Original Article

Impacts of Residential Development on Ungulates in the Rocky Mountain West

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ABSTRACT Rural residential development in the Rocky Mountain West of North America is resulting in increased conflict between ungulate habitat and infrastructure. Subdivisions, houses, and roads affect ungulates both behaviorally and demographically and reduce management options available to agencies. These habitat alterations need to be addressed if wildlife species are to coexist with humans. We reviewed literature (using 7 search engines and 16 key words) on the effects of land-use change (especially residential development) on elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), American pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*). Approximately 80 studies were directly related to the effects of human development on ungulates; however, only 25 specifically examined residential development and its influences on the focal species. Studies varied in methodology (i.e., aerial and ground surveys, pellet counts, movement rates) and analyses. The literature suggests most ungulates exhibit short-term behavioral reactions to human disturbance. However, few studies link these responses to population-level consequences or test the cumulative impact that multiple developments and development types (i.e., roads, housing, industrial development) have on seasonal habitat use and migratory behavior. Short-term and small-scale observational studies have articulated the conflict between humans and ungulates on shared habitat. Those studies need to be followed with well-designed experiments and large-scale multi-jurisdictional projects so that managers and planners can make more credible recommendations to direct future exurban development that benefits wildlife and humans. © 2012 The Wildlife Society.

KEY WORDS avoidance, cumulative effect, exurban, habituation, residential development, subdivision, ungulate, winter range.

The increase in resource exploration, mining, energy extraction, utilities, hydroelectric dams, and infrastructure has progressively altered the distribution and abundance of species (UNEP 2001, Vistnes and Nellemann 2008, Naugle 2011). Less attention has been given to the impacts residential structures have on the habitat and population dynamics of wildlife (Glennon and Kretser 2005, Hansen et al. 2005, Krausman et al. 2011). Houses may appear to have a smaller footprint than industrial infrastructure, but the piecemeal progression of residential development and the lack of comprehensive and enforceable land-use policies guarantees that residential structures and development will have a large impact on wildlife habitat (Hansen et al. 2005).

Development that occurs along the urban–rural gradient beyond urban and suburban areas has been termed exurban (Nelson 1992). It is characterized by low-density, vehicle-dependent residential development, segregated land uses, and a lack of community-based shared spaces (Ewing et al. 2005). In the 1970s, growth of rural areas exceeded growth of metropolitan regions, and by 2000, >25%

(1.39 million km^2) of the conterminous United States was occupied at exurban densities (1 unit/0.004–0.16 km^2), resulting in impacts on agricultural lands, forests, and rangelands (Brown et al. 2005). Some estimates suggest that exurbia encompasses an area 7 times larger than urban and suburban areas combined (Theobald 2005). Exurban sprawl can be especially detrimental because it results in the loss of more land to accommodate fewer people. The conditions that make valley bottoms and low-elevation foothills of the Rocky Mountain West ideal locations for new houses (e.g., low snowfall, high solar radiation) are also requirements for ungulate winter range (Safford 2003). As a consequence, ungulate habitat and new infrastructure will intersect at increasing rates.

Roads, subdivisions, and houses affect ungulate behavior and demography and reduce management options. Because the effects of exurban development vary by region; the proximity to forests, escape, and hiding cover; the presence of predators; the occurrence of hunting by humans; competition with other ungulate populations; and the type and spatial pattern of development structures, no comprehensive studies have rigorously addressed this escalating problem. Further, making comparisons across studies of species responses can be difficult due to differences in methodology, techniques,

regulatory measures, and the scale of the impact examined (Johnson and St-Laurent 2011). In general, the lack of unifying theory has made it difficult to identify common principles related to wildlife and development. Johnson and St-Laurent (2011) propose a typology for wildlife impact research that identifies a framework to classify and predict impacts with the goal of improving dialog and facilitating the review of diverse research. Our review employs Johnson and St-Laurent's (2011) typology to explore the impacts of land-use change, especially residential development at exurban densities, on white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus canadensis*), American pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) in the Rocky Mountain West.

METHODS

We conducted a literature review, across all years, on the effects of residential development by using the following electronic resources: ISI Web of Knowledge, Zoological Record; CSA Biological Sciences; CSA Illustrata: Natural Sciences, Google Scholar, and Biological Abstracts. We used a combination of the following key words: bighorn sheep, elk, energy development, exurban development, habitat quality, home range, human impact, mule deer, pronghorn, recruitment, residential development, resource selection, roads, survival, ungulate, and white-tailed deer. We focused on studies that incorporated specific responses of ungulates to human land-use change, including residential development, industrial development, roads, and other impacts. We also included literature reviews, grey literature, reports, theses, and dissertations that explored the effects of human development on wildlife and land-use policies. Articles were mined for references that were relevant and did not show up in the search criteria.

RESULTS

We reviewed >100 articles on the impacts of residential development on wildlife. Approximately 80 studies were directly related to the effects of human development on ungulates; however, only 25 specifically examined residential development and its influences on the 5 focal species (Table 1). Geographically, all but 1 study on the effects of residential development on white-tailed deer occurred in the midwestern or eastern United States. Most elk studies occurred along the Rocky Mountains. Studies on energy development were clustered in southwestern Wyoming and southern Alberta, Canada. Studies varied in methodology (i.e., aerial and ground surveys, pellet counts) and analyses of data (Smith et al. 1989, McClure et al. 2005, Cleveland et al. 2012). Different research designs and metrics alter the detection of impacts and make distinguishing comparable results difficult. For example, minimum patch size might relate to the area required to maintain species as measured by occurrence, population densities, survival, or reproductive success. Thus, a unifying framework, such as the wildlife impact typology developed by Johnson and St-Laurent (2011), is necessary to help recognize emergent patterns in the current literature and determine the most relevant research needs.

CONFLICT BETWEEN HUMAN DEVELOPMENT AND UNGULATE RANGES

Historically, settlement of the mountainous regions of the American West was constrained to valley bottoms by topography and water availability. As land was bought and sold in the early 1900s, a general pattern emerged with public lands at high elevations and private lands dominating fertile river valleys and mountain foothills that contained the most productive soils and the greatest species diversity (Ewing et al. 2005, Gude et al. 2006). Today nearly 20% of the private lands available in the West have been developed for residential, industrial, or commercial use (Travis 2007). In general, the development of valley bottoms and mountain foothills has the greatest impact on important winter habitat for ungulates. These low-elevation landscapes provide security and thermal cover, low snow cover, and high solar radiation (Armleder et al. 1994, Safford 2003, Christianson and Creel 2007). High-quality winter range is needed to offset the negative energy balance experienced by ungulates in winter due to increased energetic costs of gestation for females (Pekins et al. 1998), deep snow events (Parker et al. 1984), and loss of fat and protein due to low-quality winter nutrition (Festa-Bianchet 1989, Parker et al. 2009).

Determining the amount of winter range required to sustain a population is difficult because nutritional value of forage, exogenous effects of climate, topography, land cover, predation, and human development all interact to influence the quality of winter range (Fig. 1; Safford 2003). Snow is likely the single most important aspect of winter range in climates that experience extreme weather events (Poole and Mowat 2005). Snow depth, density, and hardness determine the amount of forage that can be reached, the ability of ungulates to avoid predators, and the timing of fine-scale daily habitat selection, movements, and migration (Parker et al. 1984). Because digestible forage is generally more abundant in open areas, ungulates must make trade-offs between the benefits and costs of forest cover, snow depth, and forage availability (Pauley et al. 1993, Serrouya and D'Eon 2008).

Summer habitat is also important because of the value of summer nutrition to ungulate population dynamics (Cook et al. 2004, Parker et al. 2009). Thus, the proximity of summer ranges to wintering areas and the quality of important migration corridors have important implications for ungulate population viability (Sawyer et al. 2009*a*). Mule deer, white-tailed deer, elk, pronghorn, and bighorn sheep commonly migrate between 50 km and 100 km in spring and autumn (Hoekman et al. 2006, Sawyer et al. 2009*a*). Unfortunately, these migration routes are increasingly threatened by exurban development, energy development, and highway mortality, especially in bottlenecks where options for avoiding development pressure are limited (Berger 2004, Gude et al. 2007).

Table 1. Review of scientific literature on the effects of residential development in North America on *Odocoileus virginianus* (Ov), *O. hemionus* (Od), *Cervus canadensis* (Cc), and *Antilocapra americana* (Aa), which summarizes study authors, study duration, whether the study was peer reviewed or not, sample size, study design, and general results. There were no studies on the effects of residential development on *Ovis canadensis*. CA, core area; Compar., comparative; CWD, chronic wasting disease; DVC, deer–vehicle collision; Exper., experimental; HR, home range; Obs., observational; Spp., species; ZOI, zone of influence.

Author: study duration	Spp.	Peer review	Sample size	Study design	General results
Anderson et al. 2011: 2003–2005	Ov	Yes	$n = 20$	Obs.	Exurban deer avoided areas near dwellings and roads most during fawning season but also during winter. Spatial patterns of residential structures may affect deer use.
Cleveland et al. 2012: 2007–2009	Cc	No	$n = 9$	Obs.	Hunting increased movement, but did not affect selection. Elk moved faster <750 m from houses and trails and selected habitat >1,600 m from human development.
Etter et al. 2002: 1995–1998	Ov	Yes	$n = 200$ ear tag, $n = 140$ VHF	Obs.	Survival of suburban deer was high compared with survival in rural populations, and the majority of deaths were caused by DVC. Dispersal was low, and HR size was comparable to similar populations.
Farnsworth et al. 2005: 1997–2002	Od	Yes	na	Obs.; Model	M had almost double the CWD infection rate of F, urban deer had almost double the infection rate of rural deer, and different sites had various levels of infection.
Grund et al. 2002: 1996–1999	Ov	Yes	$n = 31$	Obs.	HR size varied according to season. During a severe winter, 78% of HRs encompassed residential neighborhoods. Urban deer HRs were smaller than rural deer HRs.
Hebblewhite et al. 2005: 1997–1999	Cc	Yes	$n = 45$	Obs.; Compar.	Elk density was significantly higher around Banff, where predation was low. Survival and recruitment increased around Banff. Elk pellet density was $3.2\times$ higher in the central no-wolf area.
Hurst and Porter 2008: 1960–1970, 2003–2004	Ov	Yes	na	Obs.	Contemporary winter yarding areas included more residential communities than historical areas. CAs were smaller in residential areas. Deer displayed flexibility between years in selection for wintering areas.
Hygnstrom and VerCauteren 2000: 1995–1997	Ov	No	$n = 59$	Obs.	Average HR size was 276 ha, but many were smaller. Deer exhibited high fidelity to HRs with little emigration even when densities were high and hunting pressure occurred.
Kilpatrick and Spohr 2000*a*: 1995–1997	Ov	Yes	$n = 25$	Obs.	No difference in HR during year, deer moved closer to houses during bow hunting, and average HR size was smaller in developed areas. Deer did not avoid development.
Kilpatrick and Spohr 2000*b*: 1995–1997	Ov	Yes	$n = 39$	Obs.	HR and CA size did not differ between seasons. More houses were in HR during winter than fawning season. Bird feeders provided food. Highest use near houses was in Mar.
Kilpatrick and Stober 2002: 1995–1997	Ov	Yes	$n = 44$	Obs.	Deer retained CA if bait site was placed within CA, but shifted CA toward bait site if the site was within HR, but outside of CA. Deer abandoned CAs far from bait sites.
Kilpatrick et al. 2011: 2002–2003	Ov	Yes	$n = 56$	Obs.	A very small percent of deer HR and CA fell outside of the 152-m no-hunt buffer around buildings in the autumn during hunting season. Forest habitat was more important during an oak-mast year when acorns were abundant.
Kloppers et al. 2005: 2001–2002	Cc	Yes	$n = 24$	Obs.; Exper.	Aversive conditioning increased flight distance, increased elk distance from town, and decreased time spent in vigilance postures. The higher the wolf activity, the shorter the elk flight distance and distance from town.
McClure et al. 2005: 1994–1995	Od	Yes	$n = 17$ urban, $n = 14$ rural	Obs.; Compar.	Fifteen of 17 urban deer were migratory, as opposed to 8 of 14 rural deer. Deer in urban areas travelled an average of 31.5 km and deer in rural areas travelled an average of 14.5 km between winter and a shared summer range. Urban deer had lower fawn recruitment.
Piccolo et al. 2000: 1998–1999	Ov	No	$n = 21$	Obs.	Deer collared in urban forest preserves. Deer in more urban area had smaller, more linear HRs that stretched into urban areas. Deer in less developed area remained within the preserve boundaries and had smaller, centralized HRs.
Porter et al. 2004: 1997–1999	Ov	Yes	$n = 22$	Obs.	Most suburban deer moved seasonally and had small HRs compared with rural areas. Main causes of death were DVC, hunting, and accidents during culling.

(continued)

Table 1. (*continued*)

Author: study duration	Spp.	Peer review	Sample size	Study design	General results
Rhoads et al. 2010: 2004–2006	Ov	Yes	$n = 66$	Obs.	HR size of exurban deer varied according to season and increased from fawning through post-hunting seasons. Deer moved most at dusk, HR sizes approx. equal to other midwestern exurban populations.
Sawyer et al. 2005: 1998–2001	Aa, Od	Yes	$n = 34$ Aa; $n = 171$ Od	Obs.	Pronghorn migrated 116–258 km and mule deer migrated 20–158 km. A no. of significant migration-path bottlenecks were observed. Housing developments narrowed width of one bottleneck to <800 m.
Smith et al. 1989: 4 months 1983	Od	No	$n = 114$ transects	Obs.	Deer use was lowest 22.8–45.7 m from houses and higher >68.6 m from houses. Deer use was influenced up to 82.3 m from houses during winter.
Storm et al. 2007: 2003–2005	Ov	Yes	$n = 43$	Obs.	HR size of exurban deer was greater than suburban deer and less than rural deer. Deer tended (not statistically) to avoid structures during fawning. In winter, grassland outside of housing ZOI was preferred over grassland inside.
Swihart et al. 1995: varied between sites	Ov	No	varied	Obs.	Deer avoided areas with >80 houses/km^2 and had smaller HRs in urban areas. Survival was approx. equal between rural and urban areas. Deer browsed close to houses where species richness was 2× greater <50 m from houses.
Vogel 1989: 1981–1983	Ov, Od	Yes	$n = 12$ Ov, VHF; $n = 4$ Od, VHF	Obs.	Closer to development, HRs became smaller and more linear and deer became more nocturnal. Housing was more detrimental when evenly distributed. Fewer houses were present within 800 m of mule deer observations than within 800 m of white-tail deer.
Wait and McNally 2004: 1996–1998	Cc	No	$n = 30$	Obs.	Elk show significant preference toward grass–forb rangelands, sagebrush, and pinyon–juniper habitats, and avoid ponderosa pine and mixed conifer habitats. Elk avoided parcels <4 ha, and preferred parcels >24 ha.
Webb et al. 2011: 2006–2009	Cc	Yes	$n = 184$	Obs.	Annual survival of F elk was 0.76–0.85 over the 4 yr. Harvest accounted for 66.7% of mortality. The amount of human footprint (cumulative amount of ranching, energy development, and residential structures) used by elk 1 week prior to mortality did not affect survival.
Witham and Jones 1992: 1983–1989	Ov	No	$n = 103$ live captures	Obs.	Urban deer body condition varied between sites that were relatively close to each other. Some plant species seemed to regenerate after reduction in deer density.

IMPACTS OF HUMAN DEVELOPMENT ON UNGULATES

In general, 3 broad categories of effects (i.e., spatiotemporal scale, magnitude, and regulation) interact hierarchically to alter the scale of the biological impact on the species (Johnson and St-Laurent 2011). The scale of assessment has a strong influence on the probability of detecting impacts, with wider temporal and spatial scales revealing avoidance or demographic impacts when local behavioral studies often find negligible or indecisive effects (Johnson et al. 2005, Vistnes and Nellemann 2008, Hebblewhite 2011). The total magnitude of the effect depends on the size of the area developed and the length of exposure to development (Johnson and St-Laurent 2011). Single isolated activities may have a trivial impact on ungulate behavior or demography (Weisenberger et al. 1996), while effects that are large-scale and accumulate over time generally have a larger impact on populations (Nellemann and Cameron 1998). Finally, Johnson and St-Laurent (2011) report that the eventual outcome of development on wildlife is also a result of the types and effectiveness of regulatory frameworks. The importance of policies that effectively provide restrictions and guidelines regarding the location, size, and appropriateness of new developments cannot be over-stated.

BIOLOGICAL SCALE OF IMPACT

Individual Behavioral Responses

The framework for identifying the biological scale of impact developed by Johnson and St-Laurent (2011) provides a hierarchical structure to understand how various effects of human development influence ungulates (Table 2). The incremental increase in the severity of the observed biological impact likely does not follow a completely linear relationship, but reflects a general continuum from individual behavioral responses and physiological changes to population-level and community-level impacts that have broad implications for
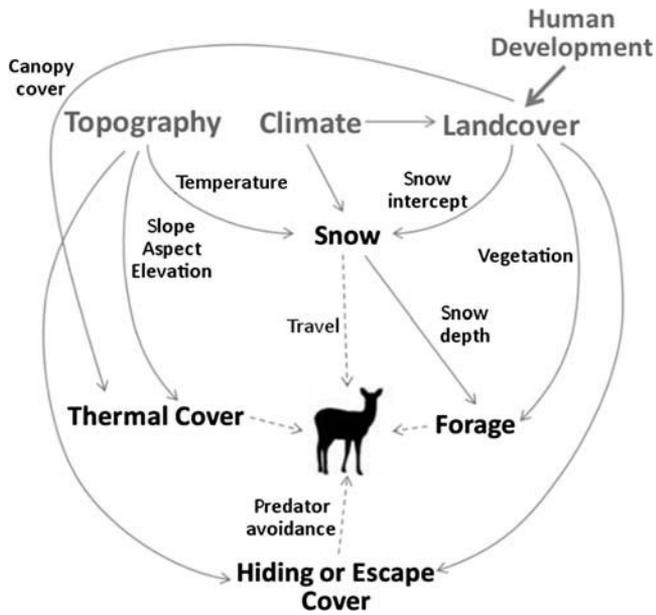
Figure 1. Factors affecting the energy balance of ungulates during the winter. Dashed lines represent factors that influence the condition of ungulates and solid arrows represent factors that influence attributes of winter range habitat. Adapted from Armleder et al. (1986).

population viability (Johnson and St-Laurent 2011). Most ungulates exhibit short-term behavioral reactions (e.g., movement away from disturbance, flight response, increased vigilance, altered foraging rates, changes in maternal activities) in response to human disturbance (Frid and Dill 2002, Stankowich 2008, Parker et al. 2009). Loud noises, aircraft, or vehicular stimuli usually affect ungulates less than pedes-

trian approach (Stankowich 2008). However, while disturbance may produce similar effects, the impacts are almost always species-specific.

Avoidance.—Human development, activity, and infrastructure can all affect ungulate populations. Anthropogenic-mediated mortality of ungulates occurs through hunting, poaching, collisions with vehicles, domestic animal predation, and injuries from building structures and toxins (Krausman et al. 2011). However, there is a growing consensus that the proximate mechanisms for species declines and extinctions are often indirect and asymmetrical (DeCesare et al. 2010). Managers are beginning to recognize the importance of complex (nonlinear) interactions and their influence on population dynamics (Polis and Strong 1996, Sinclair and Byrom 2006). Indirect effects of development include altered animal and plant community composition and biotic interactions; the complex interactions between habitat loss, alteration, and fragmentation acting simultaneously (St-Laurent et al. 2009); and behavioral avoidance of areas near development.

Avoidance responses often vary between species, development types, and seasons. For example, in a study on the effects of housing on white-tailed and mule deer populations, Vogel (1989) reported avoidance of existing development in Gallatin Valley, Montana. During residential growth in the valley (i.e., a 53.4% increase in residents from 1970 to 1980) residents reported that white-tailed deer populations encroached on historical mule deer ranges. The authors monitored both deer species (12 white-tailed deer and 4 mule deer) and reported that deer avoided houses and increased nocturnal behavior near subdivisions. Fewer houses were present within 800 m of observations of mule deer than within 800 m of observations of white-tailed deer, alluding

Table 2. Ungulate response to development along the continuum of the biological scale of impacts described by Johnson and St-Laurent (2011).

Biological scale of impact	General ungulate response	Monitoring methods	Key research
Individual behavioral responses	Movement away from disturbance, flight response, increased vigilance, altered foraging rates, changes in maternal activities, avoidance of development, and habituation. Loud noise, aircraft, and vehicular stimuli have less impact than humans on foot.	Observational studies, analysis of distributions, indirect measures of habitat use, or radiotelemetry.	Reviews by Frid and Dill (2002) and Stankowich (2008)
Individual physiological responses	Increased heart rate, respiration, and stress hormone concentration. Prolonged disturbance events may cause increased vigilance, reduced feeding time, and decreased nutrient intake leading to decreased reproductive rates. Body condition influences the timing of parturition, birth mass, and early survival of offspring.	Analysis of parasite loads, monitoring of stable isotopes, and analysis of fecal glucocorticoid hormones.	Review by Parker et al. (2009), research by Creel et al. (2002, 2009) and Millspaugh et al. (2001)
Population responses	Prolonged and severe physiological or behavioral changes can alter vital rates and be detected at higher biological scales. Few firm conclusions exist about the population-level impacts of human development on ungulates, but large-scale range abandonment has been recorded.	Long-term cumulative-effects studies.	Reviews by Hebblewhite (2011) and Laliberte and Ripple (2004), research by Sawyer and Neilson (2010), and Beckmann and Seidler (2009)
Ecological community responses	Altered interspecific relationships influence community composition and distribution. Indirect effects may cascade through a community. Ungulates may use development as a shield against predators, or alternately, predators may be drawn to development by abundant prey. Subsidized predators decrease prey populations.	Large-temporal and spatial scale, multi-level, cumulative-effects studies.	Research by Ripple et al. (2001), Hebblewhite et al. (2005), Berger et al. (2008), and Rominger et al. (2004)

to an increased avoidance of human disturbance by mule deer compared with white-tailed deer. Sensitivity to human disturbance tends to be strongest during the spring. In an exurban landscape in Illinois, white-tailed deer avoided human structures most during fawning (Storm et al. 2007, Anderson et al. 2011), and similarly, in an affluent residential area of Connecticut, deer core areas contained the lowest number of houses during fawning season (Kilpatrick and Spohr 2000a, b).

Elk also display behavioral avoidance of residential development. In Colorado, housing developments and associated infrastructure caused elk to avoid landscape patches <0.04 km². Elk preferred patches >0.24 km² with available hiding cover (Wait and McNally 2004). Housing development can also affect elk movement. In a residentially developing area north of Missoula, Montana, elk movement rates were higher <750 m from houses and trails, and elk preferred habitat >1,600 m from any human development (Cleveland et al. 2012). However, factors such as the presence of predators, the occurrence of hunting by humans, and competition with other ungulate populations can have a significant impact on behavioral responses (Hebblewhite et al. 2005, Jenkins et al. 2007).

Although no published studies specifically examined the impact of residential development on pronghorn, houses and associated infrastructure have been implicated as a major factor in blocking migration corridors (Sawyer et al. 2005). Barrier effects have the potential to influence individual dispersal, which may be essential to survival of local populations. The negative effects of fences on pronghorn populations have been well-documented. Unlike deer and elk, pronghorn rarely jump fences and require approximately 40 cm of space below the lowest wire in a fence to crawl underneath it (Yoakum 2004). Few fences are built to facilitate pronghorn movements, and consequently, fencing is a major barrier to movement. Significant research on the impacts of human disturbance on pronghorn indicates that pronghorn avoid other forms of development, such as oil and gas infrastructure and roads (Beckmann and Seidler 2009). This avoidance likely extends to residential developments. In a study on biodiversity near Sonoita, Arizona, pronghorn were never observed in exurban areas with livestock and were rarely observed in exurban areas that did not contain livestock (C. E. Bock, University of Colorado, personal communication).

Similarly, no specific research has been conducted on the effects of residential development on bighorn sheep. However, historical reports suggest that bighorn sheep once ranged far from rugged mountain terrain now considered preferred habitat (Valdez and Krausman 1999). The overwhelming expansion of urban development, resource extraction, disease, and competition with domestic livestock has reduced historical ranges by 40% (Laliberte and Ripple 2004). Thus, the large-scale declines and extirpations of bighorn sheep populations near western cities such as Tucson are likely a result of human encroachment, though no cause-and-effect studies documented the declines (Krausman et al. 2001).

Habituation.—Ungulates can habituate to temporally and spatially predictable human activity, especially when they are not hunted or harassed (Thompson and Henderson 1998). The majority of studies on the effects of residential development on ungulates have focused on white-tailed deer. These studies almost all occurred in the eastern and midwestern United States and, in general, conclude that white-tailed deer commonly habituate to human presence in suburban areas (Swihart et al. 1995, Kilpatrick and Spohr 2000a, b). White-tailed deer often have higher survival rates in urban and suburban environments, in part due to decreased movements and dispersal, decreased mortality from hunting, lack of large mammalian predators, and increased availability of ornamental plants, shrubs, fertilized yards, and supplemental feeding areas (Swihart et al. 1995, Etter et al. 2002, Grund et al. 2002, Porter et al. 2004). For example, bird feeders provided significant food resources for deer in Connecticut and likely drew deer close to houses in spring (Kilpatrick and Spohr 2000a).

Elk and mule deer can also become habituated and overabundant in urban areas (Thompson and Henderson 1998, Kloppers et al. 2005, Walter et al. 2010). While some species may display more or less habituation behavior, few studies have examined differences in levels of habituation between species. For example, even bighorn sheep and pronghorn may habituate to temporally and spatially predictable human activity, such as low levels of recreation, mining, and aircraft activity (Krausman et al. 1998, 2004; Jansen et al. 2007). The level of habituation to human activity likely varies between regions and the impact of development should be examined on a case-by-case basis.

Abundant ungulate populations in cities and towns pose a threat to human safety, cause property damage, increase disease transmission rates, and generate concerns for animal welfare (Farnsworth et al. 2005). Further, habituated animals reduce the flexibility of managers to control ungulate populations through hunting quotas and weaken public satisfaction of wildlife. Negative interactions between problem wildlife and humans in residential areas can undermine public support for management agencies and conservation initiatives (Kretser et al. 2009). Habituated ungulates may display a decrease in migratory behavior, overgraze winter ranges, and move to private lands or urban areas where hunting is not allowed (Hurst and Porter 2008, Jones et al. 2008). As more valley bottom lands are transferred from hunter-friendly ranches to subdivisions, the amount of land used as refuge by ungulates during the hunting season will likely increase. This results in a costly use of resources and reduces the effectiveness of management agencies.

Individual Physiological Responses

Responses to human activity may also include altered physiological, energetic, or nutritional states (Johnson and St-Laurent 2011). In ungulates, these responses include increased heart rate, respiration, and stress hormone concentration (Creel et al. 2009). In some cases, heart rate may increase during disturbance but quickly decrease to pre-disturbance levels with little impact on behavior or habitat

use (Weisenberger et al. 1996; Krausman et al. 1998, 2004). Because of the high energy requirements for gestating and lactating females, body condition has direct consequences on the timing of parturition, birth mass, and early survival of offspring (Parker et al. 2009). Increased human recreation (e.g., motorized and non-motorized) in elk winter range can increase the levels of stress hormones, especially when the recreation is sporadic (Cassirer et al. 1992, Creel et al. 2002). Understanding key nutritional, physiological, and behavioral changes in individuals may provide managers with the opportunity to mitigate the impacts of human disturbance before large-scale population declines occur (Creel et al. 2002).

Population Responses

Behavioral and physiological responses by ungulates to disturbance are the most studied impact due to the ease of monitoring and detecting changes. However, disturbance is only important if it decreases vital rates (i.e., reproduction and survival) and leads to a population decline (Gill et al. 2001). Few studies have been able to link behavioral or physiological responses to changes in abundance, distribution, or demography (Hebblewhite 2011, Johnson and St-Laurent 2011). However, when disturbance is severe, altered vital rates should be detected at higher biological scales. For example, McClure et al. (2005) monitored VHF-collared mule deer on 2 different winter ranges in the Cache Valley of northern Utah. They reported that deer that wintered in an urban area exhibited lower fawn recruitment (measured through fawn:F ratios) compared with deer that wintered in a rural area, even though migratory animals from the herds intermixed on a common, high-elevation summer range. Urban deer had smaller home ranges and selected concealment vegetation, which may have limited forage opportunities and resulted in the difference in fawn survival; however, the mechanisms influencing the differences between urban and rural deer were not specifically tested (McClure et al. 2005).

An understanding of the mechanisms driving population processes is important for developing effective management strategies, predicting the effects of development, and monitoring regulatory requirements (Stankowich 2008, Johnson and St-Laurent 2011). In some cases, survival rates may not be influenced by human development, especially if the majority of mortality is a result of hunting by humans (Webb et al. 2011). Further, because ungulates are generally long-lived, the effects of development on sensitive vital rates (e.g., ad F survival) are difficult to measure accurately in 2- to 3-year studies. A series of studies on mule deer and pronghorn response to energy development in the Jonah and Pinedale Anticline natural gas formations in southwestern Wyoming establish that long-term studies (>5 yr) are needed to detect population-level declines. For mule deer, the 9-year trend in abundance suggests a 36% decline since 2001 (Sawyer et al. 2009b, Sawyer and Neilson 2010), though preliminary data did not detect significant effects. Similarly, after 5 years of monitoring collared pronghorn in control and experimental areas, data revealed population-level avoidance of gas fields with the highest activity levels (Beckmann and Seidler 2009). These results are some of the first to indicate that development pressure can have negative population impacts on vital rates. Without detailed demographic data, the mechanisms influencing changes in abundance and distribution cannot be determined with confidence (Hebblewhite 2011).

Ecological Community Responses

Proximity to human development may also alter interspecific relationships (i.e., predation, competition) and, thus, influence the ecological community composition and distribution (Johnson and St-Laurent 2011). In general, increased housing densities result in a decrease in native species sensitive to human disturbance and an increase in generalist, human-adapted species (Maestas et al. 2003, Hansen et al. 2005, Duguay and Farfaras 2011). Altered species abundance and distribution can impact ecological community dynamics through trophic cascades that are mediated by human activity (Crooks and Soule 1999, Hebblewhite et al. 2005, Berger et al. 2008). For example, human developments may be attractive to ungulates due to the inherent avoidance of human infrastructure by predators (Berger 2007). Conversely, some predators may be drawn into exurban areas by abundant prey species, which results in increasing conflict with humans. Mountain lion (*Puma concolor*)–human interactions are increasing in the West (Riley and Decker 2000) and coyote (*Canis latrans*) populations have increased in residential areas (Grinder and Krausman 2001). As a consequence, public perception of wildlife may decline due to perceived risks to property and personal safety (Riley and Decker 2000, Hudenko et al. 2008).

In circumstances where predator populations are subsidized by an alternative prey species, natural predator–prey dynamics can become decoupled and increased predation can contribute to extinction of native prey (DeCesare et al. 2010). For example, research suggests that mountain lion populations in central New Mexico are subsidized by cattle and, thus, maintain higher population numbers, which has a significant negative impact on bighorn sheep populations (Rominger et al. 2004). Even a small increase in predation through altered spatial relationships among ungulates, predators, and alternate prey could lead to population-level effects in populations with low growth rates (Wehausen 1996).

CONCLUSIONS

The expansion of the human population and, in particular, the associated demand for housing space, will challenge wildlife management with unprecedented impacts on natural systems (Liu et al. 2003). We draw attention to the potential impacts that the conversion of undeveloped land into residential structures has on habitat, behavior, population dynamics, and management of ungulates. Only 25 articles reviewed specifically examined the effects of residential development on ungulates (Table 1). Not one of the studies was a replicated experiment that rigorously analyzed population-level impacts. This is of concern because the demand for new residential spaces is likely to increase in the coming

decades (Theobald 2005, Gude et al. 2007). The effects of exurban development on wildlife may even exceed those of energy- and resource-extraction activities in some areas, in part due to the lack of regulatory oversight and enforceable policies. Although no cause-and-effect studies documented the early influence of residential development on ungulate winter range during the past century, it is probable that this encroachment played a fundamental role in historical mule deer, elk, pronghorn, and bighorn sheep declines in the West (Laliberte and Ripple 2004). Certainly, the low-elevation valleys and mountain foothills that are now occupied by western cities and towns were once important winter ranges to a variety of ungulate species.

White-tailed deer populations expanded in the past century and display high adaptability to human activity. Most studies on white-tailed deer response to residential development have occurred in the eastern or midwestern United States. These studies suggest that deer often select high-quality forage near residential structures and benefit from reduced predation rates and a lack of hunting by humans in proximity to developments (Hygnstrom and VerCauteren 2000, Piccolo et al. 2000, Rhoads et al. 2010). However, there are likely behavioral differences between habituated white-tailed deer in the eastern United States, where very little habitat is available far from residential areas, and deer in the West, where large undeveloped spaces still exist (Vogel 1989). This highlights the need for future research on the response of white-tailed deer to incremental development in undeveloped habitat. Only 5 studies on mule deer and 4 studies on elk analyzed populations in relation to residential development. Results of these articles are inconclusive. In general, mule deer avoid residential areas, but studies were based on indexes of distribution and all had low samples sizes (Smith et al. 1989, Vogel 1989, McClure et al. 2005). No studies have specifically examined the impact of residential development on American pronghorn or bighorn sheep. However, historical declines in both species are likely due to expansion of residential development, resource extraction, and competition with domestic livestock (Valdez and Krausman 1999, Laliberte and Ripple 2004). Barriers to movement, especially in pronghorn migration corridors, are a threat to population persistence (Sawyer et al. 2005). As a rule, bighorn sheep and pronghorn populations require large-scale, multi-jurisdictional initiatives to protect critical migration corridors and winter ranges.

MANAGEMENT IMPLICATIONS

Wildlife persistence is unmistakably dependent on available habitat—habitat that is quickly being compromised by extensive development across the United States. The scale and measured process of piecemeal development in exurbia further confounds the ability of land planners to address cumulative effects. Single development permits, authorized over the span of years, can make it difficult for review boards and planners to decline building permits when an area already contains multiple houses (Travis 2007). Likewise, the synergies between residential and industrial developments are likely to accentuate cumulative effects in new and unforeseeable ways. Current management policies that attempt to mitigate impacts through timing or seasonal restrictions are unlikely to alleviate environmental degradation from increasing exurbanization. Thus, the cumulative impact of multiple low-density residential developments can produce significant ecological effects over time.

Studies need to be designed to evaluate the potential population-level responses of ungulates to residential development, to evaluate the effectiveness of management strategies, and monitor regulatory requirements. Several recent long-term monitoring projects on the effects of energy development on ungulates suggest that demographic impacts may take many years to detect (Beckmann and Seidler 2009, Sawyer and Neilson 2010). Further, ungulates are large and highly mobile. They can, and will, adapt to predictable human disturbance through behavioral adaptations that can mitigate negative consequences on vital rates, at least in the short term and at certain levels of development. Thus, long-term cumulative-effects studies are necessary to clarify the mechanisms that influence changes in abundance and distribution.

Understanding human expectations is also important to manage wildlife in proximity to human developments. Successful management depends on the public's understanding of conservation issues associated with exurban wildlife management and effective consultation with stakeholders (Campa et al. 2011, Hygnstrom et al. 2011, Krausman et al. 2011). The problems that face managers today are too complex to be solved by biologists or managers alone. Specific to ungulates responses to development, we suggest a need for 1) large-scale multi-jurisdictional studies that use all available location data through innovative partnerships; 2) long-term cumulative-effects studies that monitor population-level responses to the increasing growth of residential areas in the West; 3) adaptive management when information is lacking on specific guidelines; and 4) collaboration among land-use planners, wildlife managers, and ecologists to ensure that pertinent research is integrated into regulations and policies.

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