert, J. R. (2000). Egg rejection by cowbird hosts in grasslands. *Auk*, 892–901.

Phillips, J., Nol, E., Burke, D., & Dunford, W. (2005). Impacts of housing developments on wood thrush nesting success in hardwood forest fragments. *Condor*, *107*, 97–106.

Pidgeon, A. M., Radeloff, V. C., Flather, C. H., Lepczyk, C. A., Clayton, M. K., Hawbaker, T. J., & Hammer, R. B. (2007). Associations of forest bird species richness with housing and landscape patterns across the USA. *Ecological Applications*, *17*, 1989–2010.

Radeloff, V. C., Hammer, R. B., Stewart, S. I., Fried, J. S., Holcomb, S. S., & McKeefry, J. F. (2005). The wildland–urban interface in the United States. *Ecological Applications*, *15*, 799–805.

Rodewald, A. D., & Shustack, D. P. (2008). Urban flight: Understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. *Journal of Animal Ecology*, *77*, 83–91.

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, *60*, 108–115.

SAS Institute Inc. (2001). SAS Version 8.2. Cary, North Carolina.

Sauer, J. R., Hines, J. E., & Fallon, J. (2008). *The North American Breeding Bird Survey, Results and Analysis 1966-2007. Version 5. 15. 2008*. Laurel, Maryland: USGS Patuxent Wildlife Research Center.

Schlossberg, S., King, D.I. 2007. Ecology and management of scrub-shrub birds in New England: A comprehensive review. Beltsville, Maryland, report submitted to natural resources conservation service, resource inventory and assessment division.

Schlossberg, S., & King, D. I. (2008). Are shrubland birds edge specialists? *Ecological Applications*, *18*, 1325–1330.

Schlossberg, S., King, D. I., Chandler, R. B., & Mazzei, B. A. (2010). Regional synthesis of habitat relationships in shrubland birds. *Journal of Wildlife Management*, *74*, 1513–1522.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk*, *121*, 526–540.

Shochat, E., Stefanov, W. L., Whitehouse, M. E. A., & Faeth, S. H. (2004). Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. *Ecological Applications*, *14*, 268–280.

Tewksbury, J. J., Hejl, S. J., & Martin, T. E. (1998). Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology*, *79*, 2890–2903.

Thompson, F. R., III, & Capen, D. E. (1988). Avian assemblages in seral stages of a Vermont forest. *Journal of Wildlife Management*, *52*, 771–777.

Toms, J. D., Schmiegelow, F. K. A., Hannon, S. J., Villard, M.-A., & McDonald, D. B. (2009). Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? *Auk*, *123*, 438–454.

U.S. Census Bureau (2008). TIGER/Line. <http://www.census.gov/geo/www/tiger>. [accessed 06.03.09].

Wenger, S. J., & Freeman, M. C. (2008). Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology*, *89*, 2953–2959.

Zuckerberg, B., & Vickery, P. D. (2006). Effects of mowing and burning on shrubland and grassland birds on Nantucket Island, Massachusetts. *Wilson Journal of Ornithology*, *118*, 353–363.