Ecological Applications, 16(1), 2006, pp. 394–405

SONGBIRD ABUNDANCE AND PARASITISM DIFFER BETWEEN URBAN AND RURAL SHRUBLANDS

DIRK E. BURHANS[1,3] AND FRANK R. THOMPSON III[2]

[1]*Department of Fisheries and Wildlife Sciences, 202 Natural Resources Building, University of Missouri, Columbia, Missouri 65211 USA*
[2]*USDA Forest Service North Central Research Station, 202 Natural Resources Building, University of Missouri, Columbia, Missouri 65211 USA*

Abstract. Many studies have examined differences in avian community composition between urban and rural habitats, but few, if any, have looked at nesting success of urban shrubland birds in a replicated fashion while controlling for habitat. We tested factors affecting nest survival, parasitism by the Brown-headed Cowbird (*Molothrus ater*), and species abundance in shrubland habitat in rural and urban landscapes. We found no support for our hypothesis that nest survival was lower in urban landscapes, but strong support for the hypothesis that survival increased with nest height. We found strong support for our hypothesis that cowbird parasitism was greater in urban than rural landscapes; parasitism in urban sites was at least twice that of rural sites. We found strong support for an urban landscape effect on abundance for several species; Northern Cardinal (*Cardinalis cardinalis*) and Brown-headed Cowbirds were more abundant in urban landscapes, whereas Field Sparrow (*Spizella pusilla*) and Blue-winged Warbler (*Vermivora pinus*) were more abundant in rural sites. There was support for lower abundances of Blue-gray Gnatcatcher (*Polioptila caerulea*) and Indigo Bunting (*Passerina cyanea*) with increased housing density. For six other species, edge and trail density or vegetation parameters best explained abundance. Lower abundances and greater parasitism in habitat patches in urban landscapes are evidence that, for some species, these urban landscapes do not fulfill the same role as comparable habitats in rural landscapes. Regional bird conservation planning and local habitat management in urban landscapes may need to consider these effects in efforts to sustain bird populations at regional and local scales.

Key words: brood parasitism; Brown-headed Cowbird; landscape; nest predation; nesting success; shrubland; songbirds; urban.

INTRODUCTION

In the past two decades, many biologists have voiced concern about declines of neotropical migrant songbirds in response to the human-induced changes in the landscape and associated fragmentation (Terborgh 1989, Askins 2000). As human populations, housing densities, and urbanization all increase, research has increasingly focused upon urban bird communities (Marzluff et al. 2001). Many studies evaluating the effects of urbanization have compared relative abundances or diversity along a gradient from wildland to urban habitats (reviewed in Marzluff et al. 2001). Earlier songbird studies particularly emphasized the disappearance of migrant songbirds from urban areas where they formerly occurred (Robbins 1979, Aldrich and Coffin 1980, Serrao 1985). In abundance studies, greater bird diversity was often found in urban areas (e.g., Blair 1996), whereas rural areas had greater abundances of neotropical migrants or ‘‘desirable’’ native species in comparison (Nilon et al. 1995, Kluza et al. 2000).

An important component to any understanding of avian populations, however, is knowledge about breeding success. For example, studies have shown that, although birds may use forest fragments, they may not be reproducing at sustainable levels in them (Robinson et al. 1995, Faaborg 2002); thus, presence of the birds alone does not provide insights into habitat quality or into the forces driving species abundance (Marzluff et al. 2001). A number of studies have examined nesting in urban habitats, but these have typically either been single-species studies (Morneau et al. 1995) or non-replicated multi-species studies (Weber 1975). Artificial-nest studies have been used to compare nesting success between anthropogenic and natural settings (Melampy et al. 1999, Miller and Hobbs 2000), but recent work shows that artificial nests experience different predation rates than real nests (Burke et al. 2004) and that different predators are attracted to real and artificial nests (Thompson and Burhans 2004). Some artificial-nest studies have shown increases in artificial-nest predation with increasing urbanization (Jokimäki and Huhta 2000, Thorington and Bowman 2003) or

Manuscript received 14 June 2004; revised 18 May 2005; accepted 16 June 2005. Corresponding Editor: F. C. James.

[3] E-mail: burhansd@missouri.edu

decreases in predation with urbanization (Gering and Blair 1999); but even relative predation rates that assume a constant predator across treatments may not be relevant if the predator(s) responsible for the change rarely depredate real nests (Thompson and Burhans 2004).

We used a replicated design to study nesting success and abundances of songbirds in a rapidly urbanizing area in shrubland habitats embedded in urban and rural landscapes. Because the urban sites were ‘‘natural’’ or ‘‘seminatural’’ urban parks where the main citizen activities were trail use in natural surroundings, shrublands at the urban sites were similar to rural shrublands. Many studies of urban effects on songbirds have used diversity indices (Beissinger and Osborne 1982, Blair 1996) to look at a continuous ‘‘gradient’’ from rural-to-urban habitats (Beissinger and Osborne 1982, Lancaster and Rees 1979, Blair 1996). We conducted an ‘‘observational experiment’’ by comparing three replicate patches of shrubland habitat in an urban landscape to three replicate patches in a rural landscape. We used an information theoretic approach (Burnham and Anderson 2002) to test support for our hypotheses of an urban landscape effect on bird abundance, nesting success, and brood parasitism.

METHODS

Study sites

Our study was located in Boone County, Missouri, USA, and the City of Columbia within it, which is one of the six metropolitan regions of Missouri. The city of Columbia is one of the fastest growing cities in the state. Columbia experienced a population increase of 22.3% from 1990 to 2000, whereas other Missouri cities of comparable size experienced single-digit growth or population declines (OSEDA 2004).

We located shrubland bird nests in shrublands and shrubland forest edges in three urban floodplains and three rural floodplains in Boone County, from 2000 to 2002. The urban sites were in the Grindstone Nature Area (‘‘Grindstone,’’ 38°55′ N, 92°18′ W, 15.3 ha), Bear Creek Natural Area (‘‘Bear Creek,’’ 38°58′ N, 92°20′ W, 9.8 ha), and the Forum Nature Area (‘‘Forum,’’ 38°55′ N, 92°22′ W, 34.4 ha). Grindstone was managed with prescribed burns every 3–4 years. Forum and Bear Creek contained sections that were previously mowed on a biennial basis, but managers refrained from mowing these parks during the course of our study. Forum and Bear Creek also had one or more large fields (circa 5–8.5 ha) that were unmowed prior to and throughout our study, in addition to substantial portions of unmanipulated stream and forest edge. Bear Creek was reclaimed with fill as a former wastewater lagoon area >20 years before present (M. Griggs, City of Columbia Parks and Recreation, *personal communication*). We conducted research all three years (2000–2002) at all three urban sites.

Two rural sites were on Mark Twain National Forest (‘‘Hudson,’’ 38°41′ N, 92°14′ W, 8.7 ha; and ‘‘Zumwalt,’’ 38°42′ N, 92°12′ W, 10.4 ha) and one rural site was on the 920-ha Thomas S. Baskett Wildlife Research and Education Center (‘‘Baskett,’’ 38°445′ N, 92°112′ W, 19.5 ha) near Ashland, Missouri (described in Burhans 1997). Zumwalt and Baskett had reverted to shrubland from cropland; Baskett was managed by infrequent (3–4 year) prescribed burns. Hudson was a series of abandoned pastures linked by natural streams and dominated by tall fescue (*Festuca arundinacea*), but also containing patches of *Rubus*, sumac, and dispersed eastern red cedars within the fields. We conducted research all three years (2000–2002) at Baskett and from 2001 to 2002 at Zumwalt and Hudson.

All sites were composed of grasses and forbs with a large shrubby component, including shrubs such as *Rubus*, sumac (*Rhus* spp.), poison ivy (*R. radicans*), and eastern red cedar (*Juniperus virginiana*), and small-to-large sapling stands of silver maple (*Acer saccharinum*), box elder (*Acer Negundo*), and sycamore (*Platanus occidentalis*). Field edges were structurally comparable among all sites. Forest edges at both urban and rural sites were bordered by eastern red cedar, hackberry (*Celtis occidentalis*), silver maple, box elder, and oaks (*Quercus* spp). Shrub layers in the stream edges proximate to fields were typically dominated by coralberry (*Symphoricarpos orbiculatus*). Fields at both urban and rural sites had gradual or ‘‘soft edges’’; that is, the field edges graduated to forest in a shrubby continuum rather than ending abruptly (Suarez et al. 1997).

The surrounding landscape for the urban sites was approximately 17% urban impervious surface, 27% grassland/cropland, and 55% forest, whereas rural sites were approximately 29% cropland/grassland and 70% forest (based on circa 1990 TM satellite data interpreted by the Missouri Resources Assessment partnership; *available online*).[4] All sites, urban and rural, were bordered by permanent streams and subject to occasional partial flooding. Shrubland fields at all sites were bordered by forest.

Site-level habitat and landscape measurements

We measured vegetation at each site (Table 1) at four randomly located points in the shrubland and four points randomly located 10–25 m into the forest from the bole line of forest edge, because two species (Indigo Bunting, Northern Cardinal) frequently nested in forest edge proximate to the fields. We measured canopy closure with a spherical densitometer (model-C, Robert E. Lemmon, Forest Densiometers, Bartlesville, Oklahoma, USA), vertical foliage density with a robel pole (Robel et al. 1969), and cover of grass, forb, woody, litter, and bare ground in a 1 m^2 frame, at 1.78 m distance north, south, east and west of each point.

---

[4] 〈www.cerc.usgs.gov/morap〉

TABLE 1. Mean and 95% CI for site-level vegetation structure in fields and forest edges for each study site in urban and rural landscapes in Boone County, Missouri, USA, 2000–2002 ($n = 4$ plots for each row).

Site, by landscape	Grass cover (%)	Forb cover (%)	Canopy closure (%)	Foliage density†	No. small stems	No. large stems	dbh‡ (cm)
Urban							
Grindstone							
Fields	3.2 ± 4.7	12.0 ± 5.3	0.0 ± 0.0	6.8 ± 4.9	3.3 ± 5.6	1.0 ± 1.7	1.0 ± 0.0
Forest edges	1.2 ± 1.6	2.3 ± 0.6	100 ± 0.0	0.6 ± 0.4	29.3 ± 18.7	30.0 ± 6.6	5.2 ± 2.0
Forum							
Fields	2.6 ± 3.2	8.5 ± 5.0	0.0 ± 0.0	2.1 ± 2.4	1.3 ± 2.2	2.0 ± 4.7	1.0 ± 0.0
Forest edges	3.8 ± 3.3	5.8 ± 4.6	100 ± 0.0	0.7 ± 0.7	2.5 ± 5.1	28.8 ± 52.8	13.5 ± 12.9
Bear Creek							
Fields	12.4 ± 5.3	3.3 ± 5.5	0.00 ± 0.0	2.8 ± 1.7	1.3 ± 2.2	0.3 ± 0.6	2.0 ± 0.0
Forest edges	2.2 ± 1.3	3.9 ± 4.5	100 ± 0.0	0.8 ± 1.0	29.5 ± 18.9	33.5 ± 13.7	6.1 ± 4.2
Rural							
Baskett							
Fields	3.5 ± 7.1	10.6 ± 8.4	17.2 ± 26.4	2.4 ± 1.3	2.5 ± 2.3	9.8 ± 6.8	2.3 ± 1.3
Forest edges	1.6 ± 2.2	9.9 ± 6.6	91.7 ± 19.6	0.5 ± 1.0	0.3 ± 0.6	10.0 ± 7.4	15.1 ± 10.1
Hudson							
Fields	22.2 ± 15.0	0.2 ± 0.1	0.0 ± 0.0	9.1 ± 3.5	3.0 ± 6.3	2.9 ± 5.0	3.6 ± 18.1
Forest edges	1.1 ± 1.2	4.0 ± 6.9	99.5 ± 1.2	5.7 ± 1.4	8.8 ± 5.1	46.8 ± 32.8	5.3 ± 1.1
Zumwalt							
Fields	6.3 ± 2.5	3.8 ± 4.6	40.1 ± 52.7	9.9 ± 4.7	10.0 ± 15.8	72.3 ± 125.2	1.7 ± 1.5
Forest edges	2.7 ± 0.6	3.1 ± 2.5	100 ± 0.0	7.3 ± 1.6	8.8 ± 5.3	33.3 ± 12.2	10.1 ± 6.0

† Robel pole reading (Robel et al. 1969).
‡ Tree diameter at breast height.

Within a 1.78 m radius of the point we counted, by species, the number of small woody stems (<1.4 m high and ≥0.50 cm high). Within a 5.64 m radius, we measured the diameter at breast height (dbh) and identified species of large woody stems (≥1.4 m high and ≥0.50 cm dbh).

We developed maps of forest edge, trails, roads, and housing in and adjacent to each site ArcView 3.2 (ESRI, Redlands, California, USA; Table 2). We used GPS to map forest edges and trails in within a 50-m buffer around each site. We mapped the locations of roads within a 50-m buffer of each site and housing within a 400-m buffer of each site from 1998 Digital Orthographic Quarter Quadrangles and updated information collected in the field. We calculated descriptive statistics (means and 95% confidence intervals) for vegetation and landscape variable for each site and used some of this data in nest survival and abundance models as well.

TABLE 2. Densities of roads, trails, and forest edge within 50-m buffer and mean number of houses/ha within 400-m buffer of sites in Boone County, Missouri, 2000–2002.

Site	Roads (m/m^2)	Trails (m/m^2)	Forest edge (m/m^2)	Houses/ha
Urban				
Grindstone	0	0.021	0.011	0.395
Forum	0.001	0.017	0.007	1.136
Bear Creek	0	0.008	0.010	0.829
Rural				
Baskett	0.002	0.014	0.011	0.026
Hudson	0.004	0	0.018	0.015
Zumwalt	0.003	0.008	0.008	0.022

Nest monitoring

We searched for and monitored nests at urban and rural sites on alternating days. Nests were located by systematic searching of potential nest sites and behavioral cues from adult birds. We marked nest locations with plastic flagging placed at least 3 m from the nest. We focused on Field Sparrows (*Spizella pusilla*), Indigo Buntings (*Passerina cyanea*), Yellow-breasted Chats (*Icteria virens*), and Northern Cardinals (*Cardinalis cardinalis*) because their nests were easy to find and because they were common at both urban and rural sites (with the exception of Field Sparrows, whose nests were found only at rural sites).

We searched sites daily for nests and marked them with plastic flagging ≥3 m from the nest. We found 23.3%, 12.3%, 49.2%, and 15.2% of nests of the four species combined in building, laying, incubation, and nestling stages, respectively. Nests were monitored every 2–3 days (3.3 ± 1.26 [mean ± SE]) until fledging approached. Fledging was documented by early morning visits on the expected day of fledging, during which we looked for evidence such as fledgling begging calls, the sight of fledglings, parents carrying food, or parents chipping rapidly nearby. Nests empty prior to this were considered depredated unless we found evidence of premature fledging; nests where we did not observe these activities were classified as ‘‘unknown.’’ We approached nests and viewed their contents at the maximum distance possible to determine status, and were careful not to leave ‘‘dead-end trails’’ leading to the nest.

Nest site habitat and landscape measurements

We sampled vegetation after the termination of activity at each nest by laying out quadrants in the four cardinal directions centered on the nest. We measured canopy closure with a spherical densiometer at points 1.78 m north and south of the nest and calculated the mean of the two values. We measured distance to the nearest potential cowbird perch by walking (estimated at 1-m/step) to the nearest tree $\geq$3 m in height in each quadrant and calculated the mean of the four values. We measured shrub density in the nest patch by counting the number of small stems ($\geq$50 cm and $<$1.4 m high) within a 1.78 m radius of the nest. We also measured height of the nest (m) to the bottom of the nest cup and distance of the nest (m) from the main trunk of the supporting tree or shrub. If the nest was on the ground, in grass, or in vegetation with numerous small supporting stems, this distance was recorded as ‘‘0.’’ We determined Universal Transverse Mercator coordinates for each nest after the breeding season using a Trimble Pathfinder Pro XR (realtime mode) Global Positioning System (GPS) unit (Trimble, Sunnyvale, California, USA) with an accuracy level of approximately 1 m.

We determined the number of houses within a 400 m radius of each nest and the length of trail, road, and forest edge within a 50 m radius of the nest using ArcInfo 8.3 (ESRI, Redlands, California, USA). We reasoned that the influence of housing density would be relevant to nesting success at a landscape level, whereas trail and edge effects would act at the scale of the nest patch (see *Analysis*, below).

Bird abundance

We placed eight 50 m radius point count stations 200 m apart and $\geq$200 m from the entrance of each site. Point count stations were centered on the forest–field edge to standardize the amount of edge sampled by each point and to survey a greater diversity of birds. We counted birds seen or heard within a 50 m radius for a 5-min period.

We commenced point counts in the first week of May in 2001 and 2002. Each site was surveyed twice in May and twice in June. Counts were conducted between 04:45 and 08:00 Central standard Time (CST) and the order in which the count stations were surveyed was reversed between visits so that no points were always surveyed either late or early in the morning. Different observers conducted counts, but all point count personnel were trained and familiar with local avifauna, and were rotated among different sites so that no one observer always counted at the same site.

Data analysis

Nest survival.—We used a general linear model with a binomial distribution (interval nest fate = 0 if failed and 1 if successful) and a logit link function to estimate daily nest success and evaluate factors potentially affecting nest survival (Dinsmore et al. 2002, Shaffer 2004). We only considered losses due to predation because our hypotheses specifically addressed differences in nest success between urban and rural landscapes (and not factors such as weather, abandonment, etc.). We treated each interval between nest checks as an observation; this method allows time dependent variables, such as nest stage, to change from one interval to the next during the nest cycle (Shaffer 2004). Because nest observation intervals were usually $>$1 day and varied in length (mean = 3.32 days), we used the following modified logit link function: $g(\theta) = \log_e(\theta 1/t/[1 - \theta 1/t])$, where θ is the interval survival rate and t is the interval length in days (Shaffer 2004). We fit models with PROC NLMIXED (SAS 1999) by selecting a binomial response distribution and supplying this user-defined link.

We grouped variables a priori into a nest model (nest height, distance to main stem), habitat patch model (shrub–stem density, length of edge, length of trail, length of road), landscape model (housing density, urban [1 if urban site, 0 if rural site]), temporal model (nest stage, day of year), a cowbird model (presence of cowbird egg(s) and/or cowbird nestling(s) = 1, else 0), and selected combinations of these models, including a global model with all variables (Table 3). We treated the combination of year and site as a random effect in all models so this source of temporal and spatial variation would not be confounded with fixed effects. We conducted a preliminary analysis of the global model with and without a set of dummy variables that identified the bird species to determine if there was support for including species as a factor in all the candidate models.

We used an information–theoretic approach to evaluate support for our a priori models (Burnham and Anderson 2002). This approach allows for the simultaneous evaluation of strength of evidence of multiple models on the same sample. The model with the lowest value for Akaike’s Information Criterion (AIC) is the best approximating model for the data, and nested models with differences in AIC from the best model (Δ_i) of $<$2 represent potential best models (Burnham and Anderson 2002). Akaike weights (w_i) for any given model set sum to 1, and can be interpreted as the approximate probabilities of suitability for each model (Burnham and Anderson 2002). We report coefficients, and their standard errors and 95% confidence intervals, and odds ratios for the best model.

Brood parasitism.—We used binary logistic regression to model the effects of variables on whether or not a nest was parasitized. We included only nests ini-

TABLE 3. Models explaining nest survival at urban and rural old fields in Boone County, Missouri, 2000–2002.

Model	−2(L)	K	AIC	Δ_i	w_i
Nest site†	1192.22	4	1200.22	0.00	0.48
Nest site, temporal	1189.15	6	1201.15	0.93	0.30
Nest site, temporal, landscape	1186.72	8	1202.72	2.50	0.14
Nest site, temporal, nest patch	1184.54	10	1204.63	4.41	0.05
Global	1177.82	14	1205.82	5.60	0.03
Landscape‡	1208.37	4	1216.37	16.15	0.00
Null	1212.64	2	1216.64	16.42	0.00
Nest patch§	1205.17	6	1217.17	16.95	0.00
Nest patch, landscape	1201.94	8	1217.94	17.72	0.00
Temporal‖	1210.17	4	1218.17	17.95	0.00
Cowbird¶	1212.23	4	1220.23	20.01	0.00

Notes: Models are ranked from best to worst based on Akaike's information criteria (AIC), differences in AIC from best model (Δ_i), and Akaike weights (w_i); AIC is based on −2 × log likelihood (L) and the number of parameters in the model (K). Only losses due to nest predation are considered.

† Includes variables: nest height, distance to main stem.

‡ Includes variables: housing density, urban (1 if urban site, 0 if rural site).

§ Includes variables: shrub stem density, length of edge, length of trail, length of road.

‖ Includes variables: nest stage, day of year.

¶ Includes variables: cowbird eggs, (0 or ≥1), cowbird chicks (0 or ≥1).

tiated before or during the second week of July, which is the time cowbirds stop laying at these sites (Burhans 1997). Similar to the nest survival analysis, we used an information–theoretic approach to evaluate support for alternative hypotheses or models. However, some variables and models were different because we hypothesized different factors for parasitism and because the models predicted the outcome for a nest, not a nest interval. Variables were grouped into a nest characteristics model (nest height, day of year), edge model (length of edge), cowbird perch model (mean distance to cowbird perch), landscape model (housing density, urban [1 if urban site, 0 if rural site]), and combination of these models, including a global model with all variables (Table 4). We summed length of trail, road, and forest edge to make a single length of edge variable because of multicolinearity and because one or more of the former variables were completely confounded with parasitism for certain sites and yielded untenable models. We treated the combination of year and site as a random effect in all models so this source of temporal and spatial variation would not be confounded with the fixed effects.

Bird abundance.—We analyzed the count data as a measure of relative abundance (detections/visit). We rotated observers and times of counts among sites so differences in the probability of detection among observers or count times would result in minimal bias and would be accounted for in the error terms of the statistical models. We expected no habitat-related differences in the probability of detection because habitats were similar across sites. To avoid problems resulting from differences in the probability of detection among species, we analyzed species separately, and do not directly compare abundances among species. We acknowledge the recent emphasis on collecting distance or multiple-observer data to estimate effects of observer, time, species, and treatment on probability of detection (Thompson et al. 1998, Nichols et al. 2000), but the necessary data were not collected in this study.

We calculated mean detections/visit for the four visits to each point in a year for each species. Those data

TABLE 4. Parameter estimates for the best-supported models explaining nest survival and brood parasitism at urban and rural old fields in Boone County, Missouri, 2000–2002.

Model	Parameter	Coefficient	SE	95% CL	Odds ratio
Nest survival	intercept	2.415	0.159	2.077, 2.754	
	nest height	0.339	0.143	0.035, 0.645	1.41
	distance to stem	1.267	0.614	−0.044, 2.574	3.55
Brood parasitism	intercept	−0.919	1.596	−4.322, 2.482	
	landscape†	3.303	1.441	0.232, 6.374	27.19
	housing density	0.008	0.009	−0.012, 0.028	1.01
	Field Sparrow‡	−0.377	0.994	−2.496, 1.743	0.69
	Indigo Bunting‡	−2.549	1.203	−5.112, 0.015	0.08
	Yellow-breasted Chat‡	−1.283	0.909	−3.221, 0.655	0.28

Note: Models only considered losses due to nest predation.

† Categorical variable: 1 if urban, 0 if rural.

‡ Reference category for species variables was Northern Cardinal.

(8 points × 6 sites × 2 years = 96) were used in a general linear model (PROC MIXED; SAS 1999). However, to acknowledge potential correlations among counts at the same point over two years, we treated year as a repeated effect with point nested within site specified as the subject and included site as a random effect to account for potential correlations among points in the same site.

We used an information–theoretic approach to evaluate support for models representing alternative hypotheses. All models included the repeated and random effects, but had different fixed effects. We created a ''landscape'' model that had a single fixed effect of landscape (1 if urban site, 0 if rural site). We created a ''housing density'' model, which had housing density at each site as a fixed effect and an ''edge and trail'' model, which had densities of trails and forest edge for each site. We created a ''vegetation'' model with small-stem density and percent canopy cover as fixed effects. We used weighted means of small-stem density and canopy closure for each bird species calculated from the field and forest vegetation plot based on the proportion of observations of that bird species in the field and forest at each site. We also created a null model, which only had an intercept and the repeated effect of year and random effect for site. Other potential combinations of vegetation and landscape variables or combinations of the above models were not possible due to multicollinearity among the potential fixed effects.

We compared support among the above models for each species using the small sample size correction to AIC (AIC_c) because the ratio of sample size to estimated parameters was <40 (Burnham and Anderson 2002). We report results for the four species for which we monitored nests and 10 additional species for which we had sufficient detections to generate estimates of reasonable precision. We considered estimates of mean abundance for a species to be reasonably precise if half the width of the 95% CI was <50% of the mean abundance in urban or rural sites based on the landscape model.

RESULTS

Site-level vegetation structure

Vegetation structure was variable within and among sites; however, rural sites had more woody cover (as indicated by canopy cover and small and large stems) in the fields than the urban sites (Table 1). Housing density and, to a lesser degree, trail density were greater in urban sites, but roads and edges were more variable among urban and rural sites (Table 2).

Nest survival

We monitored 204 and 178 nests of the four focal species at urban and rural sites, respectively. These represented a total of 1316 nest intervals for Field Sparrows (n = 43 rural nests, no urban nests), Indigo Buntings (n = 54 urban nests, 75 rural nests), Yellow-breasted Chats (n = 19 urban nests, 29 rural nests), and Northern Cardinals (n = 131 urban nests, 31 rural nests).

The preliminary analyses of the global model with and without a set of dummy variables to identify bird species indicated lesser support for the model with species ($\Delta_i = 2.529$, $w_i = 0.220$) than the model without species ($\Delta_i = 0$, $w_i = 0.780$); therefore, we did not include species as a factor in any of the candidate models. The nest site model (Table 3) was the best-supported model and included the variables nest height and distance from the main stem. The nest site/temporal and nest site/temporal/landscape model received some support, but only because of the effects of nest site variables in those models; no other coefficients had confidence intervals that did not include 0. We found virtually no support for a landscape (urban) effect on nest survival. Therefore, we only interpreted coefficients from the nest site model and used it for predicting nest success. The odds of nest survival increased 1.42 times for each 1-m increase in nest height; the odds of survival also increased with distance to stem, but the 95% CI included 0 (Table 4). Daily nest success was 0.945 (0.934, 0.956; 95% CL) based on the nest site model for nests at the mean nest height and distance to stem.

Cowbird parasitism

Eighty-nine of 202 nests at urban sites were parasitized, whereas 25 of 174 nests at rural sites were parasitized. Northern Cardinals were parasitized 32.8% vs. 3.2% at urban vs. rural sites; Indigo Buntings were parasitized 69.2% vs. 24.7%, and Yellow-breasted Chat were parasitized 52.6% vs. 11.1% in urban and rural sites, respectively. Field Sparrow nests were only found in rural sites and parasitized at 7%.

Analysis of the global model with and without dummy variables to identify bird species indicated lesser support for the model without species ($\Delta AIC_c = 8.464$, $w_i = 0.014$) than the model with species ($\Delta AIC_c = 0$, $w_i = 0.986$); therefore, we included species as a factor in all models. The top two models were the landscape and landscape + nest characteristics models, which had a combined weight of 0.92 (Table 5). Since the landscape model had the greatest weight ($w_i = 0.68$), and none of the additional characteristics in the landscape + nest had large effects (indicated by confidence intervals not overlapping 0), further interpretations were based on the landscape model. The odds of parasitism was 27.2 times greater for nests in urban landscapes than rural landscapes; confidence limits for the effects of other variables in the model included 0 (Table 4). We estimated the probability of parasitism using the landscape model for each of the four species in urban and rural landscapes at the mean housing density; the predicted probabilities of parasitism frequencies were

TABLE 5. Models explaining brood parasitism by the Brown-headed Cowbird at urban and rural old fields in Boone County, Missouri, 2000–2002.

Model	$-2(L)$	K	AIC	Δ_i	w_i
Landscape†	368.19	8	384.19	0.000	0.64
Landscape, nest characteristics	365.64	10	385.64	1.45	0.28
Global (all variables)	362.12	13	388.13	3.94	0.07
Edge‡	380.08	7	394.08	9.89	0.01
Cowbird perch§	378.78	8	394.78	10.59	0.00
Nest characteristics‖	379.12	8	395.12	10.93	0.00
Nest characteristics, edge	377.63	9	395.64	11.45	0.00
Global without host nesting species	376.79	10	396.77	12.58	0.00
Nest characteristics, cowbird perch	376.78	10	396.78	12.59	0.00
Null	414.74	3	420.74	36.55	0.00

Notes: Models are ranked from best to worst based on Akaike's information criteria (AIC), ΔAIC (Δ_i), and Akaike weights (w_i); AIC is based on $-2 \times$ log likelihood (L) and the number of parameters in the model (K).

† Includes variables: urban (1 if urban site, 0 if rural site).

‡ Includes variables: combined length of forest, trail, and road edges.

§ Includes variables: mean distance to cowbird perch (trees $\geq$3m).

‖ Includes variables: nest height, day of year.

greater in the urban landscape than rural landscape (Fig. 1).

Bird abundance

We report on the four focal species and an additional 10 species for which we were able to estimate abundance within 50% of the true mean 95% of the time (Figs. 2–6).

We found the most support for the landscape, housing, vegetation, trails, and null models for 5, 2, 4, 1, and 1 species, respectively. We found strong support for the effect of landscape on abundances of Field Sparrow ($w_i = 0.97$), Northern Cardinal ($w_i = 0.93$), and Blue-winged Warbler (*Vermivora pinus*; $w_i = 0.89$, $\Delta \text{AIC}_c = 0$). For Black-capped Chickadee (*Poecile atricapillus*; $w_i = 0.31$), Northern Cardinal, and Brown-headed Cowbird ($w_i = 0.65$), abundances were greater in urban landscapes than rural landscapes (Fig. 2). Additional support for urban effects was seen from the housing model. The housing density model was most supported and indicated housing density was inversely related to abundance for Indigo Bunting ($w_i = 0.76$) and Blue-gray Gnatcatcher (*Polioptila caerulea*; $w_i \geq 0.88$; Fig. 3).

The vegetation model had the most support for three forest species (Acadian Flycatcher [*Empidonax virescens*; $w_i = 1.00$], Red-eyed Vireo [*Vireo olivaceus*; $w_i = 0.53$], and White-breasted Nuthatch [*Sitta caroli-*

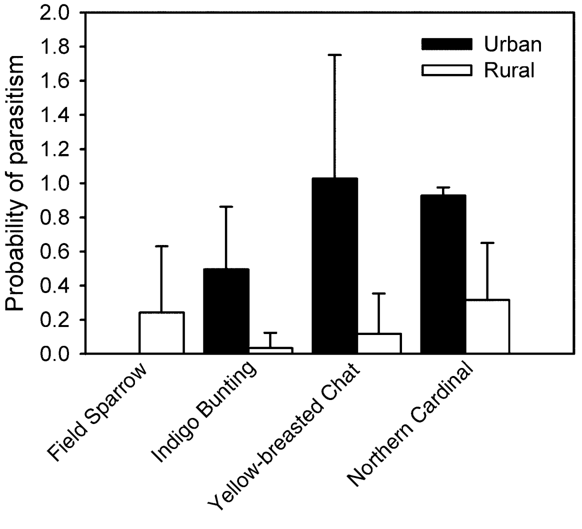

FIG. 1. Predicted probability of parasitism (mean and 95% CI) by the Brown-headed Cowbird as estimated by the landscape model (Tables 4 and 5) for four focal species breeding in urban and rural shrublands in Boone County, Missouri, USA.

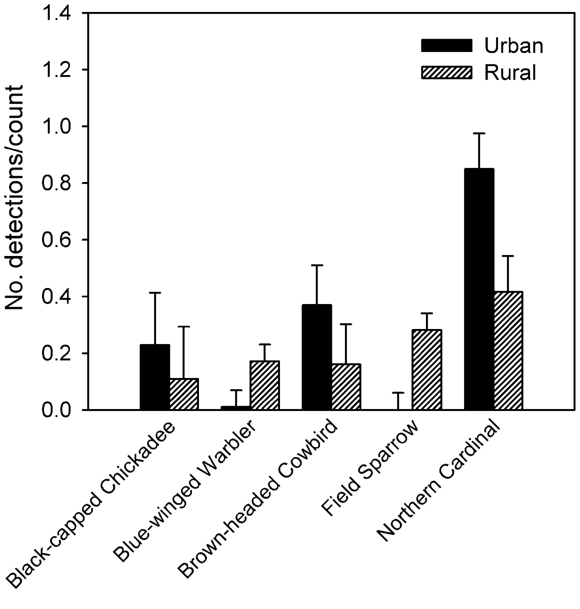

FIG. 2. Predicted number of bird detections/5-min point count (mean and 95% CI) for species in urban and rural landscapes in Boone County, Missouri. Predictions are based on the best-supported model for the species.

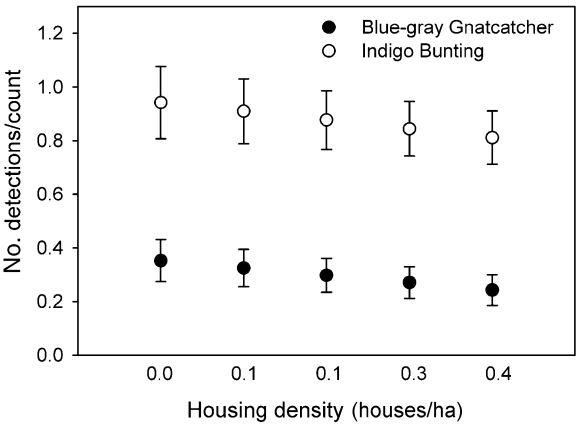

FIG. 3. Predicted number of bird detections/5-min point count (mean and 95% CI) at different levels of housing density in Boone County, Missouri. Predictions are based on the best-supported model for the species.

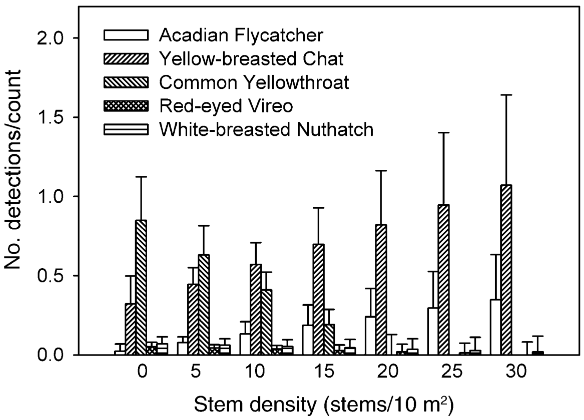

FIG. 5. Predicted number of bird detections/5-min point count (mean and 95% CI) at different levels of small stems (<1.4 m high and >0.50 cm high) in Boone County, Missouri. Stem count was weighted within a given bird species according to the proportion of birds detected in forest or field habitat by site. Predictions are based on the best-supported model for the species.

nensis; w_i = 0.42]), and two field species (Yellow-breasted Chat [w_i = 0.99] and Common Yellowthroat [*Geothlypis trichas*; w_i = 0.92]). Abundance of these species was all positively related to percent canopy closure (Fig. 4). Abundance of Acadian Flycatcher and Yellow-breasted Chat was positively related to density of small stems, and abundance for Common Yellowthroat, Red-eyed Vireo, and White-breasted Nuthatch was negatively related to density of small stems (Fig. 5). The edge and trail model was most supported for only Northern Parula (*Parula Americana*), which was predicted to be more abundant with decreasing density of trails and edges ($\Delta AIC_c = 0$, $w_i = 0.56$; Fig. 6). The null model received the most support for only Tufted Titmouse (*Baeolophus bicolor*; w_i = 0.48), but there was also some support for other models, which all had $\Delta AIC_c \leq 3.61$. For complete statistics on the bird abundance models, see the Appendix.

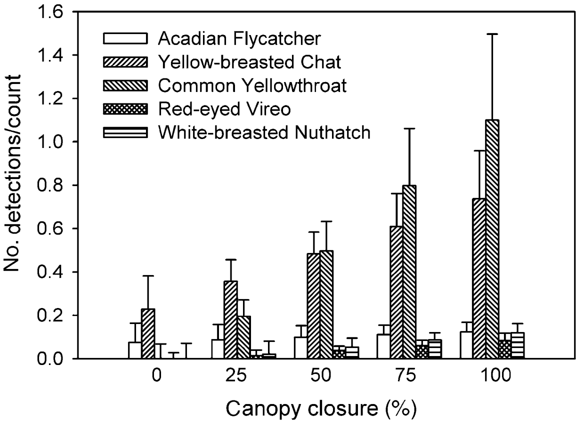

FIG. 4. Predicted number of bird detections/5-min point count (mean and 95% CI) at different levels of canopy closure in Boone County, Missouri. Canopy closure was weighted within a given species according to the proportion of birds detected in forest or field habitat by site. Predictions are based on the best-supported model for the species.

DISCUSSION

In general, we found support for our hypotheses that urban landscapes had negative effects on songbird populations. Abundances of seven species were lesser according to landscape or housing density models, and brood parasitism was greater in the urban landscape compared to the rural landscape. We did not, however, find support for our hypothesis that nest predation was higher in urban landscapes.

Nest survival

We found no evidence of an urban landscape effect on nest survival, but instead found the strongest effects

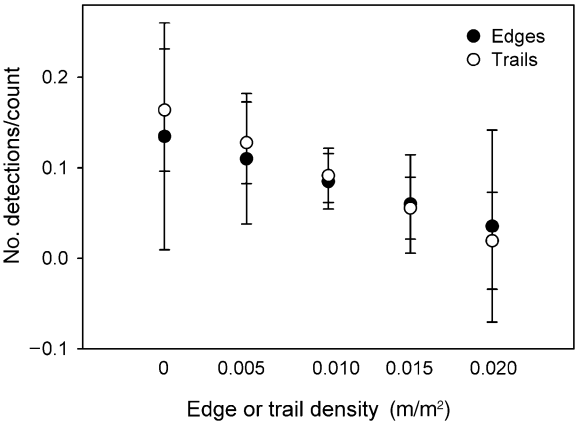

FIG. 6. Predicted number of bird detections/5-min point count (mean and 95% CI) for Northern Parula at different levels of trail and edge density (length of edge or trail/ha) in Boone County, Missouri.

at the nest site scale. In an earlier study spanning seven years, which included one of the rural sites, we similarly found that lower nests had a higher probability of becoming depredated (Burhans et al. 2002).

Conventional wisdom has been that songbird nest predation should be higher in urban and suburban locations because of greater habitat fragmentation, greater proportion of edge, and concomitantly higher densities of predators (Gates and Geysel 1978, Wilcove 1985, Robinson 1997). More recent studies have shown abundance increases for some, but not all, predators with increasing housing density (Haskell et al. 2001). Perhaps we did not observe greater nest predation in urban landscapes because we studied the same species in similar habitats in both urban and rural areas. In addition, we know that nest predation is high in these rural areas because habitat is fragmented by agricultural land uses (Robinson et al. 1995, Donovan et al. 1995). By contrast, in the heavily forested Southern Missouri Ozarks, shrubland songbirds experienced daily nest survival of 0.96 (Clawson et al. 2002) compared to 0.945 for rural and urban landscapes in this study. Nest predation, therefore, may be high in landscapes with urban or agricultural land use compared to landscapes composed of shrublands, grasslands, and forest.

Chief among the predators sometimes associated with urbanizing locations are thought to be mammals such as raccoon (*Procyon lotor*), housecat (*Felis catus*) (Banko et al. 2002), and avian predators associated with humans such as Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), and Common Grackle (*Quiscalus quiscula*) (Robinson 1997, Kluza et al. 2000). We did not count sufficient numbers of these avian nest predators to analyze differences between urban and rural landscapes. Previous video camera studies showed that snakes, particularly *Elaphe obsoleta*, were the primary nest predator at Field Sparrow and Indigo Bunting nests near one of the rural sites used in this study (Thompson et al. 1999, Thompson and Burhans 2003, 2004). Snakes also appeared to be abundant in the urban landscapes. We recorded potential predators seen at field sites during bird and nest monitoring and counted 37 and 60 predatory snakes in 2001 and 2002, respectively; 84% and 87% of these were in urban sites in 2001 and 2002, respectively. Snake species seen were similar in urban and rural landscapes; no snake species noted at the rural sites in 10 years of study was not also seen at the urban sites in 2001 and 2002, except for *Croatus horridus* and *Lampropeltis getulus*. Except for a single housecat consistently seen at one urban site, field workers did not note mammalian predators at any sites; but most of the potential mammalian nest predators are nocturnal, and would not be seen during nest-searching hours.

Cowbird parasitism

The landscape model had the strongest support in our analysis of cowbird parasitism; parasitism frequencies in the urban landscape were 2 to 10 times the amount in rural sites for each host species. As with nest predators, numerous other studies have noted that fragmentation, edge, and urbanization lead to increased numbers of cowbirds in the landscape (Gates and Geysel 1978, Robinson 1997, Thompson et al. 2000). We did not find strong support for nest site or patch effects in explaining cowbird parasitism, although two previous studies using one of our rural sites found that, for certain species, nest concealment was negatively related to frequency of parasitism, and that nests in larger shrub patches were more likely to be parasitized (Burhans 1997, Burhans and Thompson 1999). Point count models showed support for greater numbers of cowbirds in the urban landscape (Fig. 2).

Bird abundance

Several studies have shown that urban locations either lack a full component of neotropical migrants or have decreasing populations; conversely, permanent residents or short-distance migrants typically are either stable or increasing (Robbins 1979, Serrao 1985, Wilcove 1988).

The species for which urban landscape or increased housing density had a negative effect included three Neotropical migrants and one short-distance migrant (Field Sparrow). Effects were strongest for the Field Sparrow and Blue-winged Warbler. Except for a pair apparently nesting at one site in 2002 that was outside of the point count radii, we never noted Blue-winged Warblers at urban sites after migration. Similarly, we never saw Field Sparrows at the urban sites after migration, except for one singing male at the site with the Blue-winged Warblers. Although the urban sites appeared to offer habitat similar to the rural sites used by these two species, landscape considerations appeared to affect their choice not to settle in these urban areas.

Species with greater urban abundances were resident species (Northern Cardinal, Black-capped Chickadee) or Brown-headed Cowbirds. In addition to greater detections on point counts, we found over four times as many cardinal nests at urban compared to rural sites. Cardinals appeared to respond positively to urban locations, possibly because of the presence of nearby bird feeders, or perhaps because backyards adjoining our urban sites offered useful foraging and nesting areas. We also tended to find cardinal nests earlier at urban sites, with nesting typically initiating a week and a half before rural sites (D. Burhans, *personal observation*). Other studies in urban or suburban locations have found that urban populations may enjoy longer breeding seasons (Morneau et al. 1995 and references therein), perhaps because of greater warmth in urban areas.

In our study, increased trail and edge density were not necessarily concomitant with urbanization, as we found these densities to be comparable among urban and rural landscapes (Table 2). We found that trail and edge density was inversely related to bird abundance for only one species, Northern Parula, which was present in both urban and rural sites. Studies of trail impact on nesting birds have found reduced numbers of some species proximate to trails (Miller et al. 1998, Fernández-Juricic 2000), increased nest predation away from trails (Miller and Hobbs 2000), or increased nest predation close to trails (Miller et al. 1998). The species most sensitive to human disturbance in our previous studies (Indigo Bunting; Thompson and Burhans 2003) was one of the most common nesters at our urban sites, but showed an inverse relationship in relation to housing density rather than trail density (Fig. 3). Nest patch models that incorporated trail density had weak support, or no support, in the nest predation model selection process (Table 3).

Site-level vegetation parameters best explained abundance for five species, and for all of these, there was an increase in abundance with greater canopy closure (Fig. 4). These results are consistent with known habitat relationships the three forest species, Acadian Flycatcher, Red-eyed Vireo, and White-breasted Nuthatch, which typically require closed-canopy forest (Pagen et al. 2000). This result could seem counterintuitive for Yellow-breasted Chat and Common Yellowthroat, because they nest in semi-open shrubland habitats. When viewed within the context of the field habitats in this study, however, it is indicative of their preference for fields with more shrub cover (Zumwalt; Table 1). In general, vegetation relationships were consistent with previous studies that reported Yellow-breasted Chats habitats having large numbers of small stems (Annand and Thompson 1997, Burhans and Thompson 1999, Eckerle and Thompson 2001), and negative relationships between number of small stems and abundance for Common Yellowthroat, Red-eyed Vireo, and White-breasted Nuthatch.

CONSERVATION IMPLICATIONS

Wild urban parks represent potential breeding habitat for songbirds of conservation interest, as well as areas where the public may enjoy interacting with birds. Several species breeding at our urban sites, including Yellow-breasted Chat and Blue-gray Gnatcatcher, are considered priority species for the Central Hardwoods Region by the North American Bird Conservation Initiative (NABCI 2003), as are others for which we did not have sufficient detections or nests for analysis, including Kentucky Warbler (*Oporornis formosus*), White-eyed Vireo (*Vireo griseus*), Brown Thrasher (*Toxostoma rufum*), and Louisiana Waterthrush (*Seirus motacilla*). However, other priority species present at the rural sites, including Field Sparrow and Blue-winged Warbler, were rarely found in urban shrublands. Although we did not find that urban nest predation was higher for the four focal species, cowbird parasitism was substantially higher for all species in urban shrubland habitats. Cowbird parasitism may reduce productivity below sustainable levels if it reduces the number of young produced each year (Trine 1998, Donovan and Thompson 2001).

Although not amenable to analysis, we would be remiss if we did not also mention that routine park maintenance, such as mowing, appeared to influence bird use at our urban sites. Because park managers cooperated with our requests to refrain from mowing park interiors during the study, by the third year there was sufficient shrub structure for several Indigo Buntings and Yellow-breasted Chats to nest in certain sections of two urban sites where they had previously been absent. Mowing in managed parks may be undertaken for aesthetic reasons, to afford better visibility, or to help users feel ''safe.'' The latter is certainly a valid concern for park patrons and should be a consideration in any management scenario, but it may take only one complaint by a dissatisfied citizen to result in mowing of an entire parcel, rendering it unusable for nesting shrubland birds.

Higher urban abundances of cowbirds, as indicated by the abundance models, coupled with higher urban parasitism frequencies, suggests that urban-nesting birds suffer a higher risk of parasitism; yet there was no landscape effect on nest survival, indicating that nest predation was comparable between urban and rural habitats. Unlike some other studies in our region, which have found higher predation at parasitized nests (Burhans and Thompson 1999, Budnik et al. 2002, Burhans et al. 2002), we did not find that cowbird parasitism was related to increased probability of nest predation. Nonetheless, high levels of cowbird parasitism may result in a net deficit of host young, with urban locations functioning as potential ecological host population sinks (Donovan et al. 1995, Trine 1998). Urban areas could also act as potential source areas for cowbirds, as Winfree (2004) found for forested habitats, although cardinals, apparently the most abundant host at our urban sites, have been shown to be unproductive cowbird hosts (Scott and Lemon 1996).

Urban land use is becoming a greater component of landscapes (McDonnell and Pickett 1990, Pickett et al. 2001, McKinney 2002). However, ''natural'' urban locations, even if containing some breeding songbird species of conservation interest, may be of lesser quality and may not contribute to population viability as much as comparable habitats in less developed landscapes. Midwest urban locations such as ours do offer breeding habitat for some songbird species of conservation interest. However, absences and lower abundances of some species, coupled with higher cowbird parasitism, indicate that these particular urban natural areas do not fulfill the same role as comparable rural habitats. We suggest that these patterns are worth exploring in other Midwest landscapes and other regions.

ACKNOWLEDGMENTS

We thank many field assistants who helped gather information for this study, including Marjanne Manker, Kristen

Ellis, Charlie Sharp, Travis Hinkleman, Heather Heitz, Kim McGee, Sean Ernst, Faren McCord, Sarah Moody, Karel Borowiak, Shannon Dugger, Jason Porter, and Jonathan Voss. Thanks to Becky Peak for her help. Jennifer Reidy, Charles Nilon, and anonymous reviewers provided comments that greatly helped earlier versions of the manuscript. The USDA Forest Service North Central Research Station funded this study, and The University of Missouri provided study sites on the Thomas S. Basket Wildlife Research and Education Center. We thank Mike Griggs and the City of Columbia Parks and Recreation Department for their cooperation and Carol Trokey for facilitating our work on Cedar Creek District National Forest lands.

LITERATURE CITED

Aldrich, J. W., and R. W. Coffin. 1980. Breeding bird populations from forest to suburbia after thirty-seven years. American Birds **34**:3–7.

Annand, E. M., and F. R. Thompson, III. 1997. Forest bird response to regeneration practices in Central Hardwood forests. Journal of Wildlife Management **61**:159–171.

Askins, R. A. 2000. Restoring North America's songbirds. Yale University Press, New Haven, Connecticut, USA.

Banko, P. C., L. Johnson, G. D. Lindsey, S. G. Fancy, T. K. Pratt, J. D. Jacobi, and W. E. Banko. 2002. Palila (*Loxioides bailleui*). Pages 1–24 *in* A. Poole and F. Gill, editors. The birds of North America. Number 679. The Birds of North America, Philadelphia, Pennsylvania, USA.

Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on 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.

Budnik, J. M., F. R. Thompson, and M. R. Ryan. 2002. Effect of habitat characteristics on the probability of parasitism and predation of Bell's Vireo nests. Journal of Wildlife Management **66**:232–239.

Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. Condor **99**:866–872.

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

Burhans, D. E., and F. R. Thompson, III. 1999. Habitat patch size and nesting success of Yellow-breasted Chats. Wilson Bulletin **111**:210–215.

Burke, D. M., K. Ellito, L. Moore, W. Dunford, E. Nol, J. Phillips, S. Holmes, and K. Freemark. 2004. Patterns of nest predation on artificial and natural nests in forests. Conservation Biology **18**:381–388.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer-Verlag, New York, New York, USA.

Clawson, R. L., J. Faaborg, W. K. Gram, and P. A. Porneluzi. 2002. Landscape-level effects of forest management on bird species in the Ozarks of Southeastern Missouri. Pages 147–160 *in* S. R. Shifely and J. M. Kabrick, editors. Proceedings of the second Missouri Ozark Forest Ecosystem Project Symposium: post-treatment results of the landscape experiment. General Technical Report NC-227. USDA Forest Service, North Central Research Station, St. Paul, Minnesota, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology **83**:3476–3488.

Donovan, T. M., and F. R. Thompson, III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications **11**:871–882.

Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology **9**:1380–1395.

Eckerle, K. P., and C. F. Thompson. 2001. Yellow-breasted Chat (*Icteria virens*). Pages 1–28 *in* A. Poole and F. Gill, editors. The birds of North America. Number 575. The Birds of North America, Philadelphia, Pennsylvania, USA.

Faaborg, J. 2002. Saving migrant birds: developing strategies for the future. University of Texas Press, Austin, Texas, USA.

Fernádez-Juricic, E. 2000. Local and regional effects of pedestrians on forest birds in a fragmented landscape. Condor **102**:247–255.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology **59**:871–883.

Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography **22**:532–541.

Haskell, D. G., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization. Pages 243–258 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Jokimäki, J., and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor **102**:838–847.

Kluza, D. A., C. R. Griffin, and R. M. DeGraff. 2000. Housing developments in rural New England: effects on forest birds. Animal Conservation **3**:15–26.

Lancaster, R. K., and W. E. Rees. 1979. Bird communities and the structure of urban habitats. Canadian Journal of Zoology **57**:2358–2368.

Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches. Pages 1–17 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, Massachusetts, USA.

McDonnell, M. J., and S. T. A. Pickett. 1990. Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. Ecology **71**:1232–1237.

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

Melampy, M. N., E. L. Kershner, and M. A. Jones. 1999. Nest predation in suburban and rural woodlots of Northern Ohio. American Midland Naturalist **141**:284–292.

Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning **50**:227–236.

Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications **8**:162–169.

Morneau, F., C. L. Lepine, R. Decarie, M. Villard, and J. DeGranges. 1995. Reproduction of American Robin (*Turdus migratorius*) in a suburban environment. Landscape and Urban Planning **32**:55–62.

NABCI [North American Bird Conservation Initiative]. 2003. The Central Hardwoods joint venture concept plan. ⟨http://www.abcbirds.org/nabci/chjv_plan.htm⟩

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk **117**:393–408.

Nilon, C. H., C. N. Long, and W. C. Zipperer. 1995. Effects of wildland development on forest bird communities. Landscape and Urban Planning **32**:81–92.

OSEDA [Office of Social and Economic Data Analysis Website]. 2004. University of Missouri Extension. ⟨http://www.oseda.missouri.edu⟩

Pagen, R. W., F. R. Thompson, III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor **102**:738–747.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics **32**:127–157.

Robbins, C. S. 1979. Effects of forest fragmentation on bird populations. Pages 198–212 *in* Management of North Central and Northeastern forests for nongame birds. USDA Forest Service, General Technical Report NC-51, North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hurlbert. 1969. Relationships between visual obstruction and weight of grassland vegetation. Journal of Range Management **23**: 295–298.

Robinson, S. K. 1997. The case of the missing songbirds. Consequences **3**:3–15.

Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987–1990.

SAS. 1999. SAS system for Windows. Version 8. SAS Institute, Cary, North Carolina, USA.

Scott, D. M., and R. E. Lemon. 1996. Differential reproductive success of Brown-headed Cowbirds with Northern Cardinals and three other hosts. Condor **98**:259–271.

Serrao, J. 1985. Decline of forest songbirds. Records of New Jersey birds **11**:5–9.

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

Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology **11**:928–935.

Terborgh, J. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey, USA.

Thompson, F. R., III, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between forest and field habitats. Journal of Wildlife Management **67**:408–416.

Thompson, F. R., III, and D. E. Burhans. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conservation Biology **18**: 373–380.

Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk **116**:259–264.

Thompson, F. R., III, S. K. Robinson, T. M. Donovan, J. R. Faaborg, D. R. Whitehead, and D. R. Larsen. 2000. Biogeographic, landscape, and local factors affecting cowbird abundance and host parasitism levels. Pages 271–279 *in* J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds. University of Texas Press, Austin, Texas, USA.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic press, San Diego, California, USA.

Thorington, K. K., and R. Bowman. 2003. Predation rate on artificial nests increases with human housing density in suburban habitats. Ecography **26**:188–196.

Trine, C. L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology **12**:576–585.

Weber, W. C. 1975. Nest-sites of birds in residential areas of Vancouver, British Columbia. Canadian Field Naturalist **89**: 457–460.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211–1214.

Wilcove, D. S. 1988. Changes in the avifauna of the Great Smokey mountains: 1947–1983. Wilson Bulletin **100**:256–271.

Winfree, R. 2004. High offspring survival of the Brown-headed Cowbird in an invaded habitat. Animal Conservation **7**:445–453.

APPENDIX

A comparison of general linear models explaining bird mean abundances (*Ecological Archives* A016-017-A1).