Importance of Reserve Size and Landscape Context to Urban Bird Conservation

ROARKE DONNELLY* AND JOHN M. MARZLUFF†

Box 352100, Ecosystem Science and Conservation, College of Forest Resources, University of Washington, Seattle, WA 98195-2100, U.S.A.

Abstract: *We tested whether reserve size, landscape surrounding the reserve, and their interaction affect forest songbirds in the metropolitan area of Seattle, Washington (U.S.A.), by studying 29 reserves of varying size (small, medium, large) and surrounding urbanization intensity (urban, suburban, exurban). Larger reserves contained richer and less even bird communities than smaller reserves. These size effects disappeared when we removed the positive correlation of shrub diversity with reserve size, suggesting that greater habitat diversity in large reserves supported additional species, some of which were rare. Standardizing the number of individuals detected among all reserve size classes reversed the effect of size on richness in exurban landscapes and reduced the magnitude of the effect in suburban or urban landscapes. The latter change suggested that richness increased with reserve size in most landscapes because larger areas also supported larger samples from the regional bird species pool. Most bird species associated with native forest habitat (native forest species) and with human activity (synanthropic species) were present in reserves larger than 42 ha and surrounded by >40% urban land cover, respectively. Thus, we recommend these thresholds as means for conserving the composition of native bird communities in this mostly forested region. Native forest species were least abundant and synanthropic species most abundant in urban landscapes, where exotic ground and shrub vegetation was most common. Therefore, control of exotic vegetation may benefit native songbird populations. Bird nests in shrubs were most dense in medium (suburban) and large reserves (urban) and tended to be most successful in medium (suburban) and large reserves (exurban), potentially supplying another mechanism by which reserve size increased retention of native forest species.*

Key Words: exotic vegetation, forest songbird, nest predation, reserve size, urban conservation, urban landscape

Importancia del Tamaño de la Reserva y el Contexto del Paisaje para la Conservación de Aves Urbanas

Resumen: *Evaluamos si el tamaño de la reserva, el paisaje que rodea a la reserva y su interacción afecta a aves canoras de bosque en el área metropolitana de Seattle, Washington (E.U.A) estudiando 29 reservas de tamaño variable (pequeño, mediano y grande) y la intensidad urbana circundante (urbano, suburbano y exurbano). Las reservas más grandes contenían comunidades de aves más ricas y menos homogéneas que reservas más pequeñas. Estos efectos de tamaño desaparecieron cuando removimos la correlación positiva de la diversidad de arbustos con el tamaño de reserva, sugiriendo que la mayor diversidad de hábitat en las reservas grandes soportaba especies adicionales, algunas de las cuales eran raras. La estandarización del número de individuos detectados entre todas las clases de tamaño de reserva revirtió el efecto del tamaño sobre la riqueza en paisajes exurbanos y redujo la magnitud del efecto en paisajes suburbanos o urbanos. Este cambio sugirió que la riqueza incrementó con el tamaño de la reserva en la mayoría de los paisajes porque áreas mayores también soportaron muestras mayores del conjunto regional de especies de aves. La mayoría de las especies de aves asociadas con el hábitat de bosque nativo (especies nativas de bosque) y con la actividad humana (especies sinantrópicas) estuvieron presentes en reservas mayores a 42 ha y rodeadas por >40% de cobertura urbana, respectivamente. Así, recomendamos estos umbrales como medio para conservar*

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*Current address rdonnelly@ogelthorpe.edu

†Address correspondence to J. M. Marzluff; email corvid@u.washington.edu.

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la composición de comunidades de aves nativas en esta región mayormente boscosa. Las especies nativas de bosque fueron menos abundantes y especies sinantrópicas fueron más abundantes en paisajes urbanos, donde fue más común la vegetación herbácea y arbustiva exótica. Por lo tanto, el control de la vegetación exótica puede beneficiar a las poblaciones de aves canoras. Los nidos de aves en arbustos fueron más densos en reservas medianas (suburbanas) y grandes (urbanas) y tendieron a ser más exitosas en reservas medianas (suburbanas) y grandes (exurbanas), potencialmente proporcionando otro mecanismo por el cual el tamaño de la reserva incrementó la retención de especies nativas de bosque.

Palabras Clave: ave canora de bosque, conservación urbana, depredación de nidos, paisaje urbano, tamaño de reserva, vegetación exótica

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Introduction

Each year the Earth's human population grows and appropriates more natural resources for its use, including land for residential development (Vitousek et al. 1997). Much of this land use and associated land-cover conversion occurs in existing suburbs and at the suburban-exurban interface (for standard definitions of urbanization levels, see Marzluff et al. 2001). These changes to the landscape have fairly consistent effects on communities of birds and other wildlife. As landscapes become more developed and fragments of native habitat shrink, demographic and behavioral mechanisms cause bird species richness and evenness to decrease and total bird density to increase (Marzluff 2001). Richness and evenness decrease because species associated with native habitat decline in abundance and eventually go extinct as a result of decreased nest success, direct human disturbance (e.g., flushing), or area sensitivity (Whitcomb et al. 1981) and are replaced by fewer, synanthropic species (associated with humans) that proliferate (Beissinger & Osborne 1982). Colonists often increase in abundance by exploiting food and nest sites provided by humans (Marzluff 2001). These responses by bird communities to urbanization challenge bird conservation, an endeavor made more urgent by increasing per capita rates of land development (Ewing 1994) and lagging protection of native habitat (McKinney 2002).

Effective wildlife conservation in urbanizing areas requires that we know if and how native habitat patch size and surrounding development interact to determine bird community structure and underlying population function. We tested whether reserve size, urbanization intensity, and their interaction affect forest songbirds in the Seattle, Washington, metropolitan area. To elucidate mechanisms that might drive observed patterns, we relate breeding bird community composition, bird species relative abundance, and bird reproductive success to urbanization intensity, reserve size, and local vegetation. We relate bird responses to habitat composition at a large scale (urbanization intensity) and a small scale (local vegetation) because birds select habitat at multiple scales (Hilden 1965).

Methods

Study Area

The Seattle metropolitan area (47°40′N, 122°20′W) is within the Western Hemlock (*Tsuga heterophylla* [Raf.]) Zone of the Pacific Northwest (U.S.A.) (Franklin & Dyrness 1988). Because of logging, the subclimax tree Douglas-fir (*Pseudotsuga menziesii* [Mirb.]) dominates the area. The metropolitan area is composed of a large business district that is surrounded by residential developments and satellite business districts (Fig. 1). Despite its urban character, the Seattle area retains a substantial amount of relatively undisturbed native vegetation in the form of privately owned, undeveloped parcels and parks. These habitat reserves range from 1 to 1500 ha.

Site Selection

We used a stratified random-selection process to choose 29 reserves representing all possible combinations of three sizes—small (mean ± SE = 2.1 ± 0.6 ha, $n = 3$ exurban + 6 suburban + 2 urban), medium (34.7 ± 6.0 ha, $n = 2$ exurban + 6 suburban + 2 urban), and large (1471.1 ± 559.8 ha, $n = 2$ exurban + 4 suburban + 2 urban)—within three landscapes or levels of residential development intensity (exurban, suburban, and urban) below 1000 m in elevation. We quantified size and landscape with digital orthophotos and Landsat satellite images, respectively. Orthophotos indicated that all reserves had been isolated from other forest fragments for at least 5 years prior to the study and that exurban reserves were usually isolated by clearcuts, roadways, and utility corridors rather than residential development. To quantify landscape, we converted Landsat images to a three-class land cover based on impervious surface (e.g., pavement) and vegetation (following Botsford 2000; forest = 59% of 356,377 ha classified; urban forest = 19%; urban land cover = 11%; other land cover = 11%). Forest was $\geq$70% trees and $<$20% impervious surface. Urban forest was $\geq$25% trees and 20–60% impervious surface. Urban land cover was $\geq$60% impervious surface. Other land cover was $\geq$75% open water or bare soil.

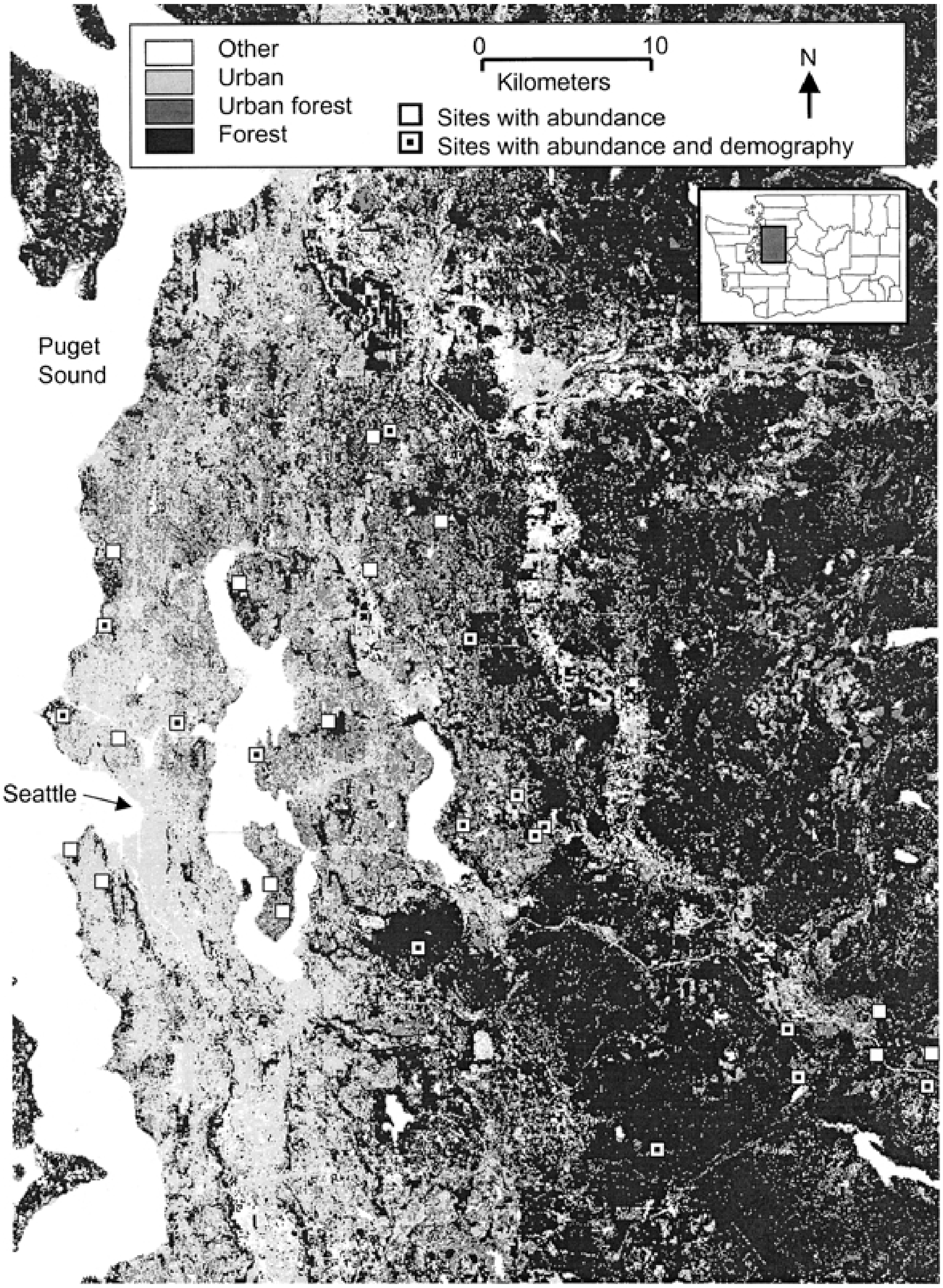

Figure 1. Classified Landsat image from 1998 showing habitat reserves where we studied bird community composition, species abundance, and bird demography.

We classified a reserve's landscape based on the dominant land cover within a 1-km buffer surrounding the reserve. We used Geographic Resource Analysis Support System and the r.le add-on programs (Baker 1997; Alberti et al. 2001) to calculate land cover representation within buffers. The buffer size was selected to reflect the size of a typical residential development and the approximate distance over which subsidized nest predators travel. Reserves with buffers dominated by forest (mean %: forest = 77, urban forest = 17, urban land cover = 5, $n = 7$), urban forest (mean%: forest = 36, urban forest = 44, urban land cover = 20, $n = 16$), and urban land cover (mean %: forest = 9, urban forest = 19, urban land cover = 72, $n = 6$) were classified as exurban, suburban, and urban, respectively. These classifications were distinct according to a discriminant analysis based on urban land cover, urban forest, mean urban patch size, and contagion ($\chi^2_8 = 111.4, p < 0.001$).

Once we identified a park or undeveloped lot as a potential study site based on size and landscape, we walked within the reserve to inspect canopy composition and drove around the reserve to determine type of urbanization. We rejected reserves with canopies dominated by younger trees (<70 yrs), canopies dominated by red alder (*Alnus rubra* [Bong.]) and big-leaf maple (*Acer macrophyllum* [Pursh]), and adjacent areas dominated by land uses other than single-family residential. The final criterion was relaxed in exurban landscapes, where single-family residential was rare by definition. We applied the aforementioned criteria because the dominant land cover before European settlement was relatively mature mixed conifer and deciduous forest (Booth 1991) and because multiple land-cover and land-use types may have confounded our design.

Bird Surveys

In 1998 we completed a pilot study at 14 reserves (5 small, 3 medium, and 6 large). We conducted five fixed-radius (50-m) point-count surveys at all reserves between 26 April and 20 July. We (R.D. and one assistant that he trained) recorded all birds that we detected in or just above the canopy by sight or sound during 10 minutes at each point. We set points within the medium and large reserves using two parallel transects with 150 m between all successive points. All points within large and medium reserves were >80 m from forest edges. In each small site, we centered points within the reserve. Extreme variation in site size necessitated varying the number of survey points per site. We established and surveyed as many points as possible up to a maximum of eight points per reserve (small, one point; medium, three to four points; large, five to eight points). In so doing we surveyed the entire area of all small and medium reserves. We did not survey more than eight points in large reserves because richness did not increase after six points (Donnelly 2002). We maintained the same survey protocol in subsequent years but reduced the number of annual visits per site to four. This reduction in survey effort was justified because the pilot study detected a mean of only 1.8 ± 0.58, 0.33 ± 0.33, and 1.33 ± 0.42 new species during the fifth visits to small ($n = 5$), medium ($n = 3$), and large reserves ($n = 6$), respectively.

We analyzed the bird survey data at the community and population levels using data from four surveys conducted in 26 reserves in 1999 (including the reserves from the 1998 pilot study) and 2 reserves in 2000. The benefit of increasing sample size with the two sites from 2000 outweighed the potential for confounding year effects because richness was consistent at sites among years ($r = 0.85, p < 0.001, n = 20$) and evenness tended to be similar at sites among years ($r = 0.31$, $p = 0.19$, $n = 20$). Greater variation in evenness among years could be explained by greater sensitivity to relative abundance.

We investigated patterns of total bird relative abundance (including all species except those noted below), species richness, Shannon evenness (Magurran 1988), and species relative abundance based on a subset of observed birds. For all analyses we deleted birds that bred primarily in riparian corridors, migrant birds that did not breed in our study area, and birds that ranged over large areas, because our survey technique was unable to assess how they were using the field sites. For further analysis of richness we controlled the increase in total number of birds with area surveyed by rarefying the data (James & Rathbun 1981) with Ecosim 7.0 (Gotelli & Entsminger 2002; options: 1000 iterations, $n = 17$). To index relative abundance at each study site, we averaged the mean number of individuals per species per point across surveys from a single year. We expressed total bird relative abundance as the sum of all species abundances within a site. Abundances of species and all birds were based on seasonal means across surveys within a breeding season rather than seasonal maximums to avoid inflating abundance estimates with young of the year and migrating individuals.

Vegetation Surveys

We quantified the vegetation in plots centered on each bird survey point. In small plots (0.02 ha) we visually estimated (1) the percent cover (vertical, unless stated otherwise) of all ground and shrub species and (2) the horizontal cover and canopy closure from 1.5 m above ground at the cardinal and subcardinal directions with a Moosehorn Coverscope (Garrison 1949). In large plots (0.08 ha) we counted the number of snags and live trees. From these data we calculated 11 vegetation indices: (1 and 2) percent cover for ground and shrub strata; (3 and 4) total percent horizontal and total canopy closure by adding all respective covers (canopy closure, $n = 8$; horizontal, $n = 4$); (5 and 6) preponderance of exotic species in the ground and shrub strata by dividing the percent cover of all species introduced to the Western Hemlock Zone or typically not found below 1000 m in elevation by the percent cover of all species; (7 and 8) diversity (Shannon-Wiener Diversity Index [Magurran 1988]) of shrubs and trees based on percent cover and number of individuals, respectively; (9, 10, and 11) relative snag density, tree density, and red alder domination. We expressed the last as the number of alders divided by all trees. We summarized the indices by site by averaging values across survey points.

Estimation of Bird Productivity

We measured two aspects of reproductive success for 1–3 years per reserve at 15 reserves (Fig. 1): the production of nestlings within a few days of fledging and the ratio of juveniles to adults caught passively in a standardized mist-net survey.

Standard nest-searching techniques were used to locate breeding attempts by birds nesting in shrubs (Martin & Geupel 1993). We searched for nests of the American Robin (avian scientific names are provided in Fig. 4 if not at first mention in text) and Swainson's Thrush within a 8-ha subsection of medium and large reserves and the entire area within small reserves.

We described nest locations based on landmarks and bearings so that we could monitor attempts without leaving cues for predators. We visited each nest every 4–5 days and on the expected day of fledging to categorize the fate of the nest. Nests were "successful" if we observed compacted nest lining, fresh feces on the nest cup or nearby vegetation, or fledglings close to the nest. Nests were "depredated" if the nest cup was disturbed or the clutch or brood was damaged or removed before nestlings were capable of temperature regulation and significant locomotion. Nests were classified as "disturbed" or "abandoned" based on signs of disturbance near the nest, the behavior of incubating or brooding adults (e.g., flushing from nest), and proximity to a likely source of disturbance (e.g., hiking trails). Nests were "substrate-collapsed" if eggs or young nestlings fell to the ground because the supporting substrate collapsed under the weight of the nest. We took care to approach nests when corvids were absent and from a variety of directions to avoid making the nest conspicuous.

Because we found nests at all stages of the nesting cycle, we calculated daily survivorship rates and their variances (Mayfield 1961; Johnson 1979). We assumed that the risk of failure was greater during the brooding stage than the incubation stage as a result of more frequent trips by birds to the nest and nestling vocalizations. Therefore, we calculated daily rates for brooding and incubation. We extrapolated these values to the nest cycle—13 days of incubation and 12 days of brooding—and multiplied the resulting nest-cycle success rate by an estimate of nest density, the number of nests found per search hour. The product indexed the probability of a successful nest. To alleviate problems caused by small sample sizes, we pooled shrub nests by site classification (i.e., size and landscape combination).

We estimated the number of juveniles produced per adult for a subset of shrub-nesting bird species by capturing birds with a modified technique for monitoring avian productivity and survivorship (Desante 1992). At each site we set and operated 10 mist nets (7 30-mm mesh and 3 38-mm mesh measuring 2.6 × 6 m) for 5.5 hours beginning at dawn between 15 May and 10 August. Each site was sampled five times annually. We aged birds according to the procedure of Pyle (1997) and banded each individual to avoid recounting. We assumed that all juveniles were produced in the immediate area and included all of them in the analysis. Our trapping method was effective at capturing the American Robin and Swainson's Thrush, but sample sizes were not large for either species. We therefore pooled nests for these species to compare nest-cycle success among design factors.

Statistics

We set α at 0.05 and completed all statistical analyses other than quantification of community nestedness with the Statistical Package for Social Sciences (SPSS 2001). To meet the assumptions of parametric tests, we transformed many vegetation parameters (all percent covers with arcsine square root; tree diversity with exponential), community metrics (evenness with arcsine square root), and bird species relative abundance (all species with log [abundance + 1]).

We tested the effects of reserve size and landscape context on bird communities and populations with full-factorial general linear models. We included vegetation parameters as covariates in models of total bird relative abundance, richness, and evenness and species relative abundance if these parameters varied with size or landscape and correlated with the response variable (Table 1). If the parameter's inclusion in a model increased the p value associated with a significant main effect or interaction by ≥ 0.15, we concluded that it was a potential mechanism or that it correlated with one.

We estimated where bird species switched from present to absent, or thresholds of occurrence, along continuous ranges of reserve size and landscape context (percent urban land cover) by adapting techniques for quantifying community nestedness. Communities were nested if species in smaller communities—those with fewer species—tended to be included in larger communities. We tested for community nestedness with respect to size and landscape by entering species presence-absence matrices for all 29 reserves into the program Nest (Lomolino 1996). For nested communities, we defined the threshold of occurrence for a species (for method, see Atmar & Patterson 1993) as the size or landscape value at the intersection of the occurrence threshold curve with the row representing that species in the matrix. To obtain a general threshold for the community, we averaged thresholds across species.

We tested the effects of reserve size and landscape context on individual nesting parameters with two techniques. First, we modeled nests found per search hour with three general linear models: a test for an effect of landscape based on small reserves, a test for an effect of landscape based on large reserves, and a test for an effect of size based on suburban reserves. We could not use full-factorial models because we did not monitor nests in medium reserves in exurban and urban landscapes. Second, we tested for differences in nests found per search hour, the mean nest-cycle success of shrub nests, and their combination by comparing overlap in 95% confidence intervals.

To determine which levels of significant main effects and interactions differed in general linear models, we completed post hoc tests. For main effects we used Hochberg's GT2 method (test statistic = H) because this method is robust to differences in sample sizes among treatments (Sokal & Rohlf 1995). Hochberg's test indicates which levels of a main effect differ but does not distinguish among combinations of size and landscape (e.g., small exurban from small suburban). Because this test does not apply to interactions, we computed Scheffe's

Table 1. Influence of reserve size, landscape context, and vegetation on bird communities, populations, and individuals based on full factorial general linear models.

Metric or species	*Factor showing association without covariate in model*[a]	F	p	*Vegetative covariate and sign of correlation*[b]	p *increase with model covariate*[c]
Community					
total bird density	landscape	5.2	0.01	% exotic ground cover +	0.11
				% horizontal shrub cover +	0.05
	size	2.7	0.09		
richness	size	19.1	<0.001	shrub diversity +	0.00
	landscape	4.3	0.03	shrub diversity +	0.06
rarefied richness	interaction	4.9	0.01		
evenness	size	4.0	0.04	shrub diversity −	0.17*
Population					
American Crow	interaction	3.9	0.01	% exotic ground cover +	0.09
				% exotic shrub cover +	0.01
				number snags −	0.01
American Robin	landscape	4.2	0.03	% exotic ground cover +	0.45*
				% exotic shrub cover +	0.20*
				number snags −	0.07
Bewick's Wren	landscape	7.0	0.01	% exotic ground cover +	0.37*
				% exotic shrub cover +	0.28*
				number snags −	0.07
Black-headed Grosbeak	landscape	4.4	0.02		
Brown Creeper	landscape	4.6	0.03	number snags +	0.03
Black-throated Gray Warbler	landscape	3.9	0.04		
Bushtit	interaction	4.5	0.01	% exotic ground cover +	0.10
				% exotic shrub cover +	0.43*
				number snags −	0.00
Chestnut-backed Chickadee	landscape	3.5	0.04		
Hammond's Flycatcher	landscape	3.6	0.04	number snags +	0.03
Hutton's Vireo	size	4.8	0.02		
	landscape	4.7	0.03		
Pine Siskin	landscape	3.6	<0.05	% exotic shrub cover +	0.85*
Spotted Towhee	landscape	5.4	0.02		
Varied Thrush	interaction	7.1	0.01		
Wilson's Warbler	landscape	3.9	0.03	% horizontal shrub cover +	0.13
				number snags −	0.40*
Winter Wren	landscape	3.8	0.04	% exotic ground cover −	0.32*
				% exotic shrub cover −	0.45*
				number snags +	0.86*
Yellow-rumped Warbler	interaction	3.4	0.02	number snags +	0.00
Individual shrub nests found per search hour	landscape	8.2	0.04		

[a] *Main effects on indices of individual breeding success were tested separately. Landscape was tested with large sites (df = 2,3). Size was tested with suburban sites (df = 2,6).*

[b] *Vegetation variables were included as covariates only if they varied with the design factor (all df = 2,26) and correlated with the response metric. Signs for covariate relationships with metrics were based on Pearson's coefficients for analyses at the community and population levels (all* n *= 29).*

[c] *Asterisk indicates inclusion of the vegetative covariate in the model led to a large change in* p *(>0.15).*

post hoc test (test statistic = S) for significant interactions following the method of Zar (1996).

Results

Communities

All bird community metrics responded to landscape and/or size. Total relative abundance of birds in exurban reserves was lower than in suburban reserves (Table 1; Fig. 2; $H = 1.9$, $p = 0.04$) and tended to be lower than in urban reserves ($H = 2.1$, $p = 0.06$). It also tended to decrease with reserve size (Table 1). Bird species richness increased with reserve size (Table 1; Fig. 3a; small to medium $H = 5.0$, $p < 0.01$; small to large $H = 9.3$, $p < 0.001$; medium to large $H = 4.3$, $p = 0.02$) and was greater in suburban reserves than in exurban reserves (Table 1; Fig. 3a; $H = 3.8$, $p = 0.04$), perhaps with the exception of the small size class. The landscape effect held

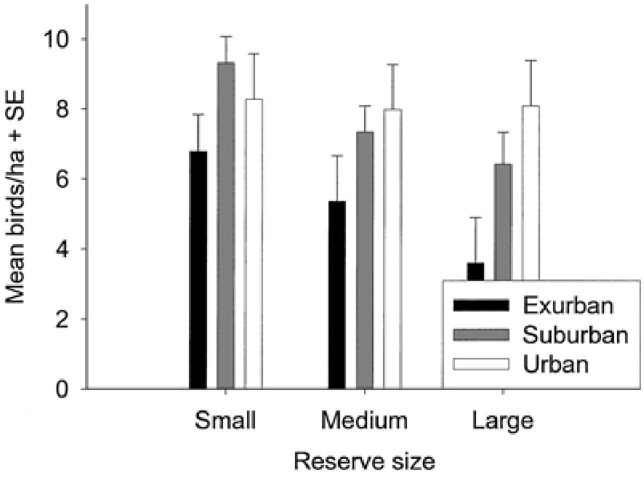

Figure 2. Total bird relative abundance as a function of habitat reserve size and urbanization intensity.

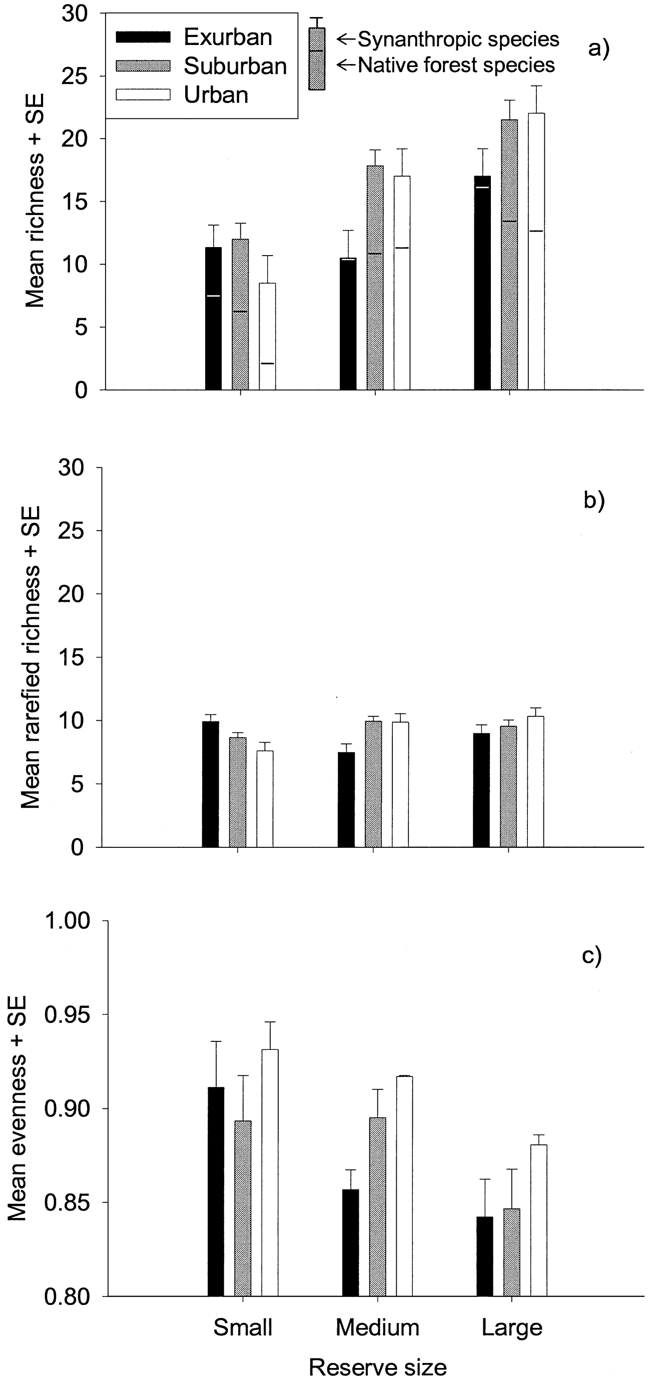

Figure 3. (a) Bird species richness, (b) rarefied bird species richness, and (c) bird community evenness as a function of habitat reserve size and urbanization intensity. In (a), horizontal lines separate native forest species (bottom) from synanthropic species (top).

with fewer than four surveys per site (Donnelly 2002) but changed with rarefaction; rarefied richness increased with urbanization intensity in medium and large reserves but showed the opposite trend in small reserves (Table 1; Fig. 3b). Evenness was greater in small reserves than large reserves (Table 1; Fig. 3c; $H = 4.8$, $p = 0.03$). This relationship disappeared when shrub diversity was included as a covariate in the model (Table 1).

Populations

Species-specific thresholds in reserve size and surrounding urbanization intensity ordered (created nested communities; sensu Atmar & Patterson 1993) the retention of native forest species (percent of perfect nesting by size: 19.2, $p < 0.01$; Fig. 4a) and gain of synanthropic species (percent of perfect nesting by landscape: 13.5, $p = 0.01$; Fig. 4b). Retention was more ordered than gain. Native forest species tended to switch from present to absent when reserves fell below 42.2 ± 15.0 ha (mean threshold of occurrence, $n = 17$). Synanthropic species were almost completely absent from the eight reserves with the least urban land cover (<6% urban land cover) and tended to switch from absent to present when urban land cover exceeded 40 ± 9.9% (mean threshold of occurrence, based on 12 species present in at least four reserves). The increases in retention of native forest species with reserve size and in gain of synanthropic species with urbanization intensity are also visible in Fig. 3a.

The relative abundance of many bird species varied with landscape (Table 1). Of those species responding to landscape, three were most abundant in exurban reserves (Black-throated Gray Warbler, Hammond's Flycatcher, Winter Wren; exurban to suburban $H = 0.04–0.1$, all $p < 0.05$; exurban to urban $H = 0.04–0.2$, all $p < 0.05$), four were most abundant in suburban reserves (Black-headed Grosbeak, Brown Creeper, Chestnut-backed Chickadee, Spotted Towhee; suburban to exurban $H = 0.03–0.12$, all $p < 0.05$; suburban to urban $H = 0.06–0.12$, all $p < 0.05$), and four were most abundant in urban reserves (American Robin, Bewick's Wren, Hutton's Vireo, Pine Siskin;

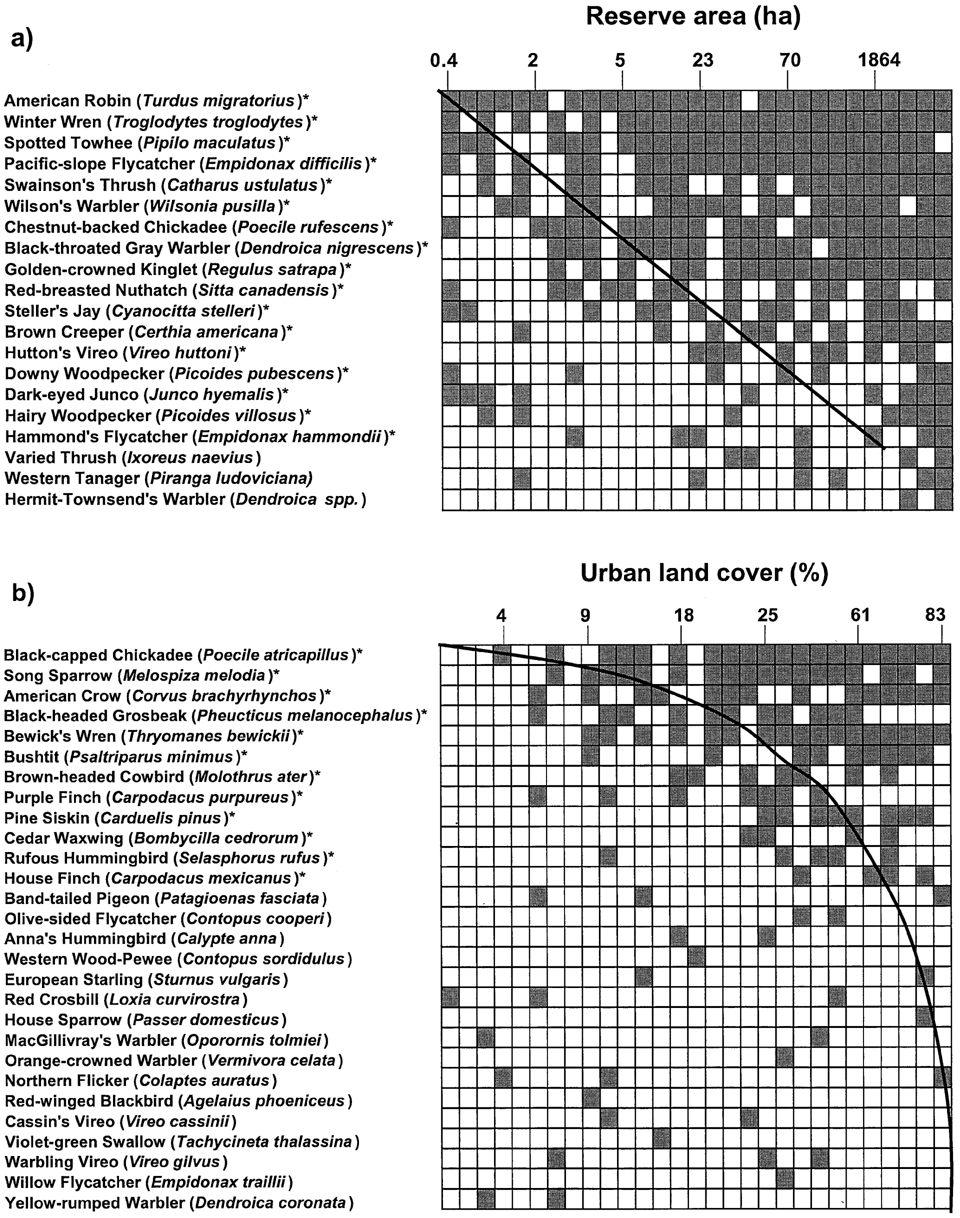

Figure 4. Ordered retention of (a) native forest and (b) synanthropic bird species in habitat reserves. Columns represent communities ranked by (a) reserve size and (b) urban land cover. Rows represent species ordered to maximize presences in the upper right and absences in the lower left. Filled and unfilled squares indicate presence and absence, respectively. The intersection of the superimposed occurrence threshold curve (shape dependent on matrix dimensions and percent fill) with a row indicates a species-specific occurrence threshold or the size or land cover value where a species tended to switch from present to absent or vice versa. We calculated mean thresholds of occurrence based on all species present in more than three reserves (marked with asterisks).

urban to suburban $H = 0.02–0.12$, all $p < 0.05$; urban to exurban $H = 0.02–0.2$, all $p < 0.05$). Only three of the species responding to landscape were not found within all three landscape levels (Bewick's Wren, Black-headed Grosbeak, Pine Siskin). In each case, they were absent from exurban reserves. Many of the associations between relative abundance and landscape dissipated when one or more vegetation variables were included in the models as covariates. Two correlated variables ($r = 0.63, p < 0.001$, $n = 29$) caused most of these effects (Table 1): exotic ground cover ($n = 3$ species; mean % cover: exurban = 2.7 ± 2.3, suburban = 17.2 ± 4.9, urban = 35.1 ± 16.2) and exotic shrub cover ($n = 4$ species; mean % cover: exurban = 0 ± 0, suburban = 4.2 ± 2.0, urban = 27.3 ± 11.6).

Five species varied in abundance with reserve size and with combinations of size and landscape (Table 1). Hutton's Vireo was more common in medium than small reserves ($H = 0.018$, $p = 0.01$). The American Crow and Bushtit were absent from exurban reserves and more common in small urban reserves than all other combinations of size and landscape (American Crow, $S = 4.4–7.3$; all $p < 0.05$; Bushtit, $S = 4.5–7.5$; all $p < 0.05$). The Varied Thrush was more abundant in medium exurban reserves than all other reserve types except medium urban reserves ($S = 4.5–6.8$, all $p < 0.05$). The Yellow-rumped Warbler was rare and was found only in small exurban reserves. Replication limited our ability to distinguish its abundance in small exurban reserves from its abundance in other combinations of size and landscape (to small suburban $S = 4.6, p = 0.04$; to medium suburban $S = 4.6$, $p < 0.05$).

Nest Success and Causes of Nest Failure

Nest predation was the most common cause of failure at shrub nests. Fifty-one percent (95 of 188) of monitored nests failed. Seventy-seven percent (59 of 76) of nests with a known cause of failure were depredated. Other causes of failure were disturbance (8%), abandonment (8%), and substrate collapse (4%).

The relative abundance of shrub nests and nest-cycle success was related to reserve size and landscape context. Nests were three to four times more abundant in medium suburban and large urban reserves than all other combinations of reserve and size (Fig. 5a). Within suburbs they appeared to be more abundant in medium reserves than small and large reserves. Within urban areas they appeared to be more abundant in large reserves than small reserves. Large urban reserves also had more nests than large reserves in other landscapes (Table 1; Fig. 5a; urban to suburban $H = 0.085, p = 0.04$; urban to exurban $H = 0.094, p = 0.01$). If landscape had an effect on the relative abundance of nests in small sites, the pattern it produced opposed the pattern observed in large sites. Nests were conspicuously absent in small urban reserves, where the search effort per unit area was high (approximately75 hours/ha/year). Nest-cycle success (combination of incubation and brooding stages) appeared to be nearly two times greater in medium sites than in sites of other sizes within suburbs and in large sites than in smaller sites within exurban areas (Fig. 5b). Similar to the pattern of nest abundance, the number of successful shrub nests found per unit search effort appeared to peak in medium sites within suburbs and within large sites in urban landscapes (Fig. 5c). These sites were three to four times more successful by this measure than other combinations of size and landscape.

The juvenile-to-adult ratio for shrub-nesting birds appeared to correlate with nest productivity only in urban landscapes. There, juveniles were more common per adult in large than small reserves (ratios: small, 0; medium, no data; large, 0.12). The opposite pattern occurred in exurban reserves (ratios: small, 0.39; medium, no data; large, 0), despite nearly equal nest abundance and nest-cycle success in small and large exurban reserves. The juvenile-to-adult ratio was lowest in medium reserves in suburbs (ratios: small, 0.27; medium, 0.13; large, 0.17), a trend that was also not apparent from monitoring nests.

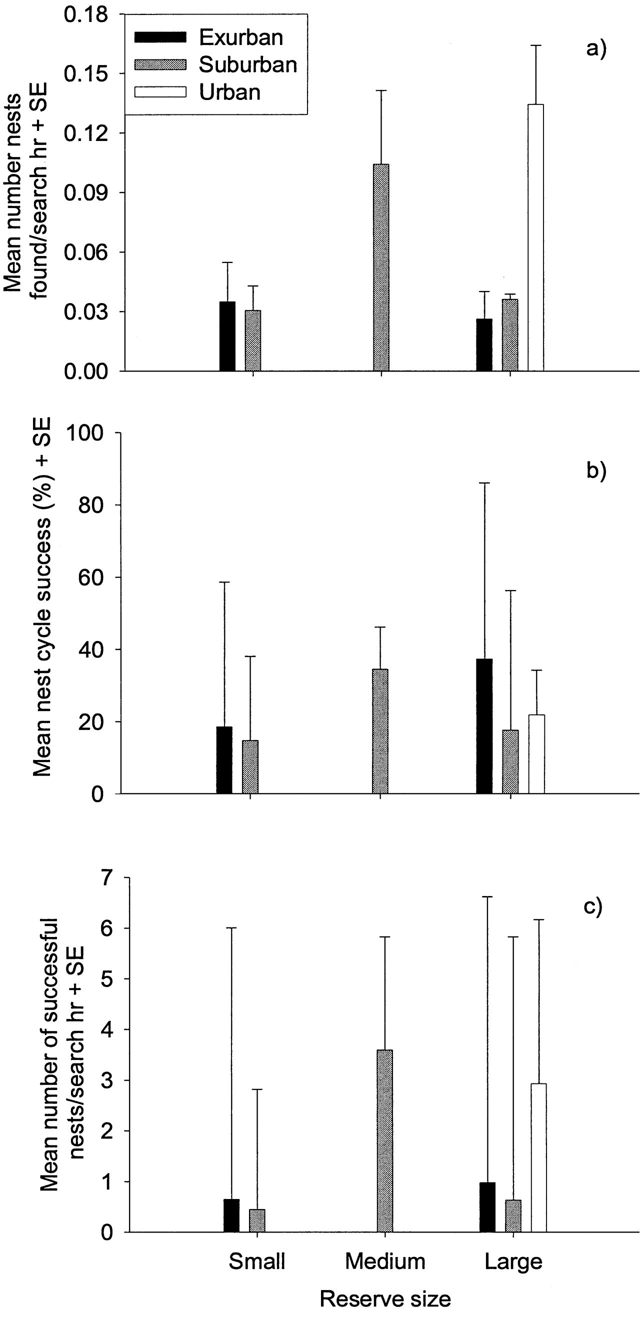

Figure 5. Shrub nest success in habitat reserves expressed as (a) nests found per search hour, (b) nest cycle success, and (c) a combination of these factors. We did not find any nests in the small urban reserve or search for nests in medium exurban and medium urban reserves.

Discussion

Communities

Bird communities generally changed with size and landscape, as predicted by the literature. As reserve size increased, richness increased (Fig. 3a) but individuals became less evenly distributed among those species (Fig. 3c). Theory argues that richness should increase with reserve size because, relative to smaller areas, larger areas (1) support larger populations that are more resistant to demographic stochasticity (MacArthur & Wilson 1967); (2) support more individual birds representing a larger proportion of species from the regional pool (passive sampling; Wiens 1989); and (3) contain greater habitat heterogeneity and more niches (β diversity). We found evidence for the second and third mechanisms. Rarefaction reduced the magnitude of the size effect on richness in suburban and urban reserves (Fig. 4b), implicating passive sampling. A biological effect of reserve size on species richness was also likely, however, because rarefaction dampened but did not remove the size effect in most landscapes. We hypothesize that greater shrub diversity in larger reserves than in smaller reserves may explain at least some of the remaining size effect because shrub diversity and richness were positively correlated (Table 1). Moreover, this hypothesis was consistent with the negative correlation of evenness with size (Fig. 3c) and its apparent explanation by shrub diversity (Table 1). Bird species responding to greater habitat diversity were rare. Thus, they lowered evenness and contributed little to rarefied richness, a sample derived from species surveys. Regardless of the mechanism driving greater richness in larger reserves, this benefit of larger reserve size appeared to hold only in suburban and urban landscapes.

Landscape had both expected and unexpected relationships with avian community composition. As expected, total bird relative abundance was greater in urban and suburban reserves than in exurban reserves. However, supplemental food and human-made nest sites could not have explained the entire effect because synanthropic species were not common within reserves. This suggests that density increased because native birds packed into forest patches when forest was rare on the landscape (Hannon & Schmiegelow 2002). The degree of packing tended to be negatively correlated with reserve size, perhaps because similar numbers of birds dispersed over more forest habitat when it was available. Unlike the pattern of total bird relative abundance, the increase in rarefied richness with urbanization intensity in medium and large sites was unexpected. The unexpected increase in species number may have resulted from our truncation of the urbanization-intensity gradient at approximately 70% impervious surface. Had we extended the gradient to the core business district (90–100% impervious surface), richness probably would have declined to a subset of the six most synanthropic bird species in this region (House Sparrow, American Crow, European Starling, Glaucous-winged Gull [*Larus glaucescens*], Herring Gull [*Larus argentatus*], Rock Dove [*Columba livia*]). We hypothesize that the dramatic reduction in species richness would have caused richness to peak at intermediate values of urbanization intensity, as documented by others (Blair 1996) and predicted by the intermediate-disturbance hypothesis (Huston 1979).

Populations

As expected, reserve size and surrounding urbanization intensity were related to the presence or absence of individual species. The number of native forest species present within bird communities decreased with reserve area as species reached individual thresholds of occurrence; most species were present at sites larger than 42 ha. This pattern could have been caused by either differential susceptibility to area-related local extinction (Bolger et al. 1991), differential dispersal ability (Darlington 1957), or an underlying arrangement of habitats in which those in smaller sites were included within larger sites, thus increasing habitat diversity (Cody 1983). We believe that local extinction was the best hypothesis because all strong dispersers—such as the long-distance migrants Black-throated Gray Warbler and Western Tanager—were not present in the smallest sites and there was no evidence of hierarchical arrangement of habitats. The gain of synanthropic species was similarly ordered, with most species being gained in reserves surrounded by >40% urban land cover. Some of these species, such as the Black-headed Grosbeak and Cedar Waxwing, were native species that probably relied more on the juxtaposition of habitats produced by urbanization than supplemental food or human-made nest sites.

The relative abundance of many native forest and synanthropic species varied with landscape or the combination of landscape with size but not with size alone. Again, this pattern agreed with the literature: area-sensitive native forest species were generally present at constant abundance or absent (Whitcomb et al. 1981), and synanthropic species generally increased in abundance with urbanization and the resources that it provided (Marzluff 2001). Most of the relationships between relative abundance and landscape appeared to be explained by exotic ground and shrub cover. Native forest species decreased and synanthropic species increased with these attributes of the local vegetation. Because exotic ground and shrub cover were positively associated with urbanization intensity, it was difficult to tell whether their explanatory power was due to the indirect effects of urbanization or the direct impacts of these variables on individual fitness. Because the species in question represent many foraging and nesting guilds, we believe that both types of effects probably occur in these communities.

Individual Nest Success

The American Robin and Swainson Thrush, two shrub-nesting thrushes, appeared to be more productive in larger (medium and large) reserves only in suburban and urban landscapes. In urban landscapes there appeared to be roughly the same number of successful nests in large reserves than in small reserves as a result of nest density rather than nest success. Nest density appeared as important as nest success in exurban landscapes. In large exurban reserves there were three times fewer successful nests than in same-sized urban reserves because of low nest density and despite relatively high nest success. Nest density and success were two to three times higher in medium suburban sites than most combinations of reserve size and landscape, resulting in the highest apparent density of successful nests. The effect of size on the productivity of shrub-nesting birds in urban and suburban reserves was consistent with greater richness in larger reserves because populations of shrub-nesting birds are likely to persist and contribute to richness where they are more productive.

The relationship of reserve size and landscape to the relative risk of predation at artificial shrub nests was very similar to that for nest success (Donnelly 2002). Risk was least in large urban, medium suburban, and small exurban reserves, suggesting that it decreased with size in urban landscapes but increased with size in exurban landscapes. The similarity of patterns of nest success and predation risk implicated nest predation as a driver of nest success. This finding was supported by the fact that most nests failed as a result of predation, and the effect of urbanization intensity on the risk of nest predation was explained by horizontal and exotic shrub cover (Donnelly 2002). Where shrub nests were more concealed, they survived longer. Despite this pattern, the abundance of diurnal, visual predators that we sampled did not positively correlate with predation risk. Instead it appeared that rats may have increased the risk of nest predation (Donnelly 2002). Recently, estimates of population productivity based on per-nest success have been questioned because re-nesting can compensate for low rates of nest success (Thompson et al. 2001) if predation rates are not very high (<65%; Schmidt & Whelan 1999). Because the overall percentage of nest failure at our sites was below this threshold, we assessed whether re-nesting compensated for nest predation and reduced annual nest success by estimating the juvenile-to-adult ratio for each site. The pattern of these ratios for shrub-nesting birds relative to reserve size and landscape context was more similar to that for risk of nest predation than for nest abundance or nest cycle success (Donnelly 2002). As a result, we hypothesize that re-nesting did not compensate for nest predation and that large reserve size was beneficial in urban and suburban reserves but may have had little effect in exurban reserves. We state the last interpretation more cautiously because it was possible that low bird density in large exurban reserves made netting less effective. Limited correlation of juvenile-to-adult ratios with nest abundance and nest-cycle success suggested that the mechanism(s) dictating risk of nest predation (e.g., rat abundance) differed from those dictating juvenile survivorship.

Conservation and Planning Implications

Reserve size was important to bird community composition in all landscapes and to breeding success in some landscapes. These relationships suggest strategies for conserving native forest birds in the Seattle metropolitan region. Richness increased with reserve size in all landscapes because larger reserves had larger samples of individuals from the regional pool of species and provided habitat for more species than small reserves. As reserves decreased in size, native forest species disappeared at predictable sizes. For example the Golden-crowned Kinglet was almost always present in reserves of >21 ha but tended to be absent from smaller reserves. Because species exhibited these thresholds of occurrence, a collection of medium and small reserves will not conserve species such as the Golden-crowned Kinglet or regional bird diversity (Patterson 1987). Policy makers can encourage retention of larger reserves within landscapes by limiting development and requiring planners in growing counties and incorporated areas to plan for large, contiguous blocks of forest (some >42 ha), especially in areas of high forest habitat diversity. Large reserves in more urban landscapes (>40% urban land cover) will support richer communities than large exurban reserves, but the difference will be due to greater colonization by synanthropic species (some of which are native).

Population abundance within reserves was influenced by landscape and rarely by the combination of landscape and reserve size. Different groups of bird species peaked in abundance in exurban, suburban, and urban reserves. The effect of landscape was explained by exotic ground and shrub cover. These covers increased in more urban landscapes and were associated with increases in synanthropic species and decreases in native forest species. It is not clear whether these plants have a direct influence on the birds or whether they correlate with other aspects of urbanization. Nonetheless, we recommend that land managers and homeowners minimize exotic ground and shrub cover in forest fragments.

The combination of reserve size and landscape setting appeared to influence breeding success and potentially determine whether populations were self-sustaining. Reserve size was beneficial to breeding birds in suburban and urban landscapes. The density of nests in shrubs was greatest in medium suburban and large urban reserves and appeared to be at least as important as nest success to overall reserve productivity. In contrast, large exurban reserves and small reserves in all landscapes had very low densities of successful nests (0 in a small urban reserve). These relationships lead us to two conclusions. First, small urban reserves have no value as breeding habitat for at least two native forest species that nest in shrubs. Second, larger reserves in more urbanized (suburban and urban) landscapes have exceptional conservation value for most native forest species, but it will often be necessary to manage human disturbances that negatively affect birds, including free-ranging domestic cats, dog walking, hiking, and refuse. Land managers can educate recreationists and homeowners adjacent to parks and route trails to steer away from some habitat set aside for wildlife conservation. Homeowners can minimize the access of potential nest predators to refuse, keep pets inside or on a leash, stay on designated hiking trails, and trap rats.

We do not recommend that the guidelines encouraging larger reserves in suburban and urban landscapes be applied to all landscapes. Although we are most concerned about the retention of native forest species, a number of synanthropic species are also native but require some level of disturbance or habitat interspersion. For example, the native Song Sparrow and Black-headed Grosbeak are present only in habitat with some fragmentation. Rohila (2002) made similar recommendations for the retention of some native cavity-nesting bird species in this region. She recommended that some landscapes contain 27-60% forest interspersed with settlement. Providing some heterogeneity of landscape will help preserve native forest species, native synanthropic species, and regional bird diversity (Pyle 1980).

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