

THE EFFECT OF EXURBAN DEVELOPMENT ON WINTERING BIRDS IN COLORADO

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ABSTRACT.—Large-scale land-use change driven by residential development has degraded native ecosystems and altered the composition of species communities. Concern over the loss of habitat for human-sensitive species has led to questions about how housing impacts bird communities along the urban to rural gradient. Yet most studies of birds in residential ecosystems are limited to the breeding season, thus the effects of housing on avian habitat use in winter are not well understood. We surveyed winter resident birds, vegetation cover and structure, and human activity along a housing gradient in a Colorado landscape undergoing exurban development. Using an occupancy-based approach, we evaluated models for species with sufficient detections ($n = 8$). We found that habitat use by six species [American Robin (*Turdus migratorius*), Black-billed Magpie (*Pica hudsonia*), Dark-eyed Junco (*Junco hyemalis*), Downy Woodpecker (*Picoides pubescens*), Pygmy Nuthatch (*Sitta pygmaea*), Townsend's Solitaire (*Myadestes townsendi*)] was positively associated with housing density at scales ranging from 100–1,000 m. In contrast, habitat use by two species [Mountain Chickadee (*Poecile gambeli*) and Steller's Jay (*Cyanocitta stelleri*)] was negatively associated with housing proximity, and human activity had no effect on habitat use for any species. Canopy cover or understory vegetation cover and structure were important covariates for predicting habitat use of all species modeled. Our results suggest that to maximize the value of residential areas for a diverse wintering bird community, areas with natural vegetation should be incorporated into development planning. Overall, we found that the resident winter birds evaluated in our study were resilient to development in exurban areas. Indeed, these species may be opportunistic in occupying residential habitats that allow them to exploit anthropogenic resources during an energetically expensive time of year. Received 24 November 2015. Accepted 23 May 2016.

Key words: exurban sprawl, habitat use, housing density, human activity, occupancy, residential development, resident birds.

Urbanization is a major driver of land-use change (Brown et al. 2005, Foley et al. 2005, Theobald 2005) and results in widespread habitat loss, while also decreasing global biodiversity and increasing local densities of human-adapted species (Crooks et al. 2004, Suarez-Rubio et al. 2011, Groffman et al. 2014). Although it is predicted that by the year 2030 approximately two thirds (66%) of the world's population will live in urban centers (United Nations 2015), high-density urban areas cover only about 1.9% of terrestrial environments. In contrast, exurban development (low-density development outside cities and towns) occupies nearly 15 times more land and often occurs at the wildland-urban interface (Marzluff and Ewing 2001, Fraterrigo and Wiens 2005, Hansen et al. 2005). Despite recent calls for research, the impacts of exurban development on species assemblages and ecosystem functions remain relatively unknown (Merenlender et al. 2009,

Gavier-Pizarro et al. 2010, Pidgeon et al. 2014, Pejchar et al. 2015).

Colorado's Front Range, at the foot of the Rocky Mountains, has experienced some of the fastest human population growth in the nation (Mitchell et al. 2002). Population growth rates were nearly 2.5 times the national average in the 1990's (Odell and Knight 2001), and the population increased at a rate of 8.75% from 2010–2015 (U. S. Census Bureau 2016). The housing development associated with, and potentially also independent of this population growth (Pendall 2003) occurred primarily on former ranch and farm lands (Knight 1999) in areas adjacent to protected public land (Odell and Knight 2001). It is likely that exurban development will continue in Colorado as the population continues to increase (U. S. Census Bureau 2016) and individuals seek out secluded and scenic living environments and vacation homes (Romme 1997).

The density of houses, the spatial configuration of houses in a development, and the proximity of houses to natural open space all have the potential to impact native plant and animal communities (Pejchar et al. 2015). Housing density in exurban areas is usually much lower than in urban areas

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(Knight 1999). This low density housing, also called exurban sprawl (Clark et al. 2009), is often associated with an expansion of roads and other infrastructure. Roads, which contribute to habitat fragmentation, have well-known impacts to wildlife populations (Trombulak and Frissell 2000). However, the ability of animals to occupy and move through landscapes with different patterns and densities of housing development is not well understood.

Birds are appropriate taxa for understanding how housing density and the human activities associated with exurban development impacts natural communities. Birds are relatively easy to observe and bird communities are considered good indicators of ecological change (Hollamby et al. 2006, Lepczyk et al. 2008). Numerous studies suggest that avian species richness generally peaks at intermediate degrees of urbanization along a gradient of rural open space to urban centers, and, that as housing density increases, a few generalist species replace many specialists (Blair 1996; Jokimäki et al. 1996, 2002; Jokimäki and Suhonen 1998; Crooks et al. 2004; Zuckerberg et al. 2011).

Nearly all previous studies on birds in exurban environments have focused on sampling avian populations exclusively during the breeding season (but see Jokimäki et al. 1996, Jokimäki and Suhonen 1998, Bock et al. 2008). Understanding how bird populations respond to exurban development during the non-breeding winter season is important because harsh conditions in temperate and northern regions (e.g., low temperatures, limited food resources) during this time of the year may play an important role in population regulation (Jokimäki et al. 2002, Manley et al. 2009).

The objective of this study was to assess habitat use of wintering birds along an exurban development gradient in northern Colorado. Specifically, we used point counts, vegetation surveys, and three measures of human development (housing density, proximity to homes, and human activity) to evaluate how resident birds respond to residential development and habitat variables in an exurban landscape. We expected that avian response to housing development and human activity would vary among species depending on their ability to adapt to human development. For example, some wintering birds may be drawn to houses to exploit anthropogenic resources, but

forest-dependent species (i.e., Steller's Jay [*Cyanocitta stelleri*]) may avoid houses, which are often associated with open or fragmented habitat (Merenlender et al. 2009). We also expected that the degree and direction of response to vegetation covariates would vary among species. For example, shrub foraging birds may respond positively to understory vegetation; whereas birds that forage in open habitat would be negatively associated with areas of high canopy cover (Lumpkin et al. 2012). We draw on our results to make recommendations for land use planning and stewardship that are compatible with the conservation of winter bird communities.

METHODS

Study Area

Our study area was located within the North Fork of the Cache la Poudre River watershed in Larimer County approximately 40 km northwest of Fort Collins, Colorado, USA. This watershed has been subject to recent and rapid expansion of relatively low density development bordered by protected public lands and undeveloped private lands (Knight 1999). Within this region, which is bounded by the Wyoming state border to the north and the Cache la Poudre River to the south, we restricted our study area by elevation (1,700 m to 2,400 m) to minimize variation in vegetation and soil type (Fig. 1). This area is characterized by ponderosa pine woodlands (*Pinus ponderosa*) and Rocky Mountain lower mountain-foothill shrubland. Dominant shrubs include mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentata*), and wax currant (*Ribes cereum*). Soils throughout the study area are similar mixtures of Rocky Loam, Stony Loam, and Loamy Foothill Range sites (Moreland 1980).

Study Design

We surveyed birds at sites selected by stratified random sampling along a housing gradient, which was based on digitized satellite imagery of houses and other spatial data in ArcGIS 10 and National Agricultural Imagery Program (USDA Farm Service Agency, Aerial Photography Field Office, Salt Lake City, UT, USA) at a scale of 1:4,000. The housing gradient was developed by incorporating housing density as a resistance layer to least-

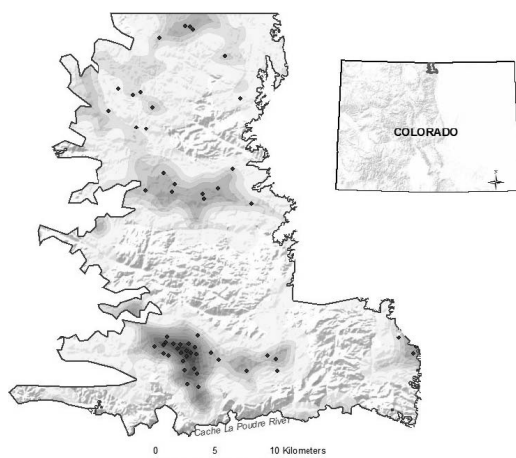


FIG. 1. Study area in northern Colorado, U.S. The study area is constrained to the south by the Cache La Poudre River and to the north by the Wyoming border. Sample sites (diamonds) were selected using a stratified random design along the exurban development gradient (grey scale). Darker shades represent more developed areas. Figure adapted from Goad et al. 2014.

cost distance analysis, which represents the mean cumulative cost, in terms of exposure to housing, of travel from any point to the boundaries of the study area (see Goad et al. 2014 for additional details). Remote undeveloped areas were excluded from sampling because the study was designed to understand where along the development gradient the effects of development become evident, rather than specifically comparing undeveloped to developed areas. Thus, the development gradient represents a range from very low (0.32 houses per km^2) to relatively high-density (50.93 houses per km^2) exurban development, as a continuous variable (Goad et al. 2014).

Stratified random sampling was used to select study sites within the development gradient. Because this study occurred during the winter when birds vocalize less frequently and activity is limited, we designed our sampling scheme to account for low detection probabilities (Mattsson and Marshall 2009). Prior to data collection, we simulated several different study designs using program GENPRES (Bailey et al. 2007) to determine adequate numbers of sites and surveys needed to detect probable differences in species occurrence (or use) across our development gradient. Fifty-three sites were ultimately included in the study; site selection was a function of

successful requests for permission to access properties and an effort to represent the gradient as evenly as possible. Adopting this design for our study on wintering bird communities was appropriate because all sampling sites can be considered independent, at least 500 m apart (range: 500–3,819 m), and the total study area was sufficiently large (66,000 ha) to allow for multi-species inference at a landscape scale (Adriaensen et al. 2003, Beier et al. 2009).

Bird Surveys

We sampled birds from December 2012–March 2013 between 0700 and 1500 MST. At each of the 53 sites along the exurban development gradient we conducted 5-min point counts with a fixed 100 m radius. Each site was surveyed by a single observer (AEM) on two to six occasions, and the mean number of sampling occasions per site was four ($\text{SE} \pm 0.20$). The number of sampling occasions per site varied due to logistical constraints (e.g., sampling days with suitable weather conditions) and this variation was independent of housing density. During each occasion we recorded all birds that were detected by sight or sound within the point count radius. All individuals were identified to the species level and the distance to and time of first detection was recorded (Mattsson and Marshall 2009). We collected information on time of day, temperature, wind speed (ranked on a scale from 0–5), and percent cloud cover at each site on each sampling occasion (Table 1). In some cases, point counts at a single site were repeated after a 5 min recess period to maximize opportunities to detect birds at sites that were arduous to access in winter weather conditions. In these cases, we allowed the detection probability to be different between the first and second surveys conducted during the same site visit (“survey effect”).

Metrics of Human Development

To investigate how residential development affects bird habitat use, we incorporated a number of site-level covariates in our analysis. These covariates included housing density and proximity, and anthropogenic sound as an index of human activity. First, using ArcGIS 10 (ESRI, Redlands, CA, USA) we measured housing density (# of houses/ha) around each site at radii of 100 m, 500 m, 1,000 m, and 1,500 m (Table 1). Second, we

TABLE 1. A list of the site and survey level covariates used in our occupancy analysis, the associated metrics and notations used in our model set, and, if applicable, references to previous studies that used similar covariates in an exurban development context. Site level covariates are variables used to model variation in occupancy (Ψ), while survey level covariates are used to model potential variation in detection probability (p).

Covariate type	Covariate name	Measurement	Covariate notation	Citation
<i>Site level</i>				
Human Development	Housing Density	100 m, 500 m, 1,000 m, and 1,500 m radius	hd100, hd500, hd1000, hd1500	(Miller et al. 2003)
	Proximity to Houses	Mean distance to nearest 5 and 10 houses	dist5, dist10	(Miller et al. 2003)
	Human Activity	Mean duration of non-natural noise during three 15 min sound surveys	HA	(Whittaker and Knight 1998)
Vegetation	Percent Canopy Cover	25 m radius	canopy cover	(Fletcher and Hutto 2008)
	Understory Vegetation Height	25 m radius	understory average height	(Fletcher and Hutto 2008)
	Understory Vegetation Percent Cover	25 m radius	understory cover	(Fletcher and Hutto 2008)
<i>Survey level</i>				
	Time	Time of day survey conducted	time	
	Wind	Categorical scale 0–5 (0: 0–2 mph; 1: 3–5 mph; 2: 6–10 mph; 3: 11–15 mph; 4: 16–20 mph; 5: 20+ mph)	wind	
	Temperature	Estimate from daily high	temp	
	Cloud Cover	Percent of sky covered by clouds	cloud	
	Survey effect	see methods	survey	

measured the mean distance from each bird sampling site to the nearest 5 and 10 houses. We chose these variables based on previous work conducted in northern Colorado, which showed that birds often respond to human development at different scales (Miller et al. 2003). While investigating how species use habitat at different spatial scales was not a primary objective of this study, we included these covariates in our model building process to accommodate species-specific variation in responses to housing variables, and to obtain unbiased estimates of our parameters. Finally, we used sound surveys as a proxy for local human activity. These data were collected using a handheld PDA provided by the National Park Service's Sound and Night Skies division (Goad et al. 2014). Sound surveys were conducted immediately following each bird survey and lasted for 15 min, during which the presence and duration of both natural and non-natural sounds

was recorded. From these data, we calculated the mean percent of time that non-natural noise was heard during surveys at each site.

Vegetation Characteristics

We measured vegetation cover and height at each site to assess habitat quality. We used ocular methods to estimate the percent canopy cover of trees, and the percent cover of understory vegetation (defined as shrub, grass, and forb cover) within 25 m radius of each site. We also measured the average height of understory vegetation within the same area (Table 1). We selected 25 m as the scale for measuring vegetation characteristics at each site because previous studies have shown that local environmental variables often explain as much or more variation in avian occurrence as do broader scale landscape variables (Fletcher and Hutto 2008).

Statistical Analysis

We used single season occupancy models to evaluate factors influencing the probability that a site is occupied, or used, by a target species (ψ) and the probability of detecting the species at occupied sites (p) (MacKenzie et al. 2006). Occupancy probabilities can be modeled as a function of site-specific covariates, while detection probabilities may be a function of either site- or survey-specific covariates. We developed a set of *a priori* models and expectations relating to model parameters, namely occupancy and detection probability, to our specified covariates (Table 1). Each model set was fit to species-specific detection history data; these data consisted of a record of the detection (1) or non-detection (0) of each species during each survey to a site. Correlations between possible predictor variables were calculated prior to our analysis to assess collinearity. Any covariates that exhibited correlation coefficients greater than a value of 0.50 were considered collinear, and only one of the two correlated predictor variables was retained in the model set (Elbroch and Wittmer 2012).

Estimates of human development (Table 1) had correlation coefficients ranging from $|r| = 0.47$ – 0.63 . Since these correlation coefficients spanned or exceeded our threshold of 0.50, we did not feel that it was appropriate to simply choose a single variable and move forward with the analysis. Therefore, we used the following model building process to eliminate these human development variables prior to the final analysis such that only one human development covariate was retained in our final model set for each species. We used a stepwise process to build and fit a set of candidate global models to each of our species-specific data sets. Preliminary analyses suggest that these data sets could each support a global model with up to eight total parameters. To determine the most influential human development covariate and fit an appropriate global model for each species we developed 14 possible global models for each species. Each global model consisted of one human development covariate, canopy cover, and one understory vegetation covariates for occupancy (Ψ [development + canopy cover + understory veg_covariate]), and three detection covariates that we expected would account for any temporal or spatial variation in detection probability based on field knowledge (p [time + canopy cover + survey

effect]). For each species, the model structure that fit best (i.e., had the lowest AICc) was retained as the global model and the associated human development covariate was used in all subsequent models.

After a global model structure was determined for each species, we followed a sequential model selection process to identify covariates that influence species detection and occupancy probabilities. Using the selected global occupancy structure for each species, we fit models where detection probability varied by our survey-specific covariates, canopy cover, or remained constant ($p[.]$) (e.g., Doherty et al. 2012). Finally, using the best supported detection probability structures (those with $\Delta AICc$ or $\Delta QAICc < 2.0$), we explored factors influencing species occupancy or use. Specifically, we considered occupancy structures with all possible combinations of the three covariates included in the global occupancy structure and a structure where occupancy remained constant across sites ($\Psi[.]$).

We fit all models to species with sufficient detections for model convergence using the R package *unmarked* (Fiske and Chandler 2011, R Core Team 2015). We used an information-theoretic approach to model selection, utilizing Akaike's Information Criterion, adjusted for small sample size (AICc) using the package *AICcmodavg* (Burnham and Anderson 2002, Mazerolle 2006). We used a bootstrap goodness-of-fit test to assess model fit and estimate overdispersion (c ; MacKenzie and Bailey 2004) for each species' data set. A total of 10,000 bootstraps were run using the global model for each data set, and if necessary, model selection criteria were adjusted for overdispersion (via QAICc). We report the occupancy and detection probability estimates for each species using the top ranked model for each dataset (Appendix 1). Because we were ultimately interested in the relationship between occupancy and various human development and vegetation covariates at the site level, we reported the effect size (i.e., the beta estimate), and associated unconditional standard error, using the top ranked model for each dataset.

RESULTS

We detected 20 wintering bird species in our study area (Appendix 2). Eight of these species

were detected with enough frequency to warrant inclusion in the occupancy analysis (Appendix 1). In all cases several top models held relatively equal weight. Therefore, we report all models with $\Delta AICc$ or $\Delta QAICc < 2.0$.

A human development or vegetation covariate was retained in the top model (the model with the lowest $AICc$ or $QAICc$ values) for American Robin (*Turdus migratorius*), Black-billed Magpie (*Pica hudsonia*), and Pygmy Nuthatch (*Sitta pygmaea*) (Table 2). The constant occupancy structure ($\Psi[\cdot]$) was included in the top model for Dark-eyed Junco (*Junco hyemalis*), Downy Woodpecker (*Picoides pubescens*), Mountain Chickadee (*Poecile gambeli*), Townsend's Solitaire (*Myadestes townsendi*), and Steller's Jay (Table 2). However, some metric of human development and/or vegetation was retained in supported occupancy structures for all species ($\Delta AICc$ or $\Delta QAICc < 2.0$), indicating that human development and/or vegetation were consistently associated with habitat use (Table 2). We used beta estimates to further investigate the relationship between bird habitat use, our metrics of human development and vegetation characteristics at each site. Habitat use of all modeled species were positively correlated with either higher housing density or closer proximity to houses (Table 3).

Housing density covariates were the most influential metrics of human development for American Robin, Dark-eyed Junco, Townsend's Solitaire, Black-billed Magpie, Downy Woodpecker and Pygmy Nuthatch (Table 2). For the American Robin, Dark-eyed Junco, and Townsend Solitaire housing density measured at a 100 m radius was the most influential human development covariate (Table 2). Housing density at 500 m was the top human development covariate for Black-billed Magpie, and housing density at 1,000 m was the top human development covariate for Downy Woodpecker and Pygmy Nuthatch. The mean distance to the five nearest houses was the top human development covariate for the Mountain Chickadee, and the mean distance to the 10 nearest houses was most influential human development covariate for the Steller's Jay (Table 2). The human activity metric was not included in the top models for any bird species.

All three vegetation covariates (canopy cover, understory cover and understory height) were represented in the top models for American Robin,

Black-billed Magpie, Downy Woodpecker, and Townsend's Solitaire. Understory height and canopy cover were both represented in the top model sets for Mountain Chickadee. Understory height was the only vegetation covariate in the top model sets for Dark-eyed Junco and Pygmy Nuthatch; and canopy cover was the only vegetation covariate represented in the top models for Steller's Jay.

Although vegetation covariates were retained in the top models for all species, the direction of the effect varied (Table 3). Habitat use was positively correlated with percent canopy cover for the Black-billed Magpie, Mountain Chickadee, Townsend Solitaire, and the Steller's Jay. The Downy Woodpecker and American Robin were negatively associated with percent canopy cover. Habitat use was positively correlated with percent cover of understory vegetation for the Black-billed Magpie, Downy Woodpecker and Mountain Chickadee. The American Robin and Townsend's Solitaire were negatively associated with the percent cover of understory vegetation (Table 3). As the average height of understory vegetation increased so did habitat use by American Robin, Dark-eyed Junco, Downy Woodpecker, Pygmy Nuthatch and Townsend's Solitaire. The Black-billed Magpie showed a decrease in habitat use at sites with higher average understory height (Table 3).

DISCUSSION

Our results demonstrate that housing density and proximity, as well as vegetation cover and height, were important predictors of habitat use for wintering birds in our region. Exurban housing density was positively associated with habitat use for six of the eight wintering bird species modeled in this study, and proximity to homes was positively associated with use for the remaining two species. Interestingly, these results are in contrast to a number of studies that have highlighted the negative impacts of exurban development on breeding birds (Miller et al. 2003, Merenlender et al. 2009, Schlossberg et al. 2011, Suarez-Rubio et al. 2011, Lumpkin et al. 2012, Glennon and Kretser 2013, Lumpkin and Pearson 2013; but see Fraterrigo and Wiens 2005).

The discrepancy between our results and previous studies could be explained by important

seasonal differences in the factors affecting survival and reproduction. During the breeding season, habitat use may be impacted by species-specific factors such as brood parasitism (Schlossberg et al. 2011) and nest predation (Lumpkin et al. 2012), both of which are generally more prevalent in areas of higher density development. Other studies have also demonstrated that resident birds are often less sensitive to human impact than long-distance migrants (Miller et al. 2003, Glennon and Kretser 2013, Lumpkin and Pearson 2013).

Resource subsidies associated with increased housing density may also explain the patterns we observed. These resources may be particularly important for birds during seasons or in ecosystems where natural sources of food and water are scarce. Exurban development can increase habitat heterogeneity and food resources, thus decreasing intra and inter-specific competition (Fraterrigo and Wiens 2005) and positively impacting certain avian species (McDonnell and Pickett 1990, McKinney 2002). For example, the granivorous Dark-eyed Junco may benefit from residential development where bird feeders and ornamental seed-bearing plants are readily available (Emlen 1974, Fraterrigo and Wiens 2005, Glennon and Kretser 2013). Similarly, ornamental plants around homes supply important winter fruit for species such as American Robins (Lepczyk et al. 2000), which forage opportunistically on both native and introduced fleshy-fruited plants (LaFleur et al. 2007).

Previous studies have also shown that generalists (i.e., Black-billed Magpie and Steller's Jay) may benefit from residential development because of an increase in the variety and availability of food sources, including refuse (Odell and Knight 2001, Miller et al. 2003, Schlossberg et al. 2011, Suarez-Rubio et al. 2011, Glennon and Kretser 2013). In the southwestern U.S., where water is a strong limiting factor due to the arid climate, avian abundance and richness increased in exurban development areas due to supplemental water features and irrigation (Bock et al. 2008). Thus, seasonality coupled with the opportunity for additional food resources in residential areas (Bock et al. 2008) could explain the neutral to slightly positive effect of exurban housing density on the distribution of wintering birds in our study (Jokimäki and Suhonen 1998).

Interestingly, habitat use of most species in our study was most strongly associated with housing densities at either a 100 or 500 m radius, whereas prior studies in similar ecosystems found that housing densities at 1,000 m (Fletcher and Hutto 2008) or 1,500 m (Miller et al. 2003) were the most important predictors of species distribution. One possible explanation for this difference could be that in the winter birds are more sensitive to changes in housing density at local scales in order to take advantage of supplemental feeding opportunities. These include birdfeeders, which have been spatially correlated with habitat use (Wilson 1994) and reproductive success in the following breeding season (Robb et al. 2008). For example, feeders may at least partially explain the positive relationship between Mountain Chickadee and Steller's Jay and housing proximity; these species regularly access this important source of energy during winter months (Bekoff et al. 1999, Carrascal et al. 2012).

Surprisingly, human activity did not explain variation in habitat use by any wintering bird in this study. This may be because some human activities such as non-motorized recreation are not detectable by sound. Alternatively birds in developed areas may adapt to rather than avoid anthropogenic sound (Nemeth et al. 2013). Nonetheless our findings indicate that the density and proximity of housing may be more important than audible anthropogenic disturbance for wintering songbirds.

For all species, some metric of vegetation (i.e., understory cover/height or canopy cover) appeared in the top models. Habitat use was associated with understory vegetation cover or height for all species, except Steller's Jay, which responded positively only to canopy cover. The Townsend's Solitaire, a known ground nester, showed a decrease in occurrence at sites where understory cover increased. Previous studies have suggested that ground nesting birds were particularly susceptible to the negative impacts of exurban development because understory vegetation is often depleted in areas of high human development, resulting in a greater risk of nest predation (Odell and Knight 2001, Hansen et al. 2005, Merenlender et al. 2009, Lumpkin et al. 2012). Our findings suggest that the Townsend's Solitaire may use habitat differently between the non-breeding season and the breeding season in our

TABLE 2. Model selection results for the best supported models on habitat use (Ψ) and detection probability (p) (ΔAIC_c or $\Delta QAIC_c < 2.0$) for each of the eight species. Δ_i is the difference in AIC_c or $QAIC_c$ for a particular model when compared with the top model, w_i is the model weight, K is the number of parameters, and $-\log \hat{\epsilon}$ is $-2 \times$ the log likelihood of the model. For species with evidence of overdispersion, we also give the estimate of the variance inflation factor (\hat{c}). $\Psi(\cdot)$ and $p(\cdot)$ represent the constant (null) structure on habitat use and detection probability, respectively.

Species	Δ_i	w_i	K	$-2 \log (\hat{\epsilon})$
American Robin				
$\Psi(\text{hd100}) p(\cdot)$	0.00	0.06	3	-41.26
$\Psi(\text{understory average height} + \text{understory cover}) p(\cdot)$	0.08	0.06	4	-40.12
$\Psi(\text{understory average height} + \text{understory cover}) p(\text{time})$	0.43	0.05	5	-39.08
$\Psi(\text{hd100} + \text{understory cover}) p(\text{wind})$	0.54	0.05	5	-39.14
$\Psi(\text{hd100}) p(\text{wind})$	0.57	0.05	4	-40.37
$\Psi(\cdot) p(\cdot)$	0.61	0.05	2	-42.69
$\Psi(\text{hd100} + \text{understory cover} + \text{canopy cover}) p(\cdot)$	0.72	0.04	5	-39.23
$\Psi(\cdot) p(\text{wind})$	0.88	0.04	3	-41.70
$\Psi(\text{hd100} + \text{average understory height} + \text{understory cover}) p(\cdot)$	1.32	0.03	5	-39.52
$\Psi(\cdot) p(\text{time})$	1.38	0.03	3	-41.95
$\Psi(\text{hd100}) p(\text{time})$	1.40	0.03	4	-40.79
$\Psi(\text{average understory height} + \text{understory cover}) p(\text{wind})$	1.40	0.03	5	-39.56
$\Psi(\text{understory cover}) p(\cdot)$	1.51	0.03	3	-42.01
$\Psi(\text{hd100} + \text{understory cover} + \text{canopy cover}) p(\text{time})$	1.53	0.03	6	-38.36
$\Psi(\text{average understory height} + \text{canopy cover}) p(\text{wind})$	1.58	0.03	5	-39.65
Black-billed Magpie				
$\hat{c} = 1.14$ $\Psi(\text{canopy cover}) p(\text{wind})$	0.00	0.16	5	-95.89
$\Psi(\cdot) p(\text{wind})$	0.04	0.16	4	-97.13
$\Psi(\text{hd500} + \text{canopy cover}) p(\text{wind})$	0.24	0.14	6	-94.74
$\Psi(\text{hd500}) p(\text{wind})$	1.41	0.08	5	-96.60
$\Psi(\text{understory cover}) p(\text{wind})$	1.56	0.07	5	-96.67
$\Psi(\text{understory average height} + \text{canopy cover}) p(\text{wind})$	1.74	0.07	6	-95.49
$\Psi(\text{hd500} + \text{understory average height} + \text{canopy cover}) p(\text{wind})$	1.91	0.06	7	-94.24
Dark-eyed Junco				
$\hat{c} = 1.81$ $\Psi(\cdot) p(\cdot)$	0.00	0.08	3	-29.25
$\Psi(\text{understory average height}) p(\cdot)$	0.00	0.08	4	-28.08
$\Psi(\text{hd100}) p(\cdot)$	0.77	0.05	4	-28.46
$\Psi(\cdot) p(\text{cloud})$	0.91	0.05	4	-28.53
$\Psi(\text{hd100} + \text{understory average height}) p(\cdot)$	1.35	0.04	5	-27.53
$\Psi(\text{understory average height}) p(\text{cloud})$	1.39	0.04	5	-27.55
$\Psi(\cdot) p(\text{wind})$	1.75	0.03	4	-28.95
$\Psi(\text{understory average height}) p(\text{wind})$	1.83	0.03	5	-27.77
$\Psi(\cdot) p(\text{survey})$	1.94	0.03	4	-29.05
$\Psi(\text{hd100}) p(\text{cloud})$	1.98	0.03	5	-27.85
Downy Woodpecker				
$\Psi(\cdot) p(\text{cover})$	0.00	0.25	3	-35.32
$\Psi(\text{understory cover}) p(\text{cover})$	1.10	0.14	4	-34.70
$\Psi(\text{understory average height}) p(\text{cover})$	1.41	0.12	4	-34.85
$\Psi(\text{hd1000} + \text{understory cover} + \text{canopy cover}) p(\text{cover})$	1.76	0.10	6	-32.53
Mountain Chickadee				
$\Psi(\cdot) p(\text{temp})$	0.00	0.12	3	-110.14
$\Psi(\text{dist5}) p(\text{temp})$	0.58	0.09	4	-109.26
$\Psi(\text{understory cover} + \text{canopy cover}) p(\text{temp})$	0.60	0.09	5	-108.05
$\Psi(\text{dist5} + \text{canopy cover}) p(\text{temp})$	0.63	0.09	5	-108.06
$\Psi(\text{dist5} + \text{understory cover} + \text{canopy cover}) p(\text{temp})$	1.15	0.07	6	-107.05
$\Psi(\text{canopy cover}) p(\text{temp})$	1.23	0.07	4	-109.58
$\Psi(\text{understory cover}) p(\text{temp})$	1.35	0.06	4	-109.65
Pygmy Nuthatch				
$\hat{c} = 1.55$ $\Psi(\text{hd1000} + \text{understory average height}) p(\text{wind})$	0.00	0.53	6	-45.61
Townsend's Solitaire				
$\Psi(\cdot) p(\text{cover})$	0.00	0.15	3	-130.04

TABLE 2. Continued.

Species	Δi	w_i	K	-2 log (L)
$\Psi(\text{hd}100)$ p(cover)	0.21	0.14	4	-128.97
$\Psi(\text{canopy cover})$ p(cover)	0.82	0.10	4	-129.28
$\Psi(\text{hd}100 + \text{canopy cover})$ p(cover)	1.17	0.09	5	-128.23
$\Psi(\text{hd}100 + \text{understory cover})$ p(cover)	1.43	0.08	5	-128.36
$\Psi(\text{understory cover})$ p(cover)	1.55	0.07	4	-129.64
$\Psi(\text{understory average height})$ p(cover)	1.58	0.07	4	-129.66
$\Psi(\text{hd}100 + \text{understory average height})$ p(cover)	1.73	0.06	5	-128.51
Steller's Jay $\hat{c} = 2.87$				
$\Psi(\cdot)$ p(time)	0.00	0.22	4	-25.40
$\Psi(\text{canopy cover})$ p(time)	0.46	0.17	5	-24.41
$\Psi(\text{distance}10_hd)$ p(time)	1.03	0.13	5	-24.69

TABLE 3. The beta values and standard errors for covariates that appeared in the supported model set ($\Delta\text{AIC} < 2.0$) for each of the bird species included in our analysis.

Covariate	β value	95% Confidence Interval	
		Lower	Upper
American Robin			
Housing Density 100 m	0.78	-0.41	1.97
Average understory height	0.79	-3.08	4.67
Understory canopy cover	-0.51	-1.85	0.83
Percent canopy cover	-0.63	-1.90	0.64
Black-billed Magpie			
Percent canopy cover	3.53	-0.76	7.82
Housing Density 500 m	2.18	-1.78	6.14
Average understory height	-1.48	-4.47	1.50
Percent understory cover	0.88	-0.83	2.58
Dark-eyed Junco			
Average understory height	0.84	-0.06	1.74
Housing Density 100 m	0.55	-0.15	1.25
Downy Woodpecker			
Percent understory cover	4.25	-4.54	13.05
Average understory height	0.76	-1.05	2.57
Housing Density 1,000 m	31.14	-144.53	206.82
Percent canopy cover	-4.42	-19.32	10.49
Mountain Chickadee			
Mean Distance to 5 Houses	-0.62	-1.53	0.30
Percent understory cover	1.03	-0.45	2.51
Percent canopy cover	1.41	-0.70	3.51
Pygmy Nuthatch			
Housing Density 1,000 m	1.92	0.54	3.31
Average understory height	2.22	0.30	4.14
Steller's Jay			
Mean Distance to 10 Houses	-1.11	-2.44	0.23
Percent canopy cover	1.31	-0.20	2.82
Townsend's Solitaire			
Housing Density 100 m	5.19	-51.33	61.71
Percent canopy cover	0.80	-0.58	2.19
Percent understory cover	-0.59	-1.81	0.62
Average understory height	1.56	-2.50	5.63

study area, perhaps due to the distribution of food resources. Townsend's Solitaires are known to feed almost exclusively on juniper trees (*Juniperus scopulorum*), a common ornamental plant, in the winter season (Poddar and Lederer 1982).

Maintaining some level of vegetation cover within exurban areas while also supporting heterogeneity in habitat structure appears important for sustaining wintering birds in exurban landscapes. This finding is consistent with previous studies showing that changes in vegetation structure alter avian communities in areas dominated by residential development (Beissinger and Osborne 1982, Blair 1996). However, not all forest species respond positively to an increase in vegetation in the presence of exurban development. Suarez-Rubio et al. (2011) found that exurban development in the eastern United States negatively impacted many native bird species during the breeding season, and that despite having an intact canopy, exurban development areas were perceived by birds as open habitat, with a corresponding decline in forest dependent species. Similar work in the Appalachians found that exurban development even without forest loss can cause the decline of more sensitive bird species and Neotropical migrants (Lumpkin and Pearson 2013). Our study suggests that wintering birds in our region generally respond positively both to housing density and to the percent cover and height of understory vegetation; thus housing developments should be designed to sustain reasonably intact vegetation communities to provide usable habitat for birds in human-dominated landscapes (Friesen et al. 1995, Odell and Knight 2001).

Our study has several important limitations that inhibit the strength and breadth of our inference on this topic. First we surveyed birds and plants during a single year and season; inter-annual variability in climate could certainly influence habitat use by wintering birds. Our results may not be transferable to years of extreme cold or drought, or to particularly mild winters. Comparing occupancy of resident birds directly between winter and breeding seasons would also strengthen our understanding of the seasonal influence of human development and habitat characteristics on these species. Second, because detection probability is likely to be lower in the winter when birds are not singing, and our data collection was limited to one season, many bird species in our system were detected too infrequently to meet model requirements. Thus, we were only able to draw inference to a subset of wintering bird species in our system. Some of these species are known to be human-adapted (e.g., Black-billed Magpie) and it is not surprising that habitat use by these species would be positively associated with housing density. Other species for which we did not have sufficient detections for modeling (e.g., Brown Creeper) may be more sensitive to human development. Thus, the limitations of our study may have lead us to unfairly conclude that the effects of exurban development on birds in this system are largely neutral or positive. To fully understand how human development affects diverse groups of wintering birds, multi-year studies that capture data on these less frequently detected species are warranted. Finally, incorporating landscape scale metrics of vegetation cover and/or proximity to protected open space, and measuring anthropogenic subsidies (e.g., supplemental water and food) directly was beyond the scope of our study. Future studies should evaluate the importance of these measures relative to patterns of housing development on wintering birds.

Our study demonstrates that housing density and proximity has a neutral or positive impact on the most common wintering birds in our region. Because some species (i.e., Mountain Chickadee and Steller's Jay) showed a neutral response to housing density but were more likely to occur in close proximity to homes, the configuration of homes in a development may be as important as housing density in influencing animal communities (Pejchar et al. 2007). We found that either

understory or canopy cover was positively associated with habitat use for all species, which suggests maintaining or restoring patches of structurally complex natural vegetation within developed areas in exurban landscapes is likely to benefit wintering birds. The synergistic effects of housing density, vegetation characteristics and seasonality should be considered in order to provide viable year-round habitat for diverse bird communities in an increasingly urbanized world.

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APPENDIX 1. Occupancy (Ψ), detection probability (p) and 95% confidence intervals for all modeled bird species.

Species	Ψ	95% Confidence Intervals		p	95% Confidence Intervals	
		Lower	Upper		Lower	Upper
American Robin	0.60	0.15	0.93	0.13	0.05	0.29
Black-billed Magpie	0.96	0.55	1.00	0.35	0.27	0.45
Dark-eyed Junco	0.28	0.14	0.48	0.28	0.15	0.46
Downy Woodpecker	0.54	0.16	0.88	0.16	0.06	0.36
Mountain Chickadee	0.80	0.51	0.94	0.40	0.26	0.57
Pygmy Nuthatch	0.99	0.70	1.00	0.36	0.25	0.49
Steller's Jay	0.62	0.37	0.82	0.07	0.03	0.18
Townsend's Solitaire	0.90	0.62	0.98	0.53	0.42	0.63

APPENDIX 2. The common and scientific names of the species detected in our study area in northern Colorado. The first eight species had sufficient detections to be included in our occupancy analyses (denoted with a *).

Common Name	Scientific Name
Downy Woodpecker*	<i>Picoides pubescens</i>
Steller's Jay*	<i>Cyanocitta stelleri</i>
Black-billed Magpie*	<i>Pica hudsonia</i>
Mountain Chickadee*	<i>Poecile gambeli</i>
Pygmy Nuthatch*	<i>Sitta pygmaea</i>
Townsend's Solitaire*	<i>Myadestes townsendi</i>
American Robin*	<i>Turdus migratorius</i>
Dark-eyed Junco*	<i>Junco hyemalis</i>
Rock Pigeon	<i>Columba livia</i>
Northern Flicker	<i>Colaptes auratus</i>
Red-tailed Hawk	<i>Buteo jamaicensis</i>
Golden Eagle	<i>Aquila chrysaetos</i>
Northern Shrike	<i>Lanius excubitor</i>
American Crow	<i>Corvus brachyrhynchos</i>
Common Raven	<i>Corvus corax</i>
White-breasted Nuthatch	<i>Sitta carolinensis</i>
Brown Creeper	<i>Certhia americana</i>
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>
House Finch	<i>Haemorhous mexicanus</i>
Common Redpoll	<i>Carduelis flammea</i>