Biodiversity across a Rural Land-Use Gradient

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Abstract: *Private lands in the American West are undergoing a land-use conversion from agriculture to exurban development, although little is known about the ecological consequences of this change. Some nongovernmental organizations are working with ranchers to keep their lands out of development and in ranching, ostensibly because they believe biodiversity is better protected on ranches than on exurban developments. However, there are several assumptions underlying this approach that have not been tested. To better inform conservation efforts, we compared avian, mesopredator, and plant communities across the gradient of intensifying human uses from nature reserves to cattle ranches to exurban developments. We conducted surveys at randomly selected points on each type of land use in one Colorado watershed between May and August of 2000 and 2001. Seven bird species, characterized as human commensals or tree nesters, reached higher densities (all* $p < 0.02$*) on exurban developments than on either ranches or reserves. Six bird species, characterized as ground and shrub nesters, reached greater densities (all* $p < 0.015$*) on ranches, reserves, or both of these types of land use than on exurban developments. Domestic dogs (*Canis familiaris*) and house cats (*Felis catus*) were encountered almost exclusively on exurban developments, whereas coyotes (*Canis latrans*) were detected more frequently (*$p = 0.047$*) on ranchlands than exurban developments. Ranches had plant communities with higher native species richness and lower non-native species richness and cover than did the other types of land use (all* $p < 0.10$*). Our results support the notion that ranches are important for protecting biodiversity and suggest that future conservation efforts may require less reliance on reserves and a greater focus on private lands.*

Biodiversidad a lo largo de un Gradiente de Uso de Suelo Rural

Resumen: *Los terrenos privados del oeste de América están experimentando una conversión del suelo de un uso agrícola a un uso urbano, aunque se conoce poco acerca de las consecuencias ecológicas de este cambio. Algunas organizaciones no gubernamentales están trabajando con granjeros para que sus tierras permanezcan sin urbanizar, ostensiblemente porque piensan que la biodiversidad se protege mejor en tierras rurales que en urbanizaciones. Sin embargo, hay varios supuestos subyacentes a este modelo que no han sido comprobadas. Para informarnos mejor sobre los esfuerzos de conservación, comparamos comunidades de aves, mesodepredadores y plantas a lo largo del gradiente de intensidad de uso humano de reservas naturales, granjas y zonas de urbanización. Realizamos muestreos en sitios seleccionados aleatoriamente en cada uso de suelo en una cuenca del Colorado entre mayo y agosto de 2000 y 2001. Siete especies de aves, caracterizadas como comensales humanos o nidificantes arbóreos, alcanzaron densidades más altas (todas* $p < 0.02$*) en urbanizaciones nuevas que en granjas o reservas. Seis especies de aves, caracterizadas como nidificantes de suelo y arbustos, alcanzaron densidades mayores (todas* $p < 0.015$*) en granjas, reservas o usos mixtos del suelo que en las nuevas urbanizaciones. Se encontraron perros (*Canis familiaris*) y gatos (*Felis catus*) domésticos casi exclusivamente en nuevas urbanizaciones, mientras que se detectaron coyotes (*Canis latrans*) más frecuentemente (*$p = 0.047$*) en granjas que en nuevas urbanizaciones. Las granjas tenían comunidades de plantas con mayor riqueza de especies nativas y menor riqueza y cobertura de especies no nativas que en todos los demás usos de suelo (todas* $p < 0.10$*). Nuestros resultados apoyan la noción de que las granjas son im-*

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portantes para la protección de la biodiversidad y sugieren que los futuros esfuerzos de conservación pueden requerir de menos confianza en las reservas y un mayor enfoque en terrenos privados.

Introduction

A profound change in human population size and land use is currently underway in the Rocky Mountain states (Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming) of the American West. With population growth rates two to three times the national rate, this region had the five fastest growing states in the country between 1990 and 2000 (Perry & Mackun 2001). Although metropolitan areas have accommodated much of this in-migration, growth in rural areas is occurring at a faster rate and is requiring more land because of the large lot sizes associated with rural development (Sullins et al. 2002). Between 1994 and 1997 in the United States, nearly 80% of the land used for constructing houses was in nonmetropolitan areas, with 57% of houses being built on lots ≥4 ha in size (Heimlich & Anderson 2001). Driven by economic and quality-of-life factors such as outdoor recreation, people are choosing to live where they play (Power 1996; Masnick 2001). Concomitantly, the region is experiencing a conversion in private land use from ranching and farming to rural residential—or exurban—development (Riebsame et al. 1996; Sullins et al. 2002).

Outside incorporated city limits, three of the principal types of land use in the Rocky Mountain West are livestock ranching, nature protection, and exurban development (Vesterby & Krupa 1997). On ranches, the primary human use is livestock production. Protected areas, or nature reserves, provide some degree of protection from the permanent conversion of natural land cover and support human uses such as nature conservation and outdoor recreation. Exurban developments are low-density residential developments (typically one house per 4–16 ha) that occur beyond incorporated city limits, with lands being used for either part-time or year-round residence. The amount of land being designated as nature reserves is increasing slowly, with small portions being acquired annually by both governmental and nongovernmental natural resource and conservation organizations. Land in ranching and development is changing rapidly, however, as private ranches are sold and converted to exurban developments. Between 1990 and 2000, approximately 12 million ha were developed at exurban densities nationwide (Theobald 2001).

Although it is seldom the focus of scientific investigation, this conversion in land use has alarmed conservationists because of its potential implications for native biodiversity (Knight 1997; Hansen & Rotella 2002; Hansen et al. 2002). Wildlife and plant communities have been well studied in and adjacent to metropolitan areas (e.g., Emlen 1974; Beissinger & Osborne 1982; Mills et al. 1989; Engels & Sexton 1994; Blair 1996; Germaine et al. 1998; Bock et al. 1999; Crooks & Soulé 1999), whereas few studies have examined wildlife communities on exurban developments (Vogel 1989; Harrison 1997, 1998; Odell & Knight 2001; Hansen & Rotella 2002) and none have assessed plant communities in exurban areas. Little is known about the ecological consequences of converting ranchland to exurban development, yet some conservationists suspect that it is resulting in a simplification of our natural heritage by promoting species that are adaptable to human-altered environments and eliminating specialist species (Knight 1997; Marzluff et al. 1998; Boren et al. 1999; Hansen & Rotella 2002).

The threat of population declines for species sensitive to exurban development has generated a new response to biodiversity protection among conservation organizations in the Rocky Mountain region. The traditional means of protecting biodiversity from intense human land uses has been to purchase land and designate it as a nature reserve. One emerging technique for conserving biodiversity is to work with ranchers to keep private land out of development. Typically, this is accomplished through conservation easements that restrict development rights but allow livestock production to continue (Morrisette 2001; Alexander & Propst 2002). This approach is becoming increasingly popular, especially among nongovernmental organizations such as The Nature Conservancy and state and local land trust groups (Morrisette 2001). To date, more than 1200 land trusts in the United States have protected over 1 million ha of land through conservation easements (Land Trust Alliance 2001).

Underlying this emerging response to biodiversity protection are some fundamental assumptions that have not been tested. First, it is assumed that biodiversity is better served on intact ranches than on land that is subdivided for rural residences (Morrisette 2001). Nongovernmental organizations continue working with ranchers even though there has been no scientific examination of this assumption. Additionally, some environmentalists argue that ranching is not compatible with the maintenance of native biodiversity in the West (Fleischner 1994; Wuerthner 1994). Second, this conservation approach is commonly used as a means by which to expand the size of nature reserves by buffering core reserve areas with private ranchlands (Morrisette 2001; Hansen & Rotella 2002). This assumes that a land-use gradient exists for biodiversity protection, in which nature reserves are the most effective, ranches the next most effective, and exurban developments the least effective for maintaining native biodiversity. Yet conservation planners acknowledge that biological resources on many existing nature reserves have been poorly inventoried (Groves et al. 2002), so the assumption that biodiversity is best protected on these lands may not be justified.

We examined biotic communities associated with these three types of land use to test the assumptions of this conservation strategy. We limited our study to avian, mesopredator, and plant communities because these groups contain many species with diverse life-history requirements, and they could be sampled reliably within our logistical constraints. We compared these three taxonomic groups along the gradient of intensifying human use from nature reserves to cattle ranches to exurban developments in one watershed.

Methods

Study Area and Sampling Design

We restricted our study to the north fork of the Cache la Poudre River watershed in northern Larimer County, Colorado (lat. 40°50′N, long. 105°15′W). The nearest metropolitan area, Fort Collins, is 40 km southeast of the watershed. The land-use matrix of the region is a mixture of private ranchland, nature reserves, and exurban developments. The plant community type is a mosaic of shrub and grassland, with some trees occurring on moister sites and higher elevations. Dominant grasses include needle-and-thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), and cheatgrass (*Bromus tectorum*). Mountain mahogany (*Cercocarpus montanus*), skunkbush sumac (*Rhus trilobata*), and bitterbrush (*Purshia tridentata*) constitute most of the shrub overstory. Common forbs include fringed sage (*Artemisia frigida*) and hairy goldaster (*Heterotheca villosa*). Average annual precipitation ranges from 33 to 46 cm, with 75% of it falling between April and September (Moreland 1980).

In this watershed, we randomly located 93 points over 20,000 ha to sample avian, mesopredator, and plant communities among the three land-use types. To reduce confounding variables among points due to biophysical features (Hansen & Rotella 2002:1121), we limited sampling points to sites with the same shrub-grassland plant community type, elevations ranging between 1740 and 2200 m, and similar mixtures of soil type (Rocky Loam, Stony Loam, Loamy Foothill Range sites) (Moreland 1980). Also, points were randomly located on areas that met the following criteria: >75 m from riparian areas, <35% slope, >20 m from built structures and roads, and >300 m from the next nearest sampling point. The 93 points covered two nature reserves (n = 30), three ranches (n = 30), and two exurban developments (n = 33). These seven sites constituted our replicates of land-use type.

Nature reserves were Wildlife Areas of the Colorado Division of Wildlife that were protected 18 and 33 years prior to our study. These lands were used principally for wildlife protection and outdoor recreation, with livestock grazing, logging, mining, and water development activities prohibited. Management activities on reserves were primarily custodial, restricted largely to road and fence maintenance.

Ranches were privately owned and used for cattle production, with grazing managed through deferred-rotation systems. Although specific grazing intensities on these ranches were not obtained, visual inspections of forage utilization suggested that all three ranches were moderately grazed. These areas have been in livestock production for >100 years.

Exurban developments have been built up over the last 25 years, the average house age being 9 years (range: 1–25). The average lot size per house was 16 ha (range: 14–20), with 93% of the houses being used for year-round residences. The amount of forage utilization varied from no livestock use to high-intensity grazing, with 72% of homeowners having at least one grazing animal (e.g., horses).

Avian Sampling

We surveyed birds at the 93 sampling points four times, twice during each of the breeding seasons (mid-May to mid-June) in 2000 and 2001. We conducted 75-m fixed-radius point counts to record bird species detected visually or aurally and the distance, in meters, to those detections. We collected distance data to obtain detectability-based density estimates, which are more reliable than traditional index counts and provide a more valid basis for inference (Rosenstock et al. 2002). Point counts were 8 minutes long, with an initial 30-second quiet period, and were conducted within a 3-hour period after sunrise. Birds that flushed upon arrival on or departure from the point and within the 75-m radius were recorded as being at the station (Ralph et al. 1995). Surveys were not conducted when it rained or when wind was >3 (19.3 km/h) on the Beaufort wind strength scale. The same observer conducted all point counts and was extensively trained in bird identification and distance estimation prior to sampling.

Mesopredator Sampling

We monitored scent stations to record the presence of medium-sized mammalian predators at each of the 93 avian sampling points between May and August of 2000 and 2001. We established scent stations by clearing vegetation, rocks, and other debris from a circle of ground 1 m in diameter (Linhart & Knowlton 1975). Soil from within that station was sifted with a 2-mm-mesh screen to create a uniform tracking surface approximately 0.5 cm thick (Roughton & Sweeny 1982; Andelt & Woolley 1996). In 2000, one fatty acid scent tablet (scented predator survey disks; Pocatello Supply Depot, Pocatello, Idaho) was placed in the center of the station as an attractant, and each station was monitored for one 4-day period. In 2001 each station was again monitored for one 4-day period, but we used a fatty acid scent tablet the first day and a perforated can of tuna (170 g) the next 3 days. Tuna cans, with labels removed, were secured to the center of the station with a 14-cm nail. Stations were examined daily for the presence of mesopredator tracks. We identified tracks left in the soil using field guides by Murie (1974) and Halfpenny and Biesiot (1986). We re-established and monitored stations for an additional day if weather or excessive use rendered them unreadable. Mesopredators observed at or near a scent station during predator sampling were recorded as being present at that point.

Vegetation Sampling

We used a modified version of the Daubenmire cover method to sample plant communities between late June and mid-July of 2001 (Daubenmire 1959). Because we kept our sampling within this period of peak plant biomass, we were only able to survey 69 points (23 per land use) of the original 93 avian and mesopredator points. Thirty-meter transects were established in the four cardinal directions (N, S, E, W) radiating out from each sampling point (no transects intersected gardens, non-native lawns, ornamental landscaping, irrigated pastures, or built structures). Sampling occurred within 20×50 cm microplots placed on the left side of each transect at 10, 20, and 30 m from the point, for a total of 12 microplots per point. Canopy coverage (i.e., cover) of individual plant species, as well as percentages of rock, litter, and bare ground, were estimated to the nearest percent within each microplot. Lichens were not recorded separately, and sedges (*Carex* spp.) and mosses were not identified to the species level. A trained plant taxonomist made all cover estimates, while another observer recorded the data to reduce observer bias. Plants that could not be identified in the field were collected and identified in the herbarium at Colorado State University. Less than 1% of species encountered could not be identified and were categorized as unknown.

Statistical Analyses

We used distance sampling data and the program Distance 3.5 to estimate bird densities (birds/ha) for species that had reliable detection functions (Thomas et al. 1998). We selected models for detection functions by using Akaike's information criterion (AIC) and by inspecting probability density functions and chi-square goodness-of-fit statistics (Buckland et al. 1993). If more than one model seemed plausible, we model-averaged density estimates to reduce bias associated with estimates from a single selected best model (Burnham & Anderson 1998). We calculated final density estimates for bird species for each study site and compared means using one-way analysis of variance (PROC GLM, SAS Institute 1999). We conducted pairwise comparisons of individual means by the least-significant-difference (LSD) method when the overall F test was significant ($p <$ 0.10). Confidence intervals were log-based because the density parameter was strictly >0, and the sampling distribution was assumed to be log normal (Burnham et al. 1987).

We used data collected from scent stations during each 4-day sampling period to estimate the proportion of points visited by mesopredator species within each land-use category. To test for statistical differences among these detection frequencies, we used Fisher's exact test (PROC FREQ, SAS Institute 1999). We also used Fisher's exact test to conduct pairwise comparisons of proportions if the overall test was statistically significant ($p < 0.10$).

For plant communities, we calculated the average cover and species richness for the microplots surveyed. We used one-way analysis of variance to test for statistical differences in cover and species richness across types of land use (PROC GLM, SAS Institute 1999). When the overall F test was significant ($p < 0.10$), we conducted a least-significant-difference means comparison. To meet assumptions of normality and homogeneity of variances, data were square-root transformed for analysis, but results are presented in the original scale. An $\alpha =$ 0.10 was established a priori for all analyses to decrease the probability of committing a Type II error.

Results

Avian Communities

We made a total of 4964 detections of 58 different bird species over two field seasons, with 39 species detected on reserves, 41 on ranches, and 52 on exurban areas. We were able to generate reliable density estimates for 17 of these species based on the total number of individuals recorded and detectability models. Seven species reached their greatest densities on exurban developments ($p < 0.02$) (Fig. 1). Six species reached their greatest densities on ranches, reserves, or both of these

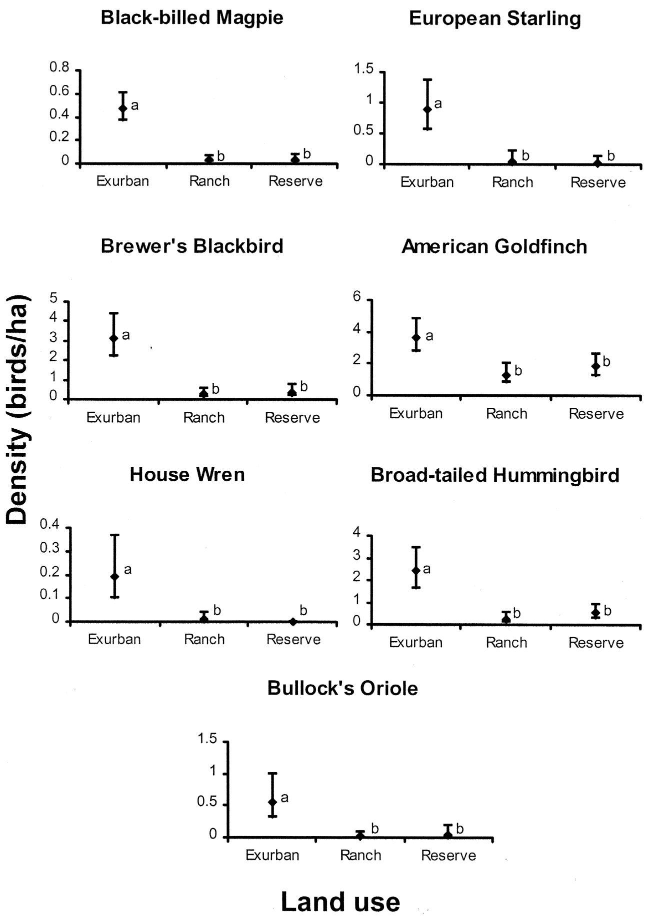

Figure 1. Densities and 90% log-based confidence intervals of bird species that reached their greatest densities on land used for exurban development. Different letters next to density estimates indicate a statistically significant difference at the 0.10 level.

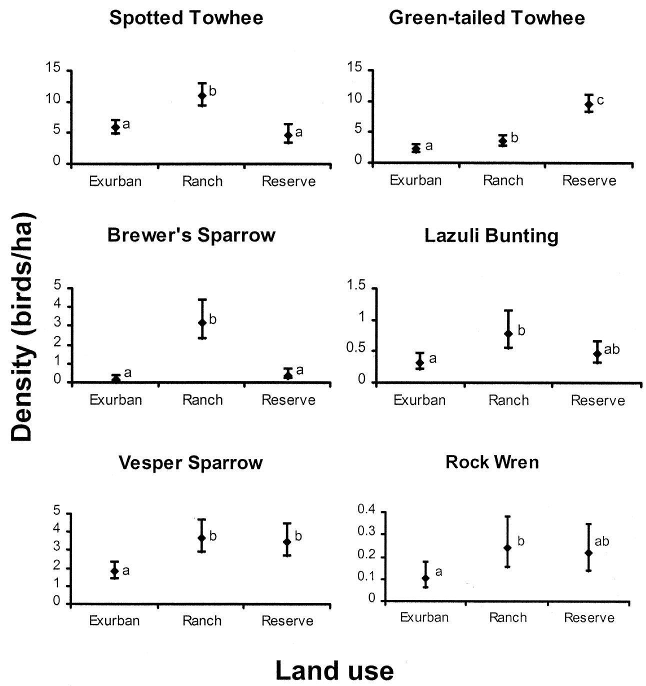

Figure 2. Densities plus 90% log-based confidence intervals of bird species that reached their greatest densities on land used for ranching or reserves. Different letters next to density estimates indicate a statistically significant difference at the 0.10 level.

types of land use ($p < 0.015$) (Fig. 2). The Lark Sparrow (*Chondestes grammacus*), Western Meadowlark (*Sturnella neglecta*), and Mourning Dove (*Zenaida macroura*) reached their greatest densities on ranches and exurban developments ($p < 0.03$). No statistical difference among sites was observed for the Brown-headed Cowbird (*Molothrus ater*) ($p = 0.50$). Although we could not obtain reliable density estimates for many species, it is worth noting that some species occurred on only one type of land use (Table 1).

Table 1. Bird species detected on only one of the types of land use in the north fork of the Cache la Poudre River watershed, Colorado.*

	Presence of species by land use (+)		
Species	*Exurban*	*Ranch*	*Reserve*
House Finch (*Carpodacus mexicanus*)	+		
Red-winged Blackbird (*Agelaius phoeniceus*)	+		
Common Raven (*Corvus corax*)	+		
Mountain Chickadee (*Parus gambeli*)	+		
Say's Phoebe (*Sayornis saya*)	+		
White-crowned Sparrow (*Zonotrichia leucophyrs*)	+		
Killdeer (*Charadrius vociferus*)	+		
Eastern Kingbird (*Tyrannus tyrannus*)	+		
Lewis' Woodpecker (*Melanerpes lewis*)	+		
Lark Bunting (*Calamospiza melanocorys*)		+	
Horned Lark (*Eremophila alpestris*)		+	
Savannah Sparrow (*Passerculus sandwichensis*)			+

** Each species was detected <12 times, so we could not obtain reliable density estimates.*

Mesopredator Communities

We detected coyotes, bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), domestic dogs, and house cats at scent stations over the two field seasons of sampling. Red foxes (two detections on ranches, one on a reserve) and striped skunks

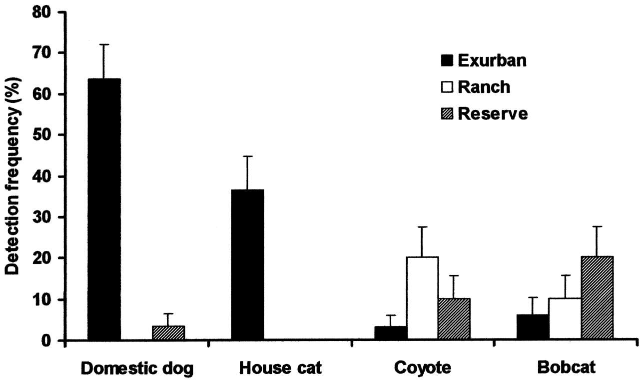

Figure 3. Frequencies (+SE) of mesopredator detections at scent stations surveyed on exurban developments, ranches, and reserves.

(two detections on ranches) were not detected often enough to allow valid statistical analyses.

Detections of domestic dogs differed among the three land-use categories ($p < 0.001$) (Fig. 3). Dogs were detected more frequently on exurban developments than either ranches or reserves (both $p < 0.001$). House cats were detected only on exurban developments ($p < 0.001$). Detections of coyotes differed statistically among the three types of land use ($p = 0.093$). Detection frequencies were higher on ranches ($p = 0.047$) than exurban developments but did not differ between ranches and reserves ($p = 0.472$) or reserves and exurban areas ($p = 0.340$). Detection frequencies of bobcats did not differ statistically across types of land use ($p = 0.262$).

Plant Communities

We identified 162 plant species among the three types of land use, 26 of which were non-native species. Cumulatively, land in exurban development had the greatest number of non-native species (Fig. 4). Mean non-native species richness and cover were higher on exurban developments and reserves than on ranches ($p < 0.03$) (Table 2). Mean native species richness was higher on ranches than on exurban developments ($p = 0.096$) and reserves ($p = 0.038$), but cover of native species did not differ among types of land use ($p = 0.204$) (Table 2).

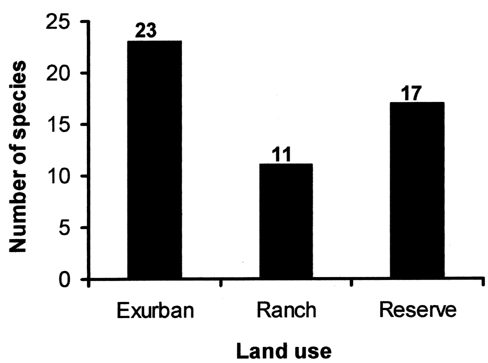

Figure 4. Cumulative number of non-native plant species by land use. The same number of microplots (n = 276) were sampled on exurban developments, ranches, and reserves.

Table 2. Mean species richness and percent cover of native and non-native plants among types of rural land use in northern Colorado.*

Land use	Mean no. of species: native (SE)	Mean no. of species: non-native (SE)	Mean percentage cover: native (SE)	Mean percentage cover: non-native (SE)
Exurban	24.4a (1.0)	4.7a (0.4)	72.0a (3.7)	26.8a (3.7)
Ranch	27.0b (1.0)	3.2b (0.3)	80.4a (3.7)	17.0b (4.1)
Reserve	23.9a (1.2)	4.5a (0.5)	75.6a (2.3)	28.4a (2.4)

**Letters next to the means within a column represent the results of pairwise comparisons using the least-significant-difference method after conducting a one-way analysis of variance. Different letters indicate statistically significant differences at the 0.10 level.*

Examining plant cover by life form revealed that ranches had the lowest forb cover ($p < 0.10$). However, ranchlands had the lowest cover of non-native grasses ($p < 0.03$) and lower cover of non-native forbs than exurban areas ($p = 0.009$) (Table 3). The dominant non-native plant, cheatgrass, differed in cover among types of land use ($p = 0.009$); cover was higher on reserves ($p = 0.002$) and exurban developments ($p = 0.050$) than on ranches.

Discussion

Our results indicate that biotic communities differ along the rural land-use gradient. Exurban developments supported greater densities of tree-nesting and human-commensal bird species (Fig. 1) and elevated numbers of domestic mammalian predators (Fig. 3). Reserves and ranches, however, had increased densities of ground and shrub-nesting bird species (Fig. 2) and virtually no domestic mesopredators (Fig. 3). Ranchlands differed from both reserves and exurban areas in that their plant communities contained a smaller proportion of non-native species (Table 2). These patterns have ecologically plausible explanations and ramifications that are supported by previous research and species life-history information.

Bird species with elevated densities on exurban developments have likely responded to human-provisioned resources on those landscapes that were mostly absent from reserves and ranches. Bird feeders were common on exurban developments, which may allow some spe-

Table 3. Mean percent cover (±SE) of native and non-native plants by life form among types of rural land use.[a]

	Forb cover		*Grass cover*		*Shrub cover*[b]
Land use	*native*	*non-native*	*native*	*non-native*	*native*
Exurban	26.1a (2.3)	5.8a (1.4)	27.1a (2.0)	21.0a (3.3)	18.8a (2.3)
Ranch	24.0a (1.7)	2.2b (0.4)	36.9b (3.1)	14.8b (4.0)	19.6a (1.6)
Reserve	30.2b (1.5)	3.8ab (0.9)	30.9ab (1.7)	24.6a (1.9)	14.5a (1.8)

[a] *Letters next to the means within a column represent the results of pairwise comparisons using the least-significant-difference method after conducting a one-way analysis of variance. Different letters indicate statistically significant differences at the 0.10 level.*
[b] *No non-native shrubs were detected.*

cies such as the Broad-tailed Hummingbird (*Selasphorus platycercus*) to reach larger populations (Calder & Calder 1992). Artificial nest boxes erected throughout exurban developments may promote occupancy by cavity-nesters, such as the European Starling (*Sturnus vulgaris*) and House Wren (*Troglodytes aedon*) (Cabe 1993; Johnson 1998). Deciduous trees used for landscaping near houses may provide the vertical habitat structure, otherwise missing from this shrub-grassland plant community, for tree-nesting birds such as the Bullock's Oriole (*Icterus bullockii*) (Barrett 1998). Finally, human garbage and waste from horses and other pets may attract species such as the Black-billed Magpie (*Pica hudsonia*) and Brewer's Blackbird (*Euphagus cyanocephalus*), allowing them to occur at elevated densities (Marzluff et al. 1994). Similar opportunistic and human-commensal bird species are known to reach elevated abundances in urban and suburban areas (Emlen 1974; Beissinger & Osborne 1982; Mills et al. 1989; Blair 1996), but further research is needed to understand how human alterations of landscapes allow these species to proliferate.

Patterns we observed in the mesopredator communities are consistent with the findings of other studies conducted on exurban developments. Domestic dogs and house cats used exurban areas almost exclusively, whereas coyotes were most common on ranchlands (Fig. 3). Odell and Knight (2001) recorded fewer coyotes and red foxes but more dogs and cats on exurban developments than on undeveloped lands. In central New Mexico, gray foxes (*Urocyon cinereoargenteous*) were tolerant of exurban developments with housing densities up to one house per 0.8–2 ha; beyond this threshold they avoided developments (Harrison 1997). Gray foxes also exhibited temporal avoidance of exurban developments. They used developments less during daytime and undeveloped areas more at nighttime, possibly because of the increased presence of dogs on developments during daytime (Harrison 1997). Although bobcats in our study showed no statistical difference among types of land use, detection frequencies were higher on the less intensive types (Fig. 3). This corroborates the results of a survey of exurban homeowners that reported bobcats being seen frequently near houses in developments but more often near undeveloped areas (Harrison 1998).

Elevated populations of human-commensal species on residential developments can be detrimental to other species (Marzluff et al. 1998). For instance, the Black-billed Magpie is a nest predator that may lower the reproductive success of other birds in an area. The Blue Jay (*Cyanocitta cristata*), a similar nest predator, has been shown to increase in numbers with urbanization and contribute to the decline of the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) (Engels & Sexton 1994). House cats and domestic dogs are subsidized mesopredators that can extend the realm of human influence and have negative impacts on wildlife populations (Churcher & Lawton 1987; Miller et al. 2001). House cats, in particular, have been implicated in the decline and extinction of scrub-breeding songbirds by two studies in California (Hawkins 1998; Crooks & Soulé 1999). Demographic evidence suggests that the long-term effect of increasing exurbanization could be added conservation problems caused by an escalating rate of expansion among opportunistic species and declining populations among sensitive species (Hansen et al. 2002).

We documented increased richness and cover of non-native plant species on exurban areas and reserves (Tables 2 & 3; Fig. 4). Human activities can change plant communities by accidentally or deliberately introducing invasive and non-native species (Mack et al. 2000). On exurban developments, disturbances caused by the construction of houses, roads, trails, or overgrazing by domestic animals may result in the increased prevalence of non-native plants. Roads and trails, in particular, are well recognized as corridors for the spread of non-native flora (Tyser & Worley 1992). Our nature reserves had few roads, but the trail systems were quite extensive and popular among motorized and nonmotorized recreationists, which may have helped spread non-native species.

Non-native plants can alter ecosystem dynamics by disrupting ecological processes and degrading the quality of wildlife habitat (Trammell & Butler 1995; Mack & D'Antonio 1998; Masters & Sheley 2001). For instance, cheatgrass proliferation in the Rocky Mountain West has altered historic fire regimes, favoring non-native, annual grasslands over native, perennial species. This invasive plant has displaced native plants and altered the occurrence of shrub-obligate songbirds that utilize these ecosystems (Rotenberry 1998). In our watershed, cheatgrass was more prevalent on reserves and exurban areas than on ranches. Also, 8 of 23 non-native plant species found on exurban developments were unique to that type of land use. Two of these species, spotted knapweed (*Centaurea maculosa*) and leafy spurge (*Euphorbia esula*), are noxious weeds that can lower the value of rangeland ecosystems, both ecologically and economically (Masters & Sheley 2001).

Finally, few bird species were completely absent from exurban areas (Table 1), but some ground and shrub-nesting bird species had elevated densities on land devoted to either ranching or reserves (Fig. 2). Previous studies indicate that floristic composition and structure are important factors associated with the distribution and abundance of these passerine species (Wiens & Rotenberry 1981; Knopf et al. 1990; Berry & Bock 1998). Brewer's Sparrows (*Spizella breweri*) reached higher densities on ranchlands than on either exurban areas or reserves, perhaps because of differences in habitat heterogeneity. Other factors may help determine species densities as well. For instance, Vesper Sparrows (*Pooecetes gramineus*) appeared sensitive to exurban development, which could be related to the elevated levels of human disturbance and increased numbers of avian and mammalian nest predators on developed areas. Demographic studies are needed to determine how these features affect population dynamics, especially for species of conservation concern such as the Vesper Sparrow and Brewer's Sparrow, which have shown long-term population declines across their ranges according to Breeding Bird Survey data (Sauer et al. 2001).

Our study was observational and was conducted in a single watershed, so inferences to other watersheds are not warranted. We assumed that sites had been in exurban development, ranching, or reserves long enough to help shape the communities we observed, but former types of land use can influence what species exist on a site. Both the reserves and the exurban developments had been in livestock ranching before their present uses. If these sites had been degraded through overgrazing before present uses, our results could be confounded. However, we observed several species of birds, predators, and plants that occurred solely on exurban developments, which suggests that, at a minimum, contemporary land uses influence what biodiversity exists on these sites. It is also important to note that our watershed is part of a region with a long evolutionary history of grazing, with factors such as climate playing more critical roles in determining plant community composition (Milchunas et al. 1988; Milchunas et al. 1990; Hart 2001).

Conservation Implications

Inferences beyond our watershed should be viewed as speculative but may serve to stimulate additional research. One generalization is that exurban developments promote non-native and human-commensal species, perhaps at the expense of other native species. Another generalization is that nature reserves may not protect biodiversity as well as they are assumed to. Both of these notions have implications for landscape-scale conservation and provide ecological justification for groups who work with private landowners to protect biodiversity.

Because privately owned ranches are often located on highly productive, low-elevation sites (Scott et al. 2001), development of these lands can be especially detrimental to wildlife. In the Greater Yellowstone Ecosystem, Hansen and Rotella (2002) showed that exurban developments occurred disproportionately close to bird hotspots. They also demonstrated that low-elevation lands serve as population sources for native bird species if they are not subdivided, but function as sinks when they are developed for rural residences. Exurban developments may have degraded habitat quality owing to human disturbance and invasive species and could operate as ecological traps, where wildlife assess land as suitable but, as a result of increased predation, competition, and parasitism, suffer reduced fitness when they attempt to reside there.

Because of biophysical factors and existing ecosystem conditions, nature reserves may currently be inadequate to fully protect biodiversity. Considering that most reserves occur on the least productive soils and at the highest elevations (Scott et al. 2001), it becomes apparent that these areas are biased toward the harsher environmental conditions. Furthermore, the population viability of some species on nature reserves could be threatened by the development of ranchlands because subpopulations on reserves rely on dispersal from undeveloped, low-elevation lands (Hansen & Rotella 2002). Reserves are often assumed to protect biodiversity, but our results suggest that reserves were somewhat ecologically degraded. Ranches can be more effective than reserves at maintaining native biotic communities in some instances, suggesting that the conversion of ranchland to exurban development has negative consequences that extend beyond administrative lines (Knight & Clark 1998; Hansen et al. 2002).

Cumulatively, these findings stress the relative importance of low-elevation ranchlands for conservation and support the emerging strategy for biodiversity protection. As private lands are increasingly converted to exurban development, the amount of low-quality habitat on western landscapes may become more prevalent and jeopardize the persistence of some species on private and public lands (Donovan & Thompson 2001; Hansen

& Rotella 2002). Efforts to protect the natural heritage of the Rocky Mountain West may require less reliance on nature reserves and a greater focus on private lands.

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