



Bird communities of the Colorado Rocky Mountains along a gradient of exurban development

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Abstract

Most insights about the effects of residential development on wildlife are based on research from urban and suburban areas. Yet exurban development is an increasingly prevalent form of human settlement in many parts of the world. Moreover because such development often occurs near the periphery of protected areas, it may have a disproportionate influence on native species. We examined bird community patterns in the Rocky Mountains of north-central Colorado across a gradient of exurban development to determine how avifauna responded to this form of settlement. Using fixed-radius point counts, we surveyed the occurrence and abundance of breeding birds in 11 developed sites and in 6 nearby undeveloped sites, all occurring in a forested matrix. We sampled ground-level habitat features at each survey point and derived digital land-cover maps from aerial photographs to characterize and quantify road development and building density. We found little evidence that land-cover varied with development intensity, yet bird abundance increased significantly with building density. Patterns of species richness were equivocal due to a highly influential observation. Principal components analysis (PCA) distinguished two axes that explained nearly 50% of the variation in the bird community and were strongly associated with road and building density. Weighted average analysis showed a marked decline in the abundance and richness of species that were insectivorous or nested in snags, suggesting that reductions in dead wood may have influenced the bird community. However, no conclusions could be drawn because dead wood was confounded with building density. Logistic regression of species occurrence and building density indicated that the incidence of some generalist species increased with building density, whereas the incidence of specialists decreased. Overall, our results suggest that development at low densities can favor habitat generalists. Similar patterns have been observed in more urbanized areas. If exurban development persists as a popular form of settlement in the Rocky Mountains, a regional plan for protecting avian habitat and limiting development dispersion will be necessary to maintain native bird communities. © 2004 Elsevier B.V. All rights reserved.

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1. Introduction

Urban development is highly conspicuous and has a considerable influence on wildlife. For example, recent studies have demonstrated that urbanization has important consequences for avian communities (Marzluff et al., 1998, 2001; McKinney, 2002). Native bird species typically decline with urbanization due to changes in both habitat and resource avail-

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ability (Beissinger and Osborne, 1982; Jokimaki and Suhonen, 1993; Blair, 1996; Clergeau et al., 1998; Germaine et al., 1998). Urban development also promotes shifts in avian community composition as generalist species increase and specialist species decrease (Emlen, 1974; Hohtola, 1978; Blair, 1996; Boren et al., 1999). Human settlement takes several forms however—urban, suburban, rural, and exurban—that are qualitatively different from one another with respect to habitat and resource modification. The effects of these forms of settlement on native species may likewise be unique, yet wildlife response to non-urban development is generally not well documented (Miller et al., 2001; Miller and Hobbs, 2002).

Exurban development and its effects on wildlife warrant particular attention. Exurban development is distinct from urban development in that it occurs outside municipal limits, perforates native ecosystems, and is often situated on the periphery of protected areas (Knight, 1999; Marzluff et al., 2001). It is increasingly common in the American West owing to the region's wealth of natural and recreational amenities (Nelson, 1992; Riebsame et al., 1996; Booth, 1999). Colorado in particular has experienced rapid exurban expansion. During the past three decades, the extent of exurban development has increased from 1.9 to 6.9% of Colorado's developed lands, outpacing both urban and suburban development with an annual growth rate of 8.3% (Theobald, 2000). Since it predominates in Colorado counties with federally designated wilderness areas (Gersch, 1996) and is often situated near bodies of water and on forest edges (Riebsame et al., 1996), exurban development may have a disproportionate effect on the biotic integrity of wildlands (Romme, 1997).

Avian species may be affected by exurban development both directly and indirectly. Changes in broad-scale land-cover patterns driven by this form of human settlement may benefit species adapted to the naturally fragmented and highly varied coniferous forests of the Rocky Mountain region (Hansen and Rotella, 2000; Theobald, 2000), whereas others may be insensitive to increased fragmentation (Hansen and Urban, 1992). Shifts in biotic processes associated with human settlement, such as predation and competition, may also influence native bird populations (Marzluff et al., 1998; Odell and Knight, 2001). Evaluating how bird communities change with in-

creasing exurban development, and identifying the proximate factors that drive these changes remain critical needs for forecasting the effects of human settlement (Marzluff et al., 1998).

McDonnell and Pickett (1990) recommended a gradient approach for examining the effects of increasing human settlement because of its capacity to distinguish critical thresholds where human impacts cause ecologically significant changes in wildlife communities (Wiens, 1989). Such thresholds may be detected in measures of building density or distance from human-dominated areas (Miller et al., 2001; e.g., Odell and Knight, 2001). Gradient-based studies are also useful for identifying the types of species most vulnerable to and those that benefit from human settlement (Marzluff et al., 1998). We employed a gradient approach to investigate how bird communities of the Colorado Rocky Mountains respond to exurban development. Specifically, we examined differences in avian community patterns along a settlement gradient, and identified factors related to changes in bird community composition. We also investigated the prevalence and richness of avian functional groups associated with settlement, and identified how the probability of individual species occurrences changed with increasing exurban development.

2. Methods

2.1. Site selection

We selected 17 study sites on the eastern slope of the Rocky Mountain Range in north-central Colorado, USA. (Fig. 1). Six sites had no residential development and were used as references. Of these, four were located in Rocky Mountain National Park and two were on US Forest Service land. The remaining 11 sites had exurban development and were located in Larimer, Boulder, or Gilpin counties. Sites were chosen to represent a gradient of exurban development as measured by building density. All sites had similar vegetation characteristics, elevation, and exposure. They occurred in coniferous forests dominated by ponderosa pine (*Pinus ponderosa*). Elevation ranged from approximately 2400 to 2750 m.

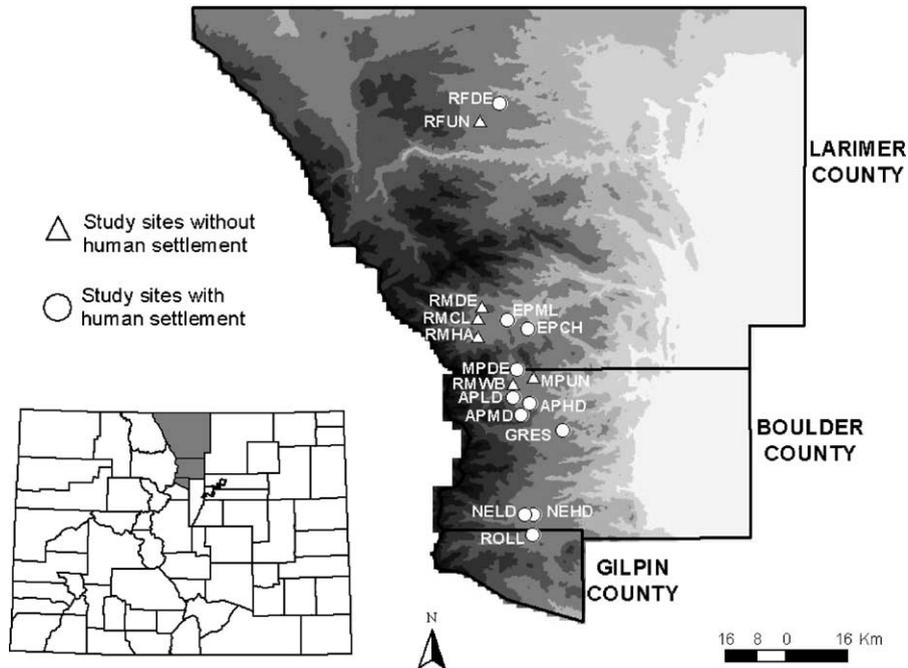


Fig. 1. Study area showing “natural” (unsettled) sites (Δ) and sites with human settlement (\circ) in the Rocky Mountain region of north-central Colorado, USA. Shading represents elevation gradient from 1450 to 4350 m, with light colors for low elevation and dark colors for high elevation.

2.2. Bird surveys

Data on bird abundance were collected at each site using fixed-radius point counts (Bibby et al., 1992; Ralph et al., 1993). Points were randomly placed along trails in undeveloped areas with 2–3 m openings in the canopy and in developed areas along narrow, unpaved roads with similar sized canopy openings. Thus, habitat differences between trails and roads were minimal and should not have biased our counts (Hutto et al., 1995). Furthermore, since roads generally interlace mountain communities, road-side surveys may integrate land-cover changes that are important for birds in developed areas and sampling near them may provide a more accurate estimate of the influence of human settlement on bird communities.

Points were positioned in areas that were comparable with respect to prevailing habitat characteristics. Because the developed sites we surveyed were small, we did not sample the same number of points at every site. We placed 9 or 10 points at each site, except for two developed areas where we placed 7 points and one

developed area where we placed 6 points. Any systematic bias in the species detected was avoided because sites with fewer points were distributed across the development density gradient.

Before the field season began, we measured the distance to a bird detection with a Bushnell Laser Rangefinder (Yardage Pro 400) to establish the maximum detection distance from survey points. We could consistently and accurately detect birds visually or aurally within 70 m of a point; therefore, no registrations were made beyond this distance and survey points were separated by a minimum of 150 m. A single observer (JMF) collected abundance data for birds at each site from 24 May to 19 July 1999, the peak of the breeding season for passerines nesting in our study sites (Kingery, 1998). We visited each site twice during the season, once between 24 May and 6 June and between 6 July and 19 July. Surveys were performed once between 05:30 and 07:00 h and between 07:30 and 09:30 h on days without rain and when wind was less than 15 km/h. Each sample point was surveyed for 5 min to maximize count efficiency (Petit et al., 1995),

and efforts were made to avoid double-counting individuals moving among points (Bibby et al., 1992). Fly-overs and birds detected outside the 70-m radius boundary were not recorded. The unit of analysis was the site, and only species occurring in ≥ 2 sites were included.

2.3. Land-cover and ground-level habitat characterization

Land-cover maps for each site were derived from 1995 to 1996 color aerial photographs (1:40,000 scale) provided by the US Forest Service. We used five categories based on the Anderson I Land Use and land-cover classification system to represent the land-cover (Anderson et al., 1976). Using a combination of unsupervised and supervised methods (ERDAS Imagine), we classified cover as dense conifer forest (closed canopy), sparse conifer forest (open canopy), or grass. Aspen and open water were digitized on-screen (ESRI, ArcView) because their spectral signatures were not distinct enough from those of other land-cover types for imaging software to delineate them. To quantify the degree of human settlement at each site, we identified and manually digitized all roads and individual buildings within the study area. We compiled these layers into a single grid-map for each site with a minimum mapping unit of 16 m².

We quantified the amount of each land-cover type for a site by first extracting the section of the land-cover map that fell within a 70-m radius circle centered on each survey point. Information on land-cover was limited to this area because it most appropriately summarized the habitat features of the locations where bird data were collected and was representative of the entire study site. The 70-m buffer distance also afforded land-cover data for a site that were spatially discrete (i.e., circles centered at points do not overlap at this buffer distance). The number of cells of each land-cover type was summed across all the points at a site. These values were then divided by the area of the polygon created by the circles. We performed this final operation to standardize the measurements of land-cover types because not all sites had the same number of points.

We measured ground-level vegetation characteristics at every point where a bird survey was performed. Vegetation was sampled only once since the features

being measured generally remained constant during the breeding season. Within a 10-m radius of each survey point, we ordinally ranked percent canopy cover, percent subcanopy cover, percent ground cover, number of snags, stumps, and undisturbed (i.e., not chopped or piled in stacks) down wood with a diameter = 5 cm using the Braun-Blanquet Cover Abundance Scale (Ralph et al., 1993). All measurements were made by ocular estimation and were averaged over the site. Upper foliage height was calculated for each point by dividing the horizontal distance from an observer to the lowermost foliage of the three tallest trees by the tangent of the angle between an observer and the foliage level. Foliage height calculations were averaged for each point and then averaged over the site.

2.4. Data analysis

We calculated Spearman's rank correlations to determine the relationships between land-cover, ground-level habitat variables and residential development. Species richness and abundance were modeled using least squares regression and building density as an independent variable to investigate how the bird community changed as residential development increased. Cook's *D* statistic was calculated to inspect the influence of potential outliers in these models. To account for differences in breeding phenology, we used the maximum count of each species and the maximum number of species recorded on the visits to a site divided by the area sampled to correct for differences in the number of bird surveys conducted at each site, as a measure of abundance and richness. The relationships between bird community patterns, land-cover and ground-level habitat variables were further examined by ordinating the bird community data using principal components analysis (PCA) based on the covariance matrix and overlaying species scores with vectors of independent variables. Although the correlation matrix is used more often in PCA, employing the covariance matrix is desirable when variables with the largest variances are more important for structuring the data than are variables that are relatively evenly distributed (McGarigal et al., 2000). In this study, we based the PCA on the covariance matrix because we wanted species with the largest variances to weigh more heavily on the princi-

pal components than species evenly distributed across the development gradient. The magnitude and direction of each vector reflects the correlation between the variable and the site score determined by PCA and is based on the Pearson correlation coefficient. PCA was favored over other ordination procedures because (1) it identifies gradients in community data without the constraint of independent variables; (2) it is designed for systems with short gradients (such as our abbreviated development gradient); and (3) its underlying algorithms are appropriate for systems in which the response variables are expected to be linear (Jongman et al., 1995).

The responses of feeding (foraging and diet) and nesting functional groups to increased human settlement were investigated by comparing the average species richness and abundance weighted by building density of each functional group. These functional groups were selected because previous studies have suggested that urbanization influences bird communities by altering resource availability (Emlen, 1974; Blair, 1996). Since the weighted average takes into account the proportional relevance of each species with respect to building density rather than weighting each species equally, this index emphasized the major shifts occurring in the bird community as development increased (Jongman et al., 1995). Weighted averages for each species were calculated as:

$$\frac{\sum_i A_{ij} E_j}{\sum_i A_{ij}}$$

where A_{ij} is the occurrence (1 or 0) or abundance of species i at site j corrected for differences in area sampled at site j , and E_j is the building density at site j . Species were classified into foraging and diet groups after Salt (1953) and Ehrlich et al. (1988) and into nesting-substrate groups according to Peterjohn and Sauer (1993) and Ehrlich et al. (1988). We used Kingery (1998) as a cross-reference to select classifications that were specific to the Rocky Mountain region (Appendix A). Weighted averages of functional groups were compared using one-way ANOVA, and differences between individual groups were tested with Tukey's honestly significant difference.

To assess how individual bird species responded to exurban development, we modeled species presence/absence data with building density using logistic regression. We pooled presence/absence data for

this analysis such that, if a species was present during either visit, it would be counted as present. All models were evaluated using the likelihood ratio and goodness-of-fit criteria (Hosmer and Lemeshow, 1989; Trexler and Travis, 1993). The contribution of the building density parameter in significant models was determined qualitatively with Wald's test. We also screened the models for evidence of a threshold response (positive or negative) to building density.

3. Results

3.1. Land-cover

The gradient of human settlement in our study sites ranged from 0 to 1.10 buildings/ha (0.24 ± 0.07 buildings/ha, mean \pm 1 S.E.; Fig. 2). Road density was strongly associated with building density ($\rho = 0.80$) and comprised a large proportion of sampled land-cover, ranging from 0 to 207 m-roads/ha (93 ± 17 m-roads/ha). Sites had an almost constant upper canopy height and density, and coniferous forest comprised a major proportion of the area sampled (Table 1). No significant relationship between building density, conifer (dense: $\rho = -0.07$; sparse: $\rho = -0.10$), grass ($\rho = 0.10$), or aspen cover ($\rho = -0.15$) was detected. Likewise, most habitat characteristics measured on the ground did not vary as building density increased (percent canopy cover: $\rho = -0.003$; % subcanopy cover: $\rho = -0.08$; percent shrub cover: $\rho = -0.13$; percent ground cover: $\rho = 0.18$; average height of upper canopy: $\rho = -0.10$). Woody debris was significantly and negatively associated with building density, however. The number of snags ($\rho = -0.71$), stumps ($\rho = -0.62$) and the amount of down wood ($\rho = -0.66$) all decreased as building density increased.

3.2. Bird community responses

We detected a total of 59 bird species at these study sites (Appendix A). The most abundant species, the Mountain Chickadee ($n = 185$), Broad-tailed Hummingbird ($n = 145$), American Robin ($n = 138$), and Dark-eyed Junco ($n = 111$), were also the most widespread, occurring at 100% of the study sites. The number of species surveyed at each site ranged from

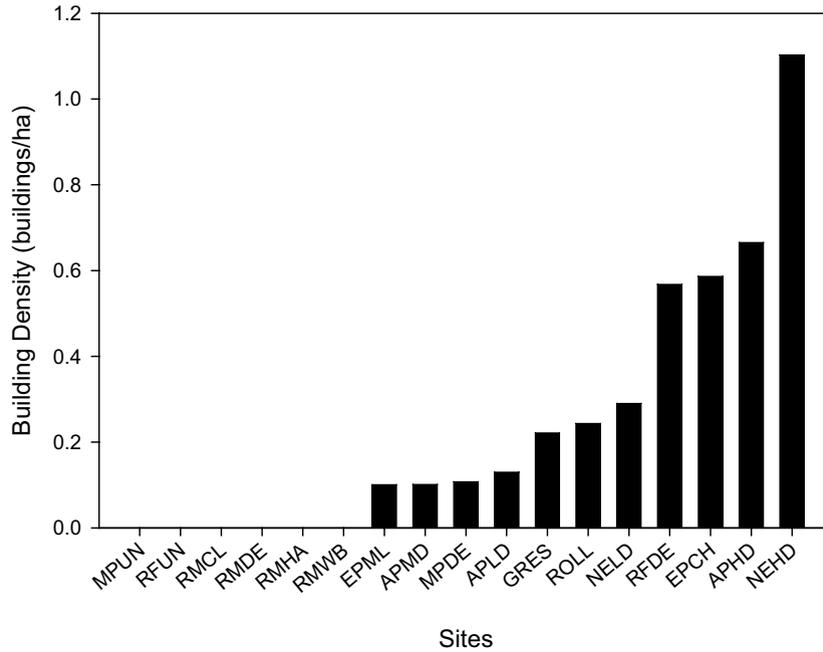


Fig. 2. The gradient of residential development (building density) across study sites in Larimer, Boulder, and Gilpin counties of north-central Colorado. Locations of sites can be found in Fig. 1.

Table 1
Vegetation characteristics of study sites in north-central Colorado, USA

Site	Dense conifer	Sparse conifer	Grass	Aspen	Canopy cover (%)	Subcanopy cover (%)	Shrub cover (%)	Ground cover (%)	Upper foliage height (m)
RFUN	0.50	0.31	0.18	0.00	4.8	2.9	1.3	2.6	13.2
RMDE	0.62	0.14	0.16	0.04	3.3	2.8	0.8	1.8	13.1
RMHA	0.26	0.15	0.53	0.06	3.0	2.1	3.2	4.8	13.2
RMWB	0.78	0.09	0.13	0.00	3.2	1.5	2.0	3.8	12.5
MPUN	0.44	0.21	0.28	0.07	4.1	3.1	2.8	4.3	15.1
RMCL	0.08	0.41	0.52	0.00	4.5	2.5	2.5	4.4	18.7
APMD	0.81	0.07	0.05	0.00	3.8	1.7	2.4	4.6	14.6
APLD	0.13	0.15	0.44	0.18	3.2	2.7	1.4	4.7	13.4
MPDE	0.62	0.09	0.03	0.25	4.6	3.7	2.3	3.7	12.6
EPML	0.29	0.21	0.31	0.10	3.5	2.8	2.0	4.5	14.4
ROLL	0.44	0.16	0.30	0.00	4.4	3.1	2.4	4.3	14.5
GRES	0.65	0.12	0.14	0.00	4.1	1.9	1.7	3.3	12.8
NELD	0.62	0.12	0.16	0.00	4.7	2.5	1.8	1.4	9.4
RFDE	0.38	0.18	0.32	0.00	3.6	1.9	2.0	3.7	15.2
APHD	0.12	0.16	0.62	0.00	2.6	1.5	1.9	5.0	12.9
EPCH	0.41	0.20	0.22	0.05	3.9	3.0	2.4	4.9	13.9
NEHD	0.45	0.13	0.25	0.00	3.5	2.5	1.7	3.5	13.4

Land-cover is reported as the mean proportion of sampled area. Percent cover was ranked using the Braun-Blanquet Cover Abundance Scale (Ralph et al., 1993). Refer to Fig. 1 for site locations.

21 to 35 (26.2 ± 0.95) and increased significantly with building density (species richness/ha = $1.74 + 0.62 (\pm 0.24)$ buildings/ha, $R^2 = 0.30$, $P = 0.02$). However, this pattern appeared to be driven by a highly influential observation at the highest building density, as indicated by outlier analysis (Cook's $D = 1.62$). When the observation was excluded, no relationship between building density and species richness was detected ($R^2 = 0.03$, $P = 0.52$). Bird abundance ranged from 6.5 to 9.6 birds/ha (7.6 ± 0.29), and there was a significant, positive relationship between building density and bird abundance (bird abundance/ha = $7.07 + 2.14 (\pm 0.82)$ buildings/ha, $R^2 = 0.31$, $P = 0.02$). Outlier analysis revealed no influential observations.

The first two axes of the PCA explained 47% of the variation in the sampled bird community (Axis 1: 27.6%; Axis 2: 19.4%). Variables loading onto Axis

I included: down wood ($r = -0.82$), snags ($r = -0.79$), stumps ($r = -0.68$), road density ($r = 0.61$), building density ($r = 0.59$), and percent ground cover ($r = 0.51$). Vectors for settlement-related variables and variables related to dead wood point in opposing directions but are approximately the same length, suggesting that both sets of variables are equally important in explaining variation in the bird community (Fig. 3). In addition, the magnitude and direction of these associations suggests that Axis 1 synthesized the response of the bird community to human settlement and can be interpreted as a gradient of development extent. Thus, bird species lying to the right of the origin reached their greatest density as development intensified.

Building density and road density also loaded onto Axis 2 (buildings: $r = 0.54$; roads: $r = 0.47$). Be-

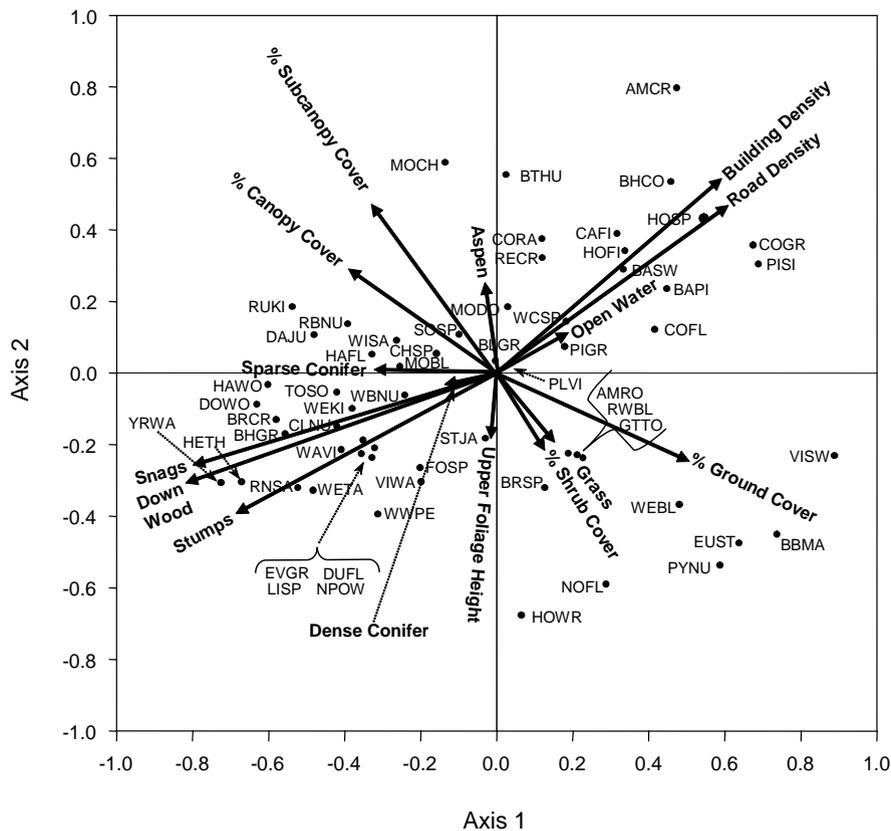


Fig. 3. Ordination diagram of principal components analysis showing the distribution of individual species (see Appendix A for species names) across the development gradient. Positions of the arrows relative to Axes 1 and 2 indicate how strongly independent variables are correlated with each axis, and therefore how related variables are to the pattern of variation in community composition shown in the diagram.

cause each principal component is uncorrelated with previously defined components, however, bird community patterns extracted by Axis 2 are unrelated to those explained by Axis 1. The correlation of building density and road density with both axes suggests that Axis 2 captured additional, unmeasured sources of variation in the bird community that are primarily related to residential development. Most habitat variables, in contrast, did not relate significantly with either of the major PCA axes, suggesting that residential development was the principal factor shaping the bird community.

3.3. Functional group responses

We recorded birds from seven foraging groups, four diet groups, and seven nesting-substrate groups during the study (Appendix A). Because averages were weighted by building density, the greater the weighted average of a functional group, the more prevalent it was in developed areas. Weighted averages of abundance and richness were not significantly different among foraging groups (abundance: $P = 0.12$; richness: $P = 0.13$; Fig. 4a); however, birds foraging in the air or on the ground were more prevalent in developed sites, whereas those that hawked, swooped, or gleaned from the bark were more common in undeveloped sites. In contrast, the weighted averages of groups classified by diet varied significantly (abundance: $P < 0.001$; richness: $P = 0.004$). The abundance and richness of granivores was significantly higher than that of insectivores (Fig. 4b). Weighted averages for density and richness by nesting substrate were also significantly different (abundance: $P = 0.001$; richness: $P = 0.003$), with species that nested on the ground, in snags, or in coniferous or deciduous trees more prevalent in undeveloped sites (Fig. 4c).

3.4. Individual responses

Whole-model tests of species occurrence were significant for 17 species, but goodness-of-fit criteria were met for only 9 species (Table 2). Building density was statistically significant ($P = 0.05$) for only one species, the White-crowned Sparrow, which declined nonlinearly as development density increased. Species whose incidence decreased with building density included the Black-headed Grosbeak, Hammond's

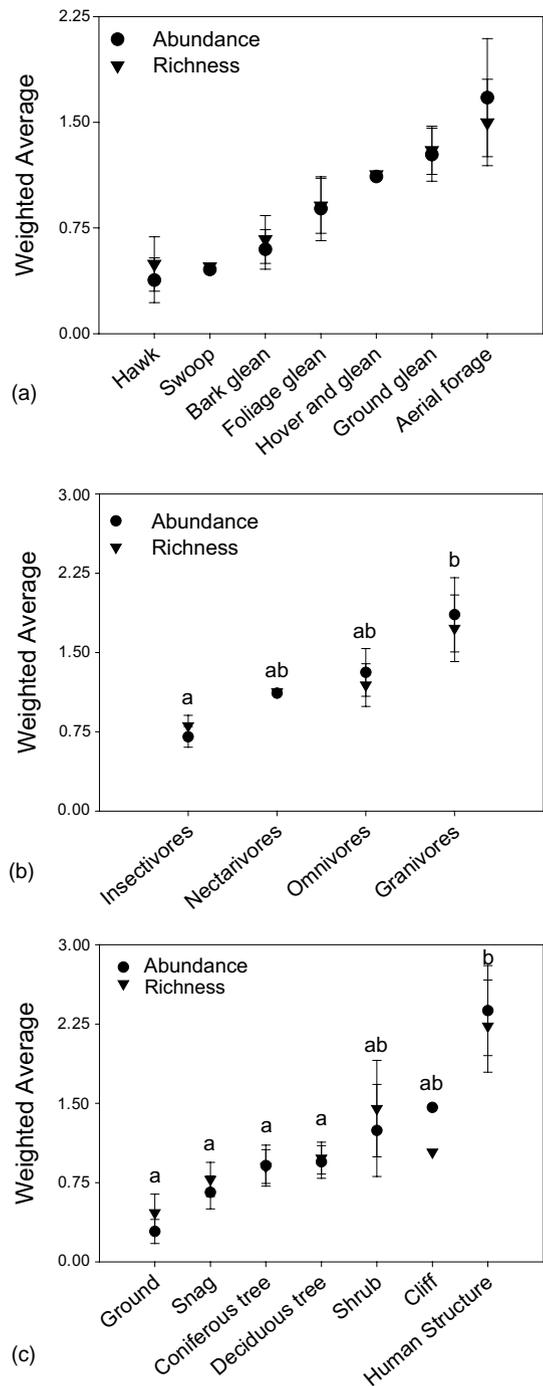


Fig. 4. Mean weighted averages (bars are ± 1 S.E.) of bird abundance and species richness for (a) foraging, (b) diet, and (c) nesting functional groups. Values with different letters are significantly different ($P < 0.05$).

Table 2

Relationship between avian species occurrence and building density in north-central Colorado, USA

Species	χ^2	Building density (\pm S.E.)	Wald statistic	P
Black-headed grosbeak	5.29*	−7.71 (5.26)	2.14	0.14
Brown-headed cowbird	5.13*	5.52 (3.39)	2.66	0.10
Cassin's finch	4.63*	4.24 (2.35)	3.27	0.07
Common grackle	4.07*	4.96 (3.35)	2.19	0.14
Hammond's flycatcher	5.47*	−14.0 (10.2)	1.89	0.16
House sparrow	4.99*	4.75 (2.62)	3.29	0.07
Northern flicker	7.46**	−8.96 (6.63)	1.83	0.17
Warbling vireo	4.55*	−5.53 (3.65)	2.29	0.13
White-crowned sparrow	5.56*	4.86 (2.56)	3.61	0.05

Results are from logistic regression in which species occurrence for combined visits was modeled with building density.

* $P < 0.05$.

** $P < 0.01$.

Flycatcher, Northern Flicker, and Warbling Vireo; whereas the incidence of the Brown-headed Cowbird, Cassin's Finch, Common Grackle, and House Sparrow increased with building density.

4. Discussion

Bird abundance clearly increased as development intensified, and synthetic gradients strongly associated with building and road density explained nearly half of the variation in the bird community. Previous work has demonstrated that changes in the composition of vegetation can alter avian community patterns in urban and suburban areas (Beissinger and Osborne, 1982; Blair, 1996). However, broad-scale vegetation patterns and most ground-level habitat characteristics were not associated with the development gradient in this study, suggesting that other aspects of exurban development influenced the bird community.

The introduction or enhancement of foraging and nesting resources may have partly influenced avian community patterns. Seed and sugar-water feeders and nest boxes were often present in residential areas. Not surprisingly, granivores were most strongly associated with development, and the incidence of two granivores, Cassin's Finch and House Sparrow, was strongly related to building density. Moreover, species that have been documented nesting in human structures (Kingery, 1998) were the dominant nesting group in developed sites. Emlen (1974) found that development favored granivorous and nectivo-

rous birds and crevice nesters in Tucson, AZ and suggested that in native ecosystems where resources are restricted, urbanization might increase species richness and/or avian biomass through resource augmentation. Black-capped Chickadees in Wisconsin, for example, obtained approximately 21% of their daily energy requirements from feeders in urban areas (Brittingham and Temple, 1992). However, Solonen (2001) showed that both Great and Blue Tits have smaller clutches and lower fledgling production in urban areas compared with rural areas, and suggested that poor food quality and reduced availability of food due to high avian density were responsible for these patterns.

Indeed, human settlement at some levels may limit avian productivity by diminishing resources, and increasing nest predation, competition for resources, and brood parasitism (Marzluff et al., 2001). However, we propose that exurban development in this study increased the abundance of some species by promoting environmental heterogeneity and reducing biotic limitations. This interpretation is consistent with the idea that human settlement can act an intermediate disturbance on the landscape (McDonnell et al., 1993; McKinney, 2002), and that habitat heterogeneity can enhance avian diversity (Willson and Comet, 1996). Many of the species that increased in abundance or incidence with building density were habitat generalists, such as House Sparrows, and Common Grackles, which may have capitalized on resource supplements provided by development (Table 2). Nilon et al. (1995) observed a similar increase in the

abundance of these species as well as in the House Finch, European Starling, and American Robin, and also found little evidence that nest predator/parasite species abundance increased in low-density developments located in a forest matrix. Habitat specialists did not appear to benefit from development at this density. The incidence of Hammond's Flycatcher, and the Warbling Vireo, species with narrowly defined habitats, decreased with development (Table 2; Kingery, 1998). Several other studies have documented declines in native forest-interior species with development (Friesen et al., 1995; Nilon et al., 1995; Hansen and Rotella, 2000). Odell and Knight (2001) found that human-sensitive avian species declined within 180 m of homes embedded in a natural shrubland matrix in Colorado exurban settlements.

Snags, down wood, and stumps were the only habitat variables correlated with the major synthetic gradients of the PCA. These variables were also negatively associated with building density, which suggests that loss of dead wood may be one mechanism through which exurban development affects bird communities in western coniferous forests. However, because the amount of dead wood was confounded with building density, this relationship bears further investigation. We did find support for a decline in birds that specialize in using snags or down wood for foraging and nesting as building density increased, but this pattern may also be related to changes in arthropod availability or predator abundance.

This study demonstrates that even at low densities, residential development may influence native bird communities. We propose some hypotheses for the observed patterns, but suggest that caution be used when making inferences about avian community response to exurban development due to our limited sample size and the short-term nature of this study. Specifically, we recommend that these hypotheses be tested in other regions where differences in avian life-history characteristics and habitat and settlement patterns may provide further opportunity to gain new insights. We also stress the need for more intensive, demographic

studies (e.g., reproductive success, survival; Marzluff et al., 2001) to identify causal relationships between residential development and bird community patterns.

Exurban development will likely persist as a popular form of settlement, especially in the Rocky Mountain region, as people search for a more scenic and secluded living environment (Romme, 1997). Educating residents of mountain communities about the impacts of development and encouraging them to change their behavior by leaving dead wood undisturbed and limiting food and nesting supplements, may be the most promising option for managing these areas so that they remain suitable for native bird species. In addition, a regional strategy for protecting suitable habitat that integrates across levels of government, including lands under county, state and federal jurisdiction, may help to secure the persistence of native species in light of growing exurban development. This approach may involve restricting the extent of exurban development, as recommended by Theobald et al. (1997) and supported by Odell and Knight (2001), or designating core areas protected from development. On a smaller scale and under different development conditions, other strategies may be sufficient (Fernandez-Juricic and Jokimaki, 2001). Regardless, the successful strategy must transcend political boundaries and consider the broader landscape context of settlement for determining how bird communities might respond to development.

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Appendix A

Names of all bird species (A.O.U., 1983) observed, with four-letter codes used in Fig. 4 and foraging, diet, and nesting groups used in functional group analyses. See Salt (1953) and Ehrlich et al. (1988) for a detailed description of foraging groups, Peterjohn and Sauer (1993) for more information about nesting groups, and Kingery (1998) for documentation of preferences.

Common name	Scientific name	Code	Foraging group	Diet group	Nesting group
American Crow	<i>Corvus brachyrhynchos</i>	AMCR	Ground gleaning	Omnivore	Deciduous tree
American Robin	<i>Turdus migratorius</i>	AMRO	Ground gleaning	Insectivore	Deciduous tree
Band-tailed Pigeon	<i>Columba fasciata</i>	BAPI	Foliage gleaning	Granivore	Coniferous tree
Barn Swallow	<i>Hirundo rustica</i>	BASW	Aerial foraging	Insectivore	Human structure
Black-billed Magpie	<i>Pica pica</i>	BBMA	Ground gleaning	Omnivore	Deciduous tree
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	Ground gleaning	Insectivore	Deciduous tree
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	BHGR	Foliage gleaning	Insectivore	Deciduous tree
Blue Grosbeak	<i>Guiraca caerulea</i>	BLGR	Ground gleaning	Insectivore	Shrub
Brown Creeper	<i>Certhia americana</i>	BRCR	Bark gleaning	Insectivore	Coniferous tree
Brewer's Sparrow	<i>Spizella breweri</i>	BRSP	Ground gleaning	Insectivore	Shrub
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	BTHU	Hover and glean	Nectarivores	Deciduous tree
Cassin's Finch	<i>Carpodacus cassinii</i>	CAFI	Ground gleaning	Granivore	Coniferous tree
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	Ground gleaning	Insectivore	Coniferous tree
Clark's Nutcracker	<i>Nucifraga columbiana</i>	CLNU	Foliage gleaning	Omnivore	Coniferous tree
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	COFL	Hawks	Insectivore	Deciduous tree
Common Grackle	<i>Quiscalus quiscula</i>	COGR	Ground gleaning	Omnivore	Deciduous tree
Common Raven	<i>Corvus corax</i>	CORA	Ground gleaning	Omnivore	Cliff
Dark-eyed Junco	<i>Junco hyemalis</i>	DAJU	Ground gleaning	Granivore	Ground
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	Bark gleaning	Insectivore	Snags
Dusky Flycatcher	<i>Empidonax oberholseri</i>	DUFL	Hawks	Insectivore	Shrub
European Starling	<i>Sturnus vulgaris</i>	EUST	Ground gleaning	Insectivore	Human structure
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	EVGR	Ground gleaning	Granivore	Coniferous tree
Fox Sparrow	<i>Passerella iliaca</i>	FOSP	Ground gleaning	Insectivore	Ground
Green-tailed Towhee	<i>Pipilo chlorurus</i>	GTTO	Ground gleaning	Insectivore	Shrub
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	Bark gleaning	Insectivore	Deciduous tree
Hammond's Flycatcher	<i>Empidonax hammondii</i>	HAFL	Hawks	Insectivore	Coniferous tree
Hermit Thrush	<i>Catharus guttatus</i>	HETH	Ground gleaning	Insectivore	Ground
House Finch	<i>Carpodacus mexicanus</i>	HOFI	Ground gleaning	Granivore	Human structure
House Sparrow	<i>Passer domesticus</i>	HOSP	Ground gleaning	Granivore	Human structure
House Wren	<i>Troglodytes aedon</i>	HOWR	Ground gleaning	Insectivore	Deciduous tree
Lincoln's Sparrow	<i>Melospiza lincolni</i>	LISP	Ground gleaning	Insectivore	Ground
Mountain Bluebird	<i>Sialia currucoides</i>	MOBL	Swoops	Insectivore	Snags
Mountain Chickadee	<i>Poecile gambeli</i>	MOCH	Foliage gleaning	Insectivore	Coniferous tree
Mourning Dove	<i>Zenaidura macroura</i>	MODO	Ground gleaning	Granivore	Deciduous tree
Northern Flicker	<i>Colaptes auratus</i>	NOFL	Ground gleaning	Insectivore	Snags
Northern Pygmy Owl	<i>Glaucidium gnoma</i>	NPOW	Foliage gleaning	Granivore	Coniferous tree
Pine Grosbeak	<i>Pinicola enucleator</i>	PIGR	Foliage gleaning	Granivore	Coniferous tree
Pine Siskin	<i>Carduelis pinus</i>	PISI	Foliage gleaning	Granivore	Coniferous tree

Appendix A (Continued)

Common name	Scientific name	Code	Foraging group	Diet group	Nesting group
Plumbeous Vireo	<i>Vireo plumbeus</i>	PLVI	Foliage gleaning	Insectivore	Coniferous tree
Pygmy Nuthatch	<i>Sitta pygmaea</i>	PYNU	Bark gleaning	Insectivore	Coniferous tree
Red Crossbill	<i>Loxia curvirostra</i>	RECR	Foliage gleaning	Granivore	Coniferous tree
Red-breasted Huthatch	<i>Sitta canadensis</i>	RBNU	Bark gleaning	Insectivore	Coniferous tree
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	RNSA	Bark gleaning	Insectivore	Deciduous tree
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	Ground gleaning	Insectivore	Deciduous tree
Ruby-crowned Kinglet	<i>Regulus calendula</i>	RUKI	Foliage gleaning	Insectivore	Coniferous tree
Song Sparrow	<i>Melospiza melodia</i>	SOSP	Ground gleaning	Insectivore	Ground
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA	Ground gleaning	Omnivore	Coniferous tree
Townsend's Solitaire	<i>Myadestes townsendi</i>	TOSO	Hawks	Insectivore	Ground
Violet-green Swallow	<i>Tachycineta thalassina</i>	VISW	Aerial foraging	Insectivore	Snags
Virginia's Warbler	<i>Vermivora virginiae</i>	VIWA	Ground gleaning	Insectivore	Ground
Warbling Vireo	<i>Vireo gilvus</i>	WAVI	Foliage gleaning	Insectivore	Deciduous tree
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	Bark gleaning	Insectivore	Deciduous tree
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	WCSP	Ground gleaning	Insectivore	Shrub
Western Kingbird	<i>Tyrannus verticalis</i>	WEKI	Hawks	Insectivore	Deciduous tree
Western Tanager	<i>Piranga ludoviciana</i>	WETA	Foliage gleaning	Insectivore	Coniferous tree
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	WISA	Bark gleaning	Insectivore	Deciduous tree
Western Wood-Pewee	<i>Contopus sordidulus</i>	WWPE	Hawks	Insectivore	Coniferous tree
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA	Foliage gleaning	Insectivore	Coniferous tree

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