

Increases in residential and energy development are associated with reductions in recruitment for a large ungulate

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Abstract

Land-use change due to anthropogenic development is pervasive across the globe and commonly associated with negative consequences for biodiversity. While land-use change has been linked to shifts in the behavior and habitat-use patterns of wildlife species, little is known about its influence on animal population dynamics, despite the relevance of such information for conservation. We conducted the first broad-scale investigation correlating temporal patterns of land-use change with the demographic rates of mule deer, an iconic species in the western United States experiencing wide-scale population declines. We employed a unique combination of long-term (1980–2010) data on residential and energy development across western Colorado, in conjunction with congruent data on deer recruitment, to quantify annual changes in land-use and correlate those changes with annual indices of demographic performance. We also examined annual variation in weather conditions, which are well recognized to influence ungulate productivity, and provided a basis for comparing the relative strength of different covariates in their association with deer recruitment. Using linear mixed models, we found that increasing residential and energy development within deer habitat were correlated with declining recruitment rates, particularly within seasonal winter ranges. Residential housing had two times the magnitude of effect of any other factor we investigated, and energy development had an effect size similar to key weather variables known to be important to ungulate dynamics. This analysis is the first to correlate a demographic response in mule deer with residential and energy development at large spatial extents relevant to population performance, suggesting that further increases in these development types on deer ranges are not compatible with the goal of maintaining highly productive deer populations. Our results underscore the significance of expanding residential development on mule deer populations, a factor that has received little research attention in recent years, despite its rapidly increasing footprint across the landscape.

Keywords: Colorado, demography, fawn ratios, land-use change, *Odocoileus hemionus*, residential development, weather, winter range

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Introduction

The human footprint is expanding rapidly on landscapes across the globe (Vitousek *et al.*, 1997; Leu *et al.*, 2008), a pattern that has been associated with reduced biodiversity, range contractions, and increased extinction risk for wildlife (Ceballos & Ehrlich, 2002; McKee *et al.*, 2004; Davies *et al.*, 2006). Infrastructure and activities related to residential development, resource extraction, transportation, recreation, and other forms of human land-use can negatively influence wildlife through a variety of means. Animals can be affected

through direct mortality, increased disturbance, altered relationships with competitors and predators, and through the loss and degradation of critical habitat resources (see reviews by Krausman *et al.*, 2011; Northrup & Wittemyer, 2013). Given that people and wildlife often select similar biophysical features of the landscape, land-use change frequently occurs in areas of high biological productivity, potentially having disproportionate effects on wildlife (Hansen *et al.*, 2005; Leu *et al.*, 2008).

Changes in land-use are often observed to influence wildlife behavior (Tuomainen & Candolin, 2011), but relatively little is known about the influence of land-use change on the demography of populations. Animals frequently avoid human infrastructure and activities by

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modifying their patterns of movement (Sawyer *et al.*, 2013) and habitat use (Nellemann *et al.*, 2007), exhibiting large-scale displacement (Sawyer *et al.*, 2006), increasing vigilance activities (McCleery, 2009), and altering foraging strategies (Robinson *et al.*, 2010). Such changes in behavior likely influence individual fitness, and ultimately, population performance, but research demonstrating these effects on the dynamics of animal populations is limited (Polfus & Krausman, 2012; Northrup & Wittemyer, 2013; Wong & Candolin, 2015). Because land conversion often occurs in spatially complex and temporally dynamic patterns (Ramalho & Hobbs, 2012), and animals alter their behavior to mediate the negative consequences of land-use change, demographic impacts may be weak, gradual, or exhibit lag effects (Hansen *et al.*, 2005; Harju *et al.*, 2010) that are difficult to detect during routine monitoring activities or over short time periods.

Residential housing and energy development are two types of land-use change that are increasing rapidly across the western United States (Vias & Carruthers, 2005; Leu *et al.*, 2008; Copeland *et al.*, 2009) and around the world (McMichael, 2000; Hansen *et al.*, 2005; International Energy Agency 2015). Over the past few decades, the intermountain west has experienced some of the highest rates of human population growth in the country (Vias & Carruthers, 2005) fueling dramatic increases in the number of residential housing units, particularly outside of metropolitan areas. Increases in rural and exurban development (low-density residential housing) have outpaced growth from other forms of residential land-use (Brown *et al.*, 2005). Low-density housing is characterized by having a highly dispersed spatial pattern, close juxtaposition to undeveloped public lands, and strong association with key habitat features (i.e., valley bottoms), factors that are likely to result in disproportionate impacts to wildlife (Theobald *et al.*, 1997; Leu *et al.*, 2008; Leinwand *et al.*, 2010). While research on the effects of rural and exurban development on wildlife is limited, there is evidence that low-density housing can reduce habitat use, survival, and reproduction for some species (Hansen *et al.*, 2005; Goad *et al.*, 2014). Infrastructure and activities related to oil and gas development (*hereafter* energy development) have also increased rapidly due to the rise in the global demand for energy (Copeland *et al.*, 2009). Between 1985 and 2006, energy development expanded by an estimated 20% per year in some areas (Walston *et al.*, 2009), with millions of additional hectares expected to be impacted in the future (Copeland *et al.*, 2009). The construction and use of wells, well pads, roads, and pipelines, along with the associated noise and vehicular traffic, have altered animal habitat-use patterns (Sawyer *et al.*, 2006; Northrup *et al.*, 2015),

have reduced survival and reproduction (Holloran *et al.*, 2010; Dzialak *et al.*, 2011), and have been linked to population declines (Sorensen *et al.*, 2008).

Over the past few decades, while land-use change has been pervasive across the intermountain west, mule deer (*Odocoileus hemionus*) populations have generally declined (Idaho Department of Fish and Game 1999; Gill, 2001; Heffelfinger & Messmer, 2003; Bergman *et al.*, 2015). Mule deer populations are known to fluctuate, but significant decreases in population estimates across multiple western states have generated concern, as mule deer are an iconic species with tremendous ecological, recreational, and economic value. Drivers of mule deer declines are largely unknown, and likely multifaceted, but evidence suggests that habitat conditions play a pivotal role (Gill, 2001; Bishop *et al.*, 2009; Hurley *et al.*, 2014; Monteith *et al.*, 2014; Shallow *et al.*, 2015). To date, research on habitat has primarily focused on the influence of forage quality, cover type, and local climate conditions on mule deer dynamics, but land-use change may also be important (Polfus & Krausman, 2012). Studies have found that mule deer reduce their selection of habitat near residential and energy development, effectively decreasing the area that is functionally available (Vogel, 1989; Sawyer *et al.*, 2009; Northrup *et al.*, 2015). While few studies have investigated the consequences of this behavior on ungulate demography, urban housing has been associated with reduced recruitment in a local mule deer herd (McClure *et al.*, 2005) and energy development has been associated with reduced survival in a population of elk (*Cervus elaphas*; Dzialak *et al.*, 2011). Given the expanding human footprint across western landscapes, it is critical for wildlife and land management agencies to quantify the impacts of land-use change on mule deer habitat and understand the degree to which different types of development may be contributing to population declines.

To examine the influence of residential and energy development on mule deer populations, we employed a unique combination of long-term data on land-use change with long-term data on mule deer recruitment. We evaluated both data types annually across western Colorado between 1980 and 2010, a time period when major changes in development and deer populations occurred. The broad extent of our study area allowed us to account for temporal dynamics in land-use change (Ramalho & Hobbs, 2012) and demography across multiple deer populations. This design provided a powerful opportunity to examine multiple factors correlated with deer performance, which would be difficult to achieve over a short time period or within a single study population. We used deer recruitment (the proportion of 7–8 month olds/100 adult females) as

our demographic rate of interest because this parameter exhibits high variation, is sensitive to environmental conditions, is minimally affected by harvest regulations, and is typically the most influential vital rate driving ungulate population growth (Gaillard *et al.*, 2000; Forrester & Wittmer, 2013).

In addition to assessing annual changes in residential and energy development on mule deer ranges, we also assessed annual variation in weather conditions and their relationship with deer recruitment. Weather factors, such as winter severity and summer precipitation, are well recognized to influence ungulate productivity through their direct effects on juvenile condition and survival and through their indirect effects on maternal condition (Hurley *et al.*, 2011, 2014; Monteith *et al.*, 2015). By including weather variables in our analysis, we were able to compare the relative associations between land-use change and recruitment to well-known associations between weather and recruitment. Specifically, we evaluated recruitment with respect to temperature and precipitation during the winter just prior to parturition, in June when fawns were born, and throughout the following summer, critical time periods for influencing both maternal condition and juvenile survival (Cook *et al.*, 2004; Gilbert & Raedeke, 2004; Hurley *et al.*, 2011). Given these considerations, our research objectives were to (i) quantify annual changes in residential development, energy development, and weather conditions within mule deer winter and summer ranges and (ii) test for associations between those annual changes in habitat conditions and annual rates of deer recruitment.

Materials and methods

Study area

We analyzed data from areas of Colorado west of Interstate 25 (164 346 km²; Fig. 1). This area included 44 deer data analysis units (DAUs) delineated by Colorado Parks and Wildlife (CPW), which are intended to represent discrete deer populations and are the primary unit for deer management in the state. These DAUs included mule deer populations that are predominantly migratory, moving seasonally between distinct winter and summer ranges. The total number of deer estimated within these units varied between 348 200 and 585 200 over the study period and comprised approximately 90% of the mule deer in the state.

For each DAU, CPW has identified mule deer winter and summer ranges, delineations that are routinely used by public and private entities for environmental assessment, resource planning, and scientific inference. Winter ranges are defined as those areas where 90% of the deer are located during an average winter from the first heavy snow to spring green-up. Summer ranges are those areas where 90% of the deer are

located during the remainder of the year. CPW used a variety of data sources to identify seasonal ranges including information from ground surveys, annual aerial surveys, telemetry collars, and expert opinion. On average, DAUs were 3735 km² in size, while winter and summer ranges were 1653 km² and 2900 km², respectively.

Land-use and weather data

We used the Spatially Explicit Regional Growth Model (SER-GoM) dataset (Bierwagen *et al.*, 2010) to estimate changes in residential development over time. This nationwide dataset models housing density on private lands by decade at a spatial resolution of 100 m. At each time step, pixels were classified as either undeveloped (0 housing units/ha) or developed at rural (<0.03 units/ha), exurban (0.03–0.59 units/ha), suburban (0.60–5.00 units/ha), or urban (>5.00 units/ha) densities. We calculated the total area and proportion of each DAU, and winter and summer ranges within DAUs, covered by each category of residential development. We used linear interpolation to estimate annual values within each decade for all developed categories (i.e., not for pixels classified as 'undeveloped'). We also calculated the total proportion of developed land as the sum of all residential development categories.

Point locations of all oil and gas wells in the study area (conventional gas, oil and carbon dioxide, unconventional gas and oil, and disposal wells) were used to examine patterns of energy development on deer ranges. Well locations were obtained from the Colorado Oil and Gas Conservation Commission and were attributed with the first date of activity (initiation of drilling). Of the 86 999 wells drilled in Colorado, the date of first activity was unknown for 8% and we excluded these from our analyses. We identified areas within 200 m, 700 m, and 2700 m of all wells at a 100-m resolution; we chose these buffer distances based on prior studies demonstrating reduced selection of habitat by mule deer within those distances of wells (Sawyer *et al.*, 2006; Northrup *et al.*, 2015). On an annual basis, we calculated the proportion of each DAU, winter and summer range within the three buffer distances of a well, given the first year that drilling was recorded for individual well sites. These areas depicted cumulative impacts of energy development over time.

To assess weather conditions that may influence deer recruitment, we used historic data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM; www.prism.oregonstate.edu). The model depicts precipitation and temperature on a monthly basis at an 800-m resolution. Across each summer range, we calculated the mean minimum temperature in June (°C), total precipitation in June (cm), cumulative average precipitation from May through September (cm), and the average maximum temperature from June through August (°C). June is the month that fawns are born, and we suspected that their survival may be reduced by cold, wet weather (Gilbert & Raedeke, 2004). Meanwhile, summer precipitation has been correlated with forage quality (Blanchard *et al.*, 2003), increased recruitment (Hurley *et al.*, 2011),

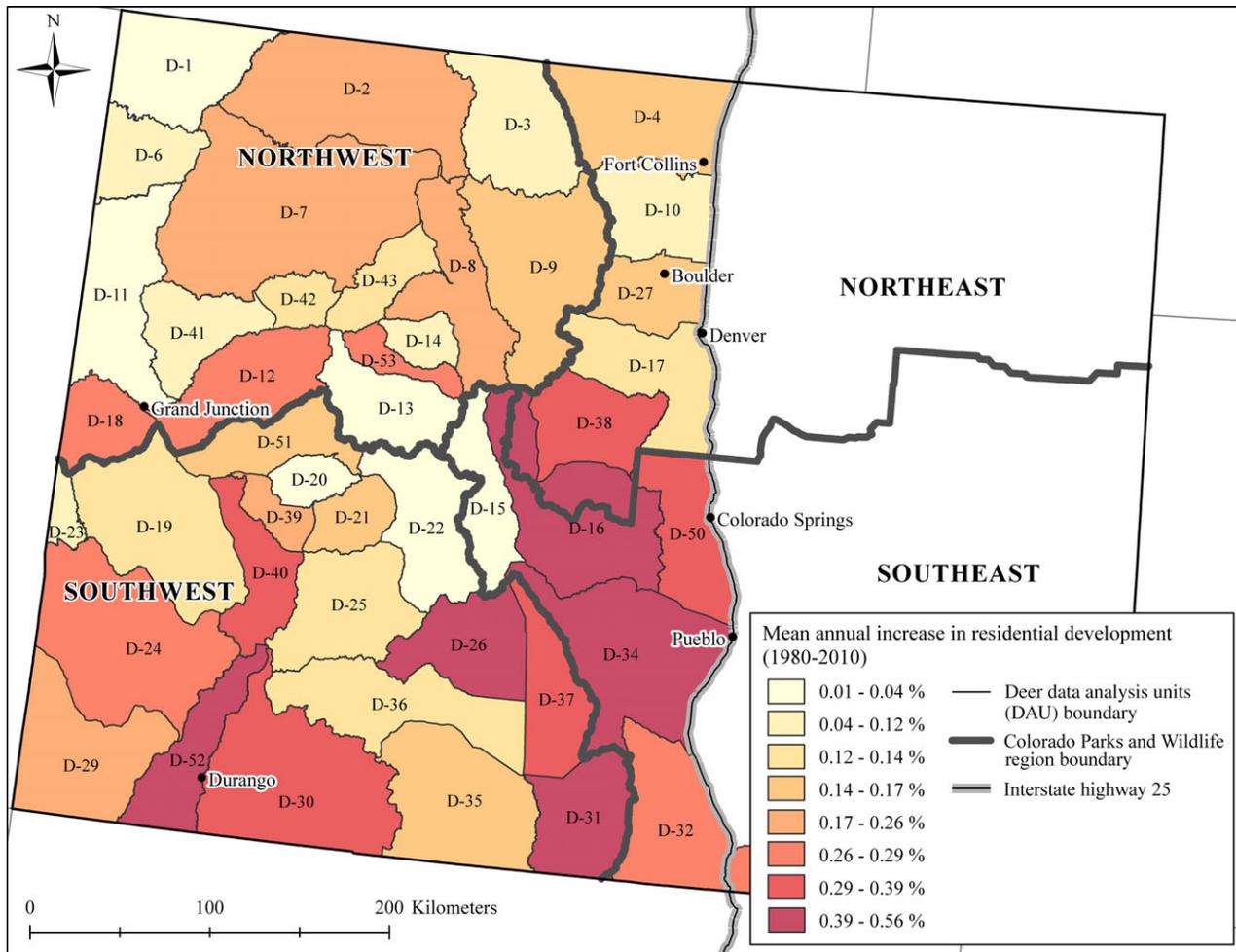


Fig. 1 Map of deer data analysis units (DAUs) and regions in Colorado designated by Colorado Parks and Wildlife. Colors represent the average annual rate of increase in total residential development between 1980 and 2010.

and maternal condition in ungulates (Cook *et al.*, 2004), while high summer temperatures have been associated with smaller litter sizes (Monteith *et al.*, 2014) and reduced recruitment (Monteith *et al.*, 2015). Across each winter range, we calculated cumulative average precipitation (cm) and average minimum temperatures ($^{\circ}\text{C}$) between December and March. These metrics were used to indicate winter severity, as harsh winters prior to parturition can reduce maternal condition in ungulates (Parker *et al.*, 2009).

Mule deer data

Between 1980 and 2010, posthunting season helicopter surveys were conducted in each mule deer DAU in most years. Surveys occurred between 1 December and 15 January; survey data collected in January were considered data from the previous calendar year (the biological birth year of the fawns). During surveys, nonrandom paths were flown across the winter ranges with the purpose of observing a representative sample of deer to assess herd composition. Deer were classified as adult females, fawns (7–8 month olds), or males based on body size and antler morphology (mean number of deer

classified/DAU/year = 1507). Annual ratios of the number of fawns/100 adult females ($n = 904$ fawn ratios) and the number of males/100 adult females ($n = 694$ male ratios) for each DAU were calculated from classification data. We also recorded CPW's estimate of the number of female deer harvested during hunting seasons in each year for each DAU.

We used annual fawn ratios as our measure of fawn recruitment. In actuality, fawn ratios (R) are a function of year-specific birth rates (B), juvenile survival rates (S_J), and adult female survival rates (S_A) following the equation:

$$R = 100 \times B \times \frac{S_J}{S_A}$$

Given that juvenile survival in ungulates is extremely variable, while the birth rate and adult female survival tend to be consistently high (Gaillard *et al.*, 2000; Forrester & Wittmer, 2013), these ratios are strongly correlated with juvenile survival and thus recruitment (Raithel *et al.*, 2007; Harris *et al.*, 2008). While fawn ratios were the primary response variable in our analyses, male ratios and the number of females harvested were included as key covariates. Male ratios largely depend on variation in annual male survival,

which is primarily driven by DAU-specific harvest rates in Colorado (Bergman *et al.*, 2011). High male ratios have been found to be inversely related to fawn ratios, presumably as a consequence of density-dependent effects (Bergman *et al.*, 2011, 2015). Female harvest was included as a covariate because the fawn ratio is expected to be higher when more adult females are killed.

Examining associations between changes in land-use and weather with deer recruitment

We quantified annual changes in residential development, energy development, and weather conditions between 1980 and 2010, years when mule deer ratios were also collected. We estimated the temporal trends in these conditions for each DAU, winter and summer ranges by fitting linear mixed models (LMMs; Pinheiro & Bates, 2000) with 'year' as the explanatory variable. We included DAU as a random intercept to account for repeated measurements over time. In addition to estimating mean trends in habitat conditions across DAUs, we also estimated trends for individual DAUs by treating DAU as a fixed effect and interacting DAU with 'year'.

Because there was high potential for multicollinearity among variables, we did not initially fit a single global model, but first investigated the univariate relationships between covariates and fawn recruitment and assessed the correlations among covariates. We used LMMs with a random intercept for DAU; land-use and weather variables that were associated with fawn ratios (80% confidence intervals were nonoverlapping zero) were retained for further modeling (Table S1). We evaluated residential development variables with respect to recruitment only in the current year t (no lag effects), due to linear interpolation of many values. Because the proportions of urban and suburban development within DAUs were so small (<0.05%), we limited our analyses to proportions of rural, exurban, and total development. Energy development variables were evaluated with respect to fawn recruitment in year t and year $t-1$, as we assumed that there may be lag effects for energy impacts, which has been found for other species (Harju *et al.*, 2010). We assessed all summer and winter weather metrics with respect to fawn recruitment in year t , and we also assessed the lag effects (year $t-1$) for summer and winter precipitation and temperature. We expected that cold, wet weather in June could be especially detrimental for fawn survival, so we tested for an interaction between June temperatures and precipitation. We found evidence for this interaction ($\beta = 0.2032$, $SE = 0.0961$; 95% confidence interval did not overlap zero) and thus included June temperature and precipitation as a 'June weather' interaction term (with main effects) for all further modeling. We also tested for an interaction between winter temperature and precipitation, as we expected that cold winters with high precipitation would be particularly detrimental to subsequent recruitment. There was no evidence for a significant interaction ($\beta = 0.0538$, $SE = 0.0374$; 95% confidence interval was overlapping zero), and so we excluded this effect from further modeling.

From those variables associated with fawn recruitment, we first examined pairwise correlations among variables within

each land-use or weather factor. When variables were highly correlated (Pearson's correlation coefficient $r > |0.6|$), we retained the variable that exhibited a stronger relationship with recruitment based on univariate t -values. Among the residential development variables, % total development across the DAU had the strongest univariate relationship with fawn ratios (Table S1). This variable was highly correlated with all other development variables ($r \geq 0.70$) except for exurban development on winter range ($r = 0.56$) so we retained only these two variables for further analyses. For energy development, the variables associated with fawn ratios were % summer range $_{(t-1)}$ and winter range $_{(t \text{ and } t-1)}$ within 2700 m of a well (Table S1). Due to a high correlation between those variables ($r \geq 0.93$), we only retained % winter range within 2700 m of well $_{(t-1)}$. Except for summer maximum temperatures, all weather variables were associated with fawn recruitment. June minimum temperatures were correlated with winter minimum temperatures $_{(t \text{ and } t-1)}$ ($r \geq 0.60$), and winter temperatures were also correlated across years $_{(t \text{ and } t-1)}$ ($r = 0.68$); we removed winter temperatures from further analyses.

Our final variable set included % total development across the DAU $_{(t)}$, % exurban development on winter range $_{(t)}$, % winter range within 2700 m of a well $_{(t-1)}$, summer precipitation $_{(t)}$, winter precipitation $_{(t \text{ and } t-1)}$, and June weather $_{(t)}$. We checked for correlations among these variables, but none were highly correlated ($r < 0.4$). We then tested for interactions between some variables across factors with respect to fawn recruitment. We tested for an interaction between energy development and total residential development because we expected that there may be a synergistic effect between these development types on mule deer. We also tested for interactions between energy development on winter range and winter precipitation and between exurban development on winter range and winter precipitation; we assumed that the impacts of development on winter range may be particularly pronounced during harsh winters. There was only evidence for an interaction between energy development and precipitation on winter ranges ($\beta = 0.0112$, $SE = 0.0044$; 95% confidence interval did not overlap zero) so we retained this interaction (and its main effects) for further modeling.

From those variables that were retained, we then conducted model selection on all subsets of variables (Table S2). We used LMMs with a random intercept for DAU and assessed model assumptions by checking residual and fitted values and using quantile-quantile plots of the residuals of fixed and random effects. Where energy development and precipitation on winter range occurred in the same model, we also tested a model with an interaction between those variables (31 additional models). Given a strong association between male deer ratios in year $t-1$ with fawn ratios in year t (Table S1; Bergman *et al.*, 2011), and an association between female harvest and fawn ratios in year t (Table S1), we also included these variables as nuisance parameters in all models. We did not have male ratio data in year $t-1$ for all observations of fawn ratios, but male ratios were highly temporally correlated ($r = 0.75$) so we used linear

interpolation to generate missing values between years with observed ratios. When the first male ratio in a time series for a DAU was missing, we assumed that the ratio in year t was the same as in year $t + 1$. Univariate coefficients for the association between fawn recruitment (year t) and male ratios (year $t-1$) for the actual data ($\beta = -0.1104$, $SE = 0.0412$) and the interpolated data ($\beta = -0.1284$, $SE = 0.0400$) were similar.

We calculated AIC_c , ΔAIC_c , and the weight of each model (Burnham & Anderson, 2002). Because several models had similar AIC_c scores, we averaged all models (based on model weights) with weights > 0 to obtain final parameter estimates. The coefficient for a variable was averaged from all models where that variable was present, using unconditional standard errors (Burnham & Anderson, 2004). Additionally, we calculated standardized coefficients (averaged across the same top set of models) to assess the relative effects of different covariates on fawn recruitment (Schielzeth, 2010). To estimate standardized coefficients, we ran models using predictor variables that were centered and scaled. All models were fit with maximum-likelihood estimation using the package 'lme4' (Bates *et al.*, 2013) in program R version 3.0.2 (R Core Team 2013). Model averaging was conducted with the R package 'MuMIn' (Barton, 2013).

Results

Changes in land-use and weather

Between 1980 and 2010, an additional 1 004 331 ha of DAUs were impacted by changes in residential development (96% was rural or exurban), representing a 37% increase in residential land-use in deer DAUs within that time. Increases in residential development were significant for all density classes, particularly on mule deer winter ranges (Table 1). On average, 23.8% of deer winter ranges overlapped with residential development in 1980, while 31.2% overlapped with development in 2010. On average, 14.0% of deer summer ranges overlapped with development in 1980 and 19.5% in 2010. Increases in residential development varied widely among deer DAUs (Fig. 1). By 2010, between 0.7% and 66.0% of DAU winter ranges overlapped with residential development, while between 0.8% and 46.0% of summer ranges overlapped with residential development.

Table 1 Model parameters from testing for temporal changes to mule deer winter and summer ranges from residential development, energy development, and weather conditions from 1980 to 2010. We report the mean changes in habitat conditions across all deer data analysis units (DAUs) and for individual DAUs (estimated using random coefficients). We also report temporal trends in fawn ratios (fawns/100 adult female deer), male ratios (males/100 adult female deer), and female deer harvest, which are relevant to the entire DAU

Habitat variable	Deer range	All DAUs			Range of β among DAUs
		Estimate	SE	t	
Residential development (%)					
Rural	Winter	0.1016	0.0073	13.96	-0.600, 0.716
Exurban	Winter	0.1357	0.0046	29.24	0.010, 0.835
Total development	Winter	0.2460	0.0057	43.27	0.000, 0.850
Rural	Summer	0.1127	0.0051	22.19	-0.270, 0.651
Exurban	Summer	0.0658	0.0022	30.17	0.000, 0.332
Total development	Summer	0.1845	0.0045	40.78	0.017, 0.650
Energy development (%)					
200 (m)	Winter	0.0299	0.0022	13.76	0.000, 0.318
700 (m)	Winter	0.1259	0.0083	15.21	0.000, 1.229
2700 (m)	Winter	0.2376	0.0117	20.39	0.000, 1.441
200 (m)	Summer	0.0128	0.0013	9.94	0.000, 0.262
700 (m)	Summer	0.0658	0.0053	12.51	0.000, 1.018
2700 (m)	Summer	0.1754	0.0105	16.64	0.000, 1.908
Weather variables					
Winter Precip (cm)	Winter	-0.0067	0.0106	-0.63	0.012, 0.075
Winter Min Temp (°C)	Winter	0.0294	0.0041	7.23	-0.055, 0.053
June Min Temp (°C)	Summer	0.0440	0.0033	13.33	-0.276, -0.052
June Precip (cm)	Summer	-0.0141	0.0058	-2.42	-0.090, 0.150
Summer Precip (cm)	Summer	-0.1622	0.0161	-10.10	0.005, 0.046
Summer Max Temp (°C)	Summer	0.0200	0.0032	6.34	0.002, 0.052
Fawn ratio	DAU	-0.4986	0.0598	-8.34	-8.501, 0.172
Male/female ratio	DAU	0.6825	0.0317	21.51	-3.076, 1.276
Female harvest	DAU	-7.8143	1.4400	-5.43	-26.590, -0.077

Over the course of the study, the area within 200 m, 700 m, and 2700 m of wells on mule deer ranges increased by 118 295, 539 830, and 1 250 654 ha, respectively. Given these three buffer distances, this equated to an increase in the area impacted on deer ranges of 246%, 146%, and 56%, respectively. The proportions of both winter and summer ranges affected by energy development increased significantly over time at all spatial scales, although winter ranges experienced the greatest impacts (Table 1). In 1980, across all DAUs, the average proportion of winter range within 200 m of a well was 0.2%, within 700 m was 2.5%, and within 2700 m was 16.7%; in 2010, it was 1.1%, 6.3%, and 23.8%, respectively. Similarly, in 1980, the average proportion of summer range within 200 m of a well was 0.1%, within 700 m was 1.2%, and within 2700 m was 10.3%; in 2010, it was 0.5%, 3.2%, and 15.6%, respectively. Increases in energy development varied widely among DAUs (Table 1). By 2010, up to 9% of a winter range was within 200 m of well, up to 39% was within 700 m of well, and up to 80% was within 2700 m of a well. By 2010, up to 8% of a summer range was within 200 m of a well, up to 29% was within 700 m of a well, and up to 68% was within 2700 m of a well.

Seasonal temperature metrics increased significantly over time, while seasonal precipitation metrics significantly decreased. The only exception to this pattern was winter precipitation which displayed no temporal trend (Table 1). Between 1980 and 2010, models estimated that on average, June mean minimum temperatures increased from 3.91 °C to 5.23 °C, summer mean maximum temperatures increased from 21.98 °C to 22.58 °C, winter mean minimum temperatures increased from -10.72 °C to -9.84 °C, June precipitation decreased from 3.42 cm to 3.00 cm, and summer precipitation decreased from 26.29 cm to 21.42 cm.

Changes in mule deer ratios

The mean fawn ratio across all DAUs over the course of the study was 56.0 fawns/100 adult females (SE = 13.6), with mean ratios in different DAUs ranging between 42.9 and 76.6. Across all DAUs, in 1980 the modeled mean ratio was 65.4 (SE = 1.4), and in 2010, it was 50.4 (SE = 1.3, Table 1). Over the course of the study, recruitment decreased by an average of 0.5 fawns/100 adult females/year (Table 1). Rates of change were highly variable among DAUs. Forty DAUs exhibited declining trends over time, while 4 DAUs exhibited slightly increasing trends (Fig. 2), with the rates of change varying between -8.50 to 0.15 fawns/100 adult females/year. Between 1980 and 2010, the ratio of adult male to adult female mule deer significantly increased (Table 1). In 1980, the mean was 13.5

adult males/100 adult females (SE = 1.1), and by 2010, the mean was 34.0 adult males/100 adult females (SE = 1.0). Female deer harvest significantly decreased over time (Table 1), as in 1980 the mean number of females harvested in a DAU was 384.1 (SE = 52.5) and by 2010 it was 149.7 (SE = 49.3).

Associations between changes in land-use and weather with deer recruitment

We ran a total of 160 models to investigate the effects of land-use change and weather on fawn recruitment. These models included all subsets of our final seven variables (refer to Methods for details) with additional models to test for an interaction between precipitation and energy development on winter range (Table S2). A total of 28 models had a weight > 0 and were included in model averaging. Considering those models, the top model accounted for 21% of the model weight and included all variables (and interactions) except for exurban development on winter range. The second best model, accounting for 16% of the model weight, included the same variables, but omitted summer precipitation.

Fawn ratios decreased in association with increasing residential development, energy development, June minimum temperatures, and winter precipitation prior to parturition (Table 2, Figs 3 and 4a). Fawn ratios increased in association with winter precipitation in the previous year (lag effect; Table 2, Fig. 3). There was a significant interaction between energy development and precipitation on winter range, suggesting that

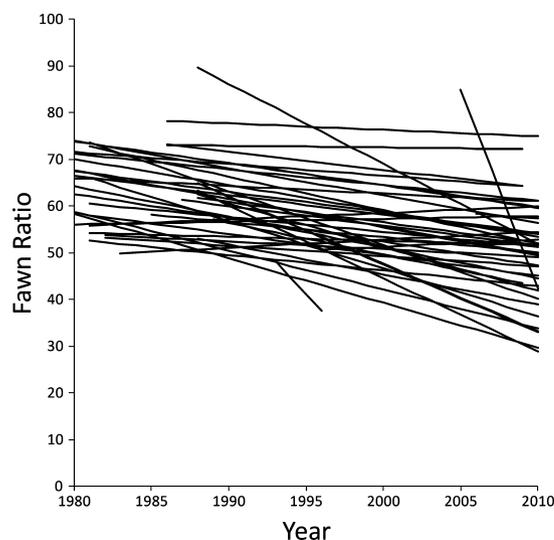


Fig. 2 Temporal trends in mule deer fawn ratios (the proportion of 7–8 month olds/100 adult females) for deer data analysis units in Colorado, 1980–2010.

Table 2 Unstandardized and standardized model-averaged coefficients (and 95% confidence intervals) for associations between mule deer fawn ratios and habitat variables for deer data analysis units (DAUs) in western Colorado. Model parameters are listed in order of the magnitude of their standardized coefficients, and identify whether they are correlated with fawn ratios in the current year (t) or the following year (lag effect; $t-1$). 'Range' signifies whether the variable was summarized across the winter range, summer range, or over the entire DAU

Model parameter	Range	Unstandardized coefficients				Standardized coefficients			
		β	SE	L95%	U95%	β	SE	L95%	U95%
Intercept	–	68.351	5.294	57.975	78.727	56.923	1.387	54.204	59.642
Total residential develop _(t)	DAU	–0.310	0.128	–0.561	–0.059	–2.892	1.178	–5.201	–0.583
Energy Develop _(t-1)	Winter	–0.191	0.083	–0.354	–0.028	–1.462	1.149	–3.714	0.790
Winter Precip _(t-1)	Winter	0.308	0.115	0.083	0.533	1.317	0.492	0.353	2.281
Winter Precip _(t)	Winter	–0.508	0.190	–0.880	–0.136	–1.215	0.504	–2.203	–0.227
June Min Temp _(t)	Summer	–1.133	0.440	–1.995	–0.271	–1.214	0.879	–2.937	0.509
Energy Develop _(t-1) * Winter Precip _(t)	Winter	0.012	0.004	0.004	0.020	1.083	0.414	0.272	1.894
June Min Temp _(t) * June Precip _(t)	Summer	0.198	0.095	0.012	0.384	0.949	0.454	0.059	1.839
Summer Precip _(t)	Summer	0.142	0.082	–0.019	0.303	0.886	0.508	–0.110	1.882
% Exurban development _(t)	Winter	–0.124	0.207	–0.530	0.282	–0.734	1.206	–3.098	1.630
Male/female ratio _(t-1)	DAU	–0.054	0.044	–0.140	0.032	–0.600	0.492	–1.564	0.364
Female deer harvest _(t)	DAU	0.001	0.001	–0.001	0.003	0.469	0.526	–0.562	1.500
June Precip _(t)	Summer	–0.739	0.190	–1.111	–0.367	0.366	0.500	–0.614	1.346

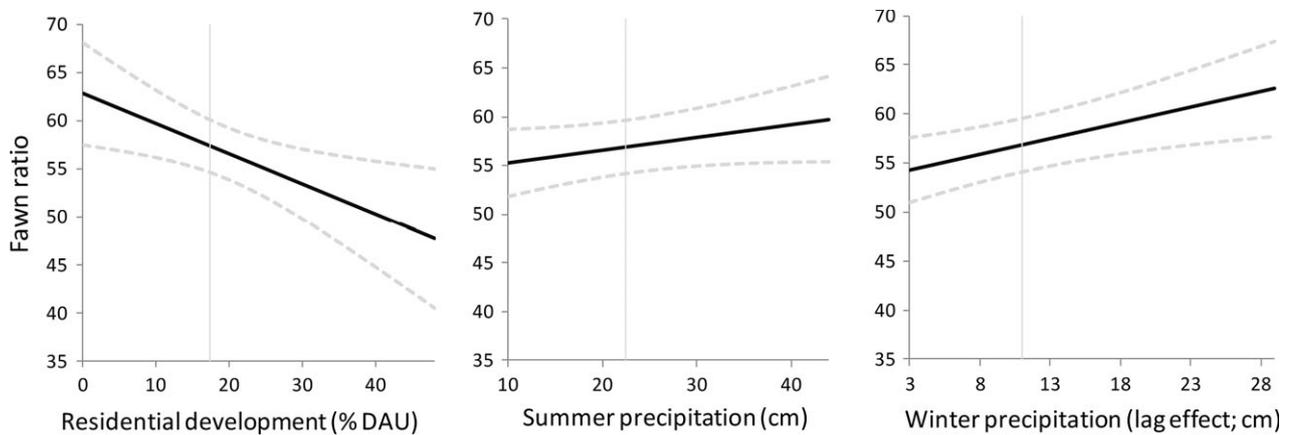


Fig. 3 Modeled predicted effects of the proportion of residential development (across deer data analysis units), summer precipitation, and winter precipitation on mule deer fawn ratios in western Colorado. The effects of residential development and summer precipitation are depicted for the current year (t), and winter precipitation is depicted in the previous year (two winters prior to parturition; year $t-1$). Predictions are based on the top linear mixed-effect model and are shown across the observed range of variation for covariate values. Median covariate values are depicted by the gray lines.

winter severity had the greatest effect on fawn recruitment when energy development was minimal and dampened as the proportion of energy development increased (Fig. 4b). Fawn recruitment was predicted to be highest when both winter precipitation and energy development were low. There was also a significant interaction between June temperature and precipitation, which indicated that cold weather was most beneficial for fawn recruitment when precipitation was low,

while warm weather was most beneficial when precipitation was high (Fig. 5). There were other variables that were included in the top model set, but had coefficients with confidence intervals overlapping zero. These were summer precipitation and female deer harvest, which both had a positive association with recruitment, and exurban development and the male ratio (in the previous year), which both had a negative association with recruitment (Table 2).

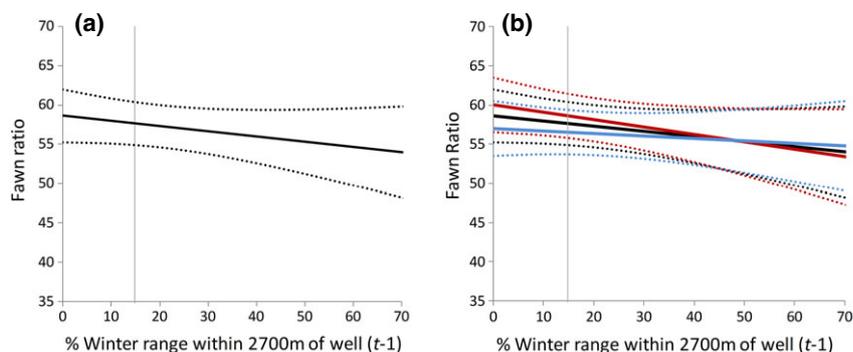


Fig. 4 Modeled predicted effects of the interaction between energy development (the proportion of winter range within 2700 m of a well) and winter precipitation on mule deer fawn ratios in western Colorado. Energy development is modeled with a lag effect (year $t-1$), and winter precipitation is modeled just prior to parturition (year t). Predicted fawn ratios for a) the observed range of energy development values given the median amount of winter precipitation (11.0 cm) and b) for the 25% (red lines), 50% (black lines), and 75% (blue lines) quartiles of winter precipitation values. The median value of energy development is depicted with a gray line.

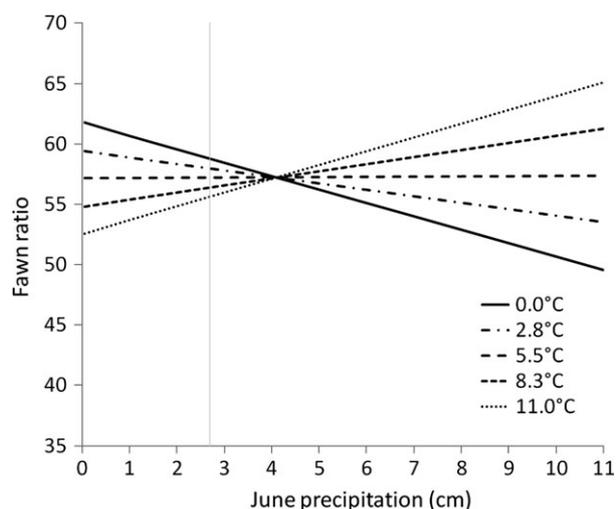


Fig. 5 Modeled predicted effects of the interaction between June minimum temperature and precipitation on mule deer fawn ratios in Colorado (modeled for the current year t). Predictions were based on the top linear mixed-effect model and are shown across the range of observed temperature and precipitation values. The median value for June precipitation is depicted by the gray line.

Standardized coefficients of the main effects suggested that residential development had the largest effect on fawn recruitment, having approximately 2 times the magnitude of any other effect. Fawn ratios were predicted to vary by approximately 15 fawns/100 adult females across the observed range of residential development values. Energy development had the second largest effect on recruitment, followed closely by the weather variables (Table 2).

Discussion

Land-use change due to residential and energy development is projected to increase rapidly in the western

United States (Theobald, 2005; Copeland *et al.*, 2009) and around the world (Seto *et al.*, 2012; International Energy Agency 2015). Land-use change is often associated with shifts in animal behavior (Tuomainen & Candolin, 2011) and habitat use (Nellemann *et al.*, 2007), with most studies focusing on short-term effects (<10 years) at relatively local scales (within a municipality or county; Pejchar *et al.*, 2015). Researchers have hypothesized that land-use change may have long-term or lagged effects on animal population dynamics (Hansen *et al.*, 2005; Harju *et al.*, 2010), but this has rarely been evaluated empirically. We combined broad-scale, long-term data on land-use change and mule deer demography to conduct the first analysis to quantify the impacts from residential and energy development to deer habitat and to correlate those changes with deer demographic performance. Our results indicate that declining recruitment rates are correlated with expanding residential and energy development, particularly within deer winter ranges. Comparing the relative associations between recruitment and land-use and weather factors, we found that residential housing had two times the magnitude of effect of any other factor correlated with recruitment and that energy development had an effect size similar to key weather variables known to be important to juvenile deer survival (Hurley *et al.*, 2011, 2014; Monteith *et al.*, 2015).

While residential development and energy development were associated with declining fawn recruitment, the specific mechanisms responsible for these correlations are unknown. Land-use change causes direct habitat loss and fragmentation through the construction of infrastructure, and indirect habitat loss through deer avoidance of infrastructure and related activities (Vogel, 1989; Sawyer *et al.*, 2009; Northrup *et al.*, 2015); these consequences likely

reduce the carrying capacity of the landscape. It has also been documented that deer migrating through areas with high densities of energy development detour from established routes, increase rates of movement, and reduce stopover use (Sawyer *et al.*, 2013), impacts that may increase energetic costs while decreasing access to high-quality forage. Additionally, mule deer may suffer higher mortality rates in developed landscapes compared to natural areas (but see Hebblewhite & Merrill, 2011). Deer in close proximity to residential housing can experience increased vehicle collisions, harvest, poaching, accidents (i.e., entrapment in fences), and predation from domestic pets (Porter *et al.*, 2004; Krausman *et al.*, 2011). Deer in the vicinity of energy development may also experience higher rates of vehicle collisions, harvest, and poaching, particularly as a function of the associated road network (Dzialak *et al.*, 2011). We suspect that several of these factors contribute to the negative association between land-use change and deer recruitment, but experimental research is needed to identify the specific mechanisms responsible.

Both types of land-use change were correlated with declining recruitment rates, but the relationship with residential housing was much stronger than that of energy production. We suspect that risks for mule deer are more pervasive around residential housing where human activities are continuous or may increase over time (i.e., as the human population and housing densities increase), compared to areas impacted by energy development where disturbance typically declines over time (i.e., as new drilling and construction of infrastructure wane, see Northrup *et al.*, 2015). Rural and exurban housing are also likely to be constructed in areas of particularly high-quality mule deer habitat, especially on winter ranges where the same biophysical features selected by deer are also often selected by people (i.e., low-elevation valley bottoms with minimal snow and high solar radiation; Hansen *et al.*, 2005; Leu *et al.*, 2008). Differences in the magnitude of the correlation between residential and energy development may also stem from disparities in land ownership, and the associated development patterns and management practices, that are associated with these two development types. In the intermountain west, energy development occurs primarily on federally owned public property where land management agencies are required to consider impacts to natural resources, including wildlife. Meanwhile residential development occurs primarily on private property with few constraints and often in areas where planning jurisdictions have limited capacity to incorporate conservation considerations into development decisions (Miller *et al.*, 2008). We suspect

that these differences contribute to a stronger negative association between recruitment and residential housing, yet to date, there has been much more research on the effects of energy development on ungulates (Polfus & Krausman, 2012). Our findings underscore the need to understand the effects of low-density housing on mule deer and other wildlife, despite the conservation challenges associated with private property.

Weather conditions have long been recognized to influence ungulate fecundity and juvenile survival through both direct effects on fawns and indirect effects on maternal condition; our results largely echo findings from other studies. Winter precipitation just prior to parturition was negatively correlated with recruitment, presumably by taxing the energetic demands of pregnant females (Parker *et al.*, 2009). Conversely, winter precipitation in the previous year ($t-1$; two winters before parturition) was positively associated with recruitment in year t . This pattern likely resulted from changes in adult female body condition. Harsh winters reduce subsequent fecundity and increase the number of nonlactating adult females during the summer. These females should be in excellent condition the following year, which likely gives a boost to fecundity rates in year t (Parker *et al.*, 2009; Monteith *et al.*, 2013). As other investigators have found (Gilbert & Raedeke, 2004), cold, wet June weather was negatively associated with fawn recruitment, presumably due to the detrimental effects of harsh weather on neonates. That said, June precipitation in western Colorado is usually very low (median value was 2.7 cm), and under typical dry conditions, warm weather was more negatively associated with recruitment than cool weather (Fig. 5). Warmer temperatures have been related to shorter durations of spring and summer green-up, reducing the availability of high-quality forage to ungulates (Middleton *et al.*, 2013; Monteith *et al.*, 2015), a mechanism that may be responsible for lower fawn ratios in our study. Relative to other weather metrics, the positive correlation between overall summer precipitation and recruitment was nonsignificant (Table 2). Late summer rainfall is generally scarce across the intermountain west, causing higher precipitation to be associated with increased recruitment (Hurley *et al.*, 2011), presumably due to improved forage quality. Colorado, however, regularly benefits from late summer monsoon rains, which likely reduces the importance of this variable in our study system.

Of the three buffers around oil and gas wells that we evaluated, only the 2700-m buffer was correlated with recruitment, and the effect was consistently associated with an interaction with winter precipitation (Table S1, Table 2). While Sawyer *et al.* (2006) found that mule

deer resource selection declined within 2700 m of a well pad in the Green River Basin of Wyoming, Northrup *et al.* (2015) found that deer reduced their selection of habitat around well pads at smaller buffer distances in the Piceance Basin of Colorado (generally <800 m). We suspect that recruitment in our study was correlated with the larger buffer distance due to the broad spatial extent of the analysis, as associations were summarized across multiple habitat and terrain types. With respect to the interaction, both energy development and winter precipitation were negatively correlated with fawn ratios (Table 2, Fig. 4a), but the influence of winter severity dampened as a greater proportion of the winter range was impacted by energy development (Fig. 4b). We hypothesize that this relationship is a function of the effects of both these factors on maternal condition, with subsequent implications for recruitment. Both energy development and winter precipitation values were estimated before fawns were born, and would have influenced adult female deer on winter range just prior to parturition. We speculate that female deer on ranges with widespread energy development may have diminished body condition as a consequence of direct and indirect losses of habitat (Sawyer *et al.*, 2006, 2009; Northrup *et al.*, 2015). If body condition is already reduced in these deer, with ensuing effects on recruitment, the additional influence of harsh winter weather may be minimal.

We were interested in assessing the relative strength of correlations between land-use change and weather variables with mule deer recruitment, but we expect that the cumulative effects of these factors, and other factors outside the scope of our study, are driving observed variation in deer productivity. Variation in forage quality, harvest, predation, disease and interspecific competition (with domestic livestock and wild ungulates) can all influence ungulate demographic rates (Gross & Miller, 2001; Cook *et al.*, 2004; Bergman *et al.*, 2011; Brodie *et al.*, 2013; Hurley *et al.*, 2014). While we did not have data with comparable spatial or temporal extents to investigate these other factors, we suspect that some are highly important in the dynamics of deer across our study area (e.g., forage quality; Bishop *et al.*, 2009; Bergman *et al.*, 2014). For those land-use and weather factors that we did investigate, their long-term temporal trends are highly disconcerting for mule deer. The intermountain west continues to experience some of the highest rates of human population growth in the United States, with extensive changes in land-use projected along the urban–wildland interface (Theobald & Romme, 2007). At the same time, climate change models forecast increases in temperature and reductions in summer precipitation (Ray *et al.*, 2008), patterns that were negatively correlated

with deer recruitment. Finally, model-averaged coefficients demonstrated that increasing male ratios were weakly associated with declining recruitment (although confidence intervals overlapped zero). Male ratios closely correspond to harvest management, and increases in ratios that are intended to boost male numbers and hunter satisfaction, may inadvertently decrease productivity through density-dependent effects (Bergman *et al.*, 2011, 2014). Combined with those factors that we could not address in our analysis, we suspect that further losses of habitat, unfavorable climate conditions, and high male ratios may pose considerable challenges for maintaining deer recruitment rates in the future.

We detected significant relationships between deer recruitment and habitat conditions, but it is important to acknowledge the drawbacks of our analysis that limit our scope of inference. The correlations we detected between recruitment and habitat conditions do not demonstrate causation, as our analyses relied on long-term observational data. Additionally, the data sources used in this analysis were coarse. Fawn ratios are strongly correlated with juvenile survival (Raithel *et al.*, 2007; Harris *et al.*, 2008), but are not a precise measure of the number of recruits that are added annually to a population. This is particularly true for our early-winter fawn ratios (collected Dec–Jan) which did not incorporate the survival of juveniles through the end of winter. In addition, we were not able to identify the effects of different types of residential and energy development disturbances on recruitment, although studies have found that behavioral responses of mule deer vary in association with distinct activities at energy wells (Sawyer *et al.*, 2009; Northrup *et al.*, 2015). The extensive spatiotemporal scale of our study also limited the data sources available for tracking changes in habitat conditions. We used the best information available, but these included model-based estimates (SERGoM residential development data, PRISM climate data), relatively large grain sizes for some variables (800 m pixel size of PRISM data), and coarse temporal resolution for others (SERGoM data). We believe that population and habitat data depicted important trends in these variables over time, but also expect that considerable noise was inherent in these datasets. Despite these drawbacks, we were able to use extensive spatiotemporal variation to identify a critical link between deer demography and landscape conditions, relationships that should be investigated further with finer-scale data.

Our findings have important implications for the conservation of mule deer in Colorado. Adequate, high-quality winter range has been hypothesized to be the primary factor limiting mule deer in the state

(Bergman *et al.*, 2015), and our findings support this speculation as land-use changes on winter ranges were more strongly correlated with declining recruitment than changes on summer ranges. Indeed, over the course of the study, an additional 1 335 992 ha of winter range was impacted by land-use change, such that by 2010, an average of 31% of winter ranges were affected by residential development and 24% were affected by energy development (at the 2700 m buffer distance). If healthy mule deer populations are going to be maintained, conservation practitioners, policy-makers, and land-use planners will need to collectively work to ensure that seasonal habitats, particularly winter ranges, are well preserved. DAUs with larger proportions of privately owned land will be particularly susceptible to increases in residential development and should be prioritized for conservation. Wildlife professionals will need to work closely with state and municipal governments to adopt land-use regulations and incentives to minimize subdivisions, and encourage land trusts and open space agencies to implement conservation easements for habitat protection (Pruetz & Standridge, 2008; Reed *et al.*, 2014). DAUs with larger proportions of public land may be more productive over time, particularly those with minimal energy development. For those DAUs experiencing high levels of energy development, wildlife professionals will need to encourage federal land management agencies to minimize the spatial extent and density of wells (Sawyer *et al.*, 2006) and avoid sensitive periods when scheduling drilling activities (e.g., winter months; Northrup *et al.*, 2015). While research is needed on the mechanisms responsible for the correlation between land-use change and declining mule deer recruitment, our results suggest that additional development will likely exacerbate reductions in recruitment, a pattern that should be carefully considered when wildlife agencies specify long-term population objectives.

Short-term and local-scale research on the effects of residential development on ungulates largely indicate limited impacts on habitat use (e.g., Goad *et al.*, 2014), but our analysis suggests that such development may have substantial long-term effects on population processes. Indeed, we observed stronger correlations between deer recruitment and residential housing than for weather factors that are well known to drive annual variation in ungulate productivity. Unfortunately, quantifying the impacts of residential development on animals is challenging (Polfus & Krausman, 2012); opportunities for experimental research are limited, the new construction of housing units occurs gradually, there is high potential for a diversity of direct and indirect effects, animals are likely to alter their behavior to mitigate demographic impacts, and population-level

consequences may take several years to manifest. Given these constraints, reliable long-term datasets that track animal population dynamics with respect to changes in landscape conditions will be critical for elucidating the role of potentially important, but subtle factors, before they degrade populations beyond recovery.

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References

- Barton K (2013) MuMIn: multi-model inference, R package version 1.9.13.
- Bates D, Maechler M, Bolker B, Walker S (2013) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. <http://CRAN.R-project.org/package=lme4>.
- Bergman EJ, Watkins BE, Bishop CJ, Lukacs PM, Lloyd M (2011) Biological and socioeconomic effects of statewide limitation of deer licenses in Colorado. *Journal of Wildlife Management*, **75**, 1443–1452.
- Bergman EJ, Bishop CJ, Freddy DJ, White GC, Doherty PF Jr (2014) Habitat management influence overwinter survival of mule deer fawns in Colorado. *Journal of Wildlife Management*, **78**, 448–455.
- Bergman EJ, Doherty PF Jr, White GC, Holland AA (2015) Density dependence in mule deer: a review of evidence. *Wildlife Biology*, **21**, 18–29.
- Bierwagen BG, Theobald DM, Pyke CR, Choate A, Crothd P, Thomase JV, Morefield P (2010) National housing and impervious surface scenarios for integrated climate impact assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 20887–20892.
- Bishop CJ, White GC, Freddy DJ, Watkins BE, Stephenson TR (2009) Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs*, **172**, 1–29.
- Blanchard P, Festa-Bianchet M, Gaillard J-M, Jorgenson JT (2003) A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. *Journal of Wildlife Management*, **67**, 477–484.
- Brodie J, Johnson H, Mitchell M *et al.* (2013) Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. *Journal of Applied Ecology*, **50**, 295–305.
- Brown DG, Johnson KM, Loveland TR, Theobald DM (2005) Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications*, **15**, 1851–1863.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York, NY.
- Burnham KP, Anderson DR (2004) Multimodel inference – understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**, 261–304.
- Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904–907.
- Cook JG, Johnson BK, Cook RC, Rigs RA, Delcurto T, Bryant LD, Irwin LL (2004) Effects of summer-autumn nutrition and parturition data on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.
- Copeland HE, Doherty KE, Naugle DE, Pocerwicz A, Kiesecker JM (2009) Mapping oil and gas development potential in the US intermountain west and estimating impacts to species. *PLoS One*, **4**, e7400.
- Davies RG, Orme CDL, Olson V *et al.* (2006) Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society Series B*, **273**, 2127–2133.
- Dzialak M, Webb SL, Harju SM, Winstead JB, Wondzell JJ, Mudd JP, Hayden-Wing LD (2011) The spatial pattern of demographic performance as a component of sustainable landscape management and planning. *Landscape Ecology*, **26**, 775–790.

- Forrester TD, Wittmer HU (2013) A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Review*, **43**, 292–308.
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gilbert BA, Raedeke KJ (2004) Recruitment dynamics of black-tailed deer in the western Cascades. *Journal of Wildlife Management*, **68**, 120–128.
- Gill RB (2001) Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife Special Report Number 77, Fort Collins, Colorado.
- Goad EH, Pejchar L, Reed SE, Knight KL (2014) Habitat use by mammals varies along an exurban development gradient in northern Colorado. *Biological Conservation*, **176**, 172–182.
- Gross JE, Miller MW (2001) Chronic wasting disease in mule deer: disease dynamics and control. *Journal of Wildlife Management*, **65**, 205–215.
- Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH, Jones K (2005) Effects of exurban development on biodiversity: patterns, mechanism, and research needs. *Ecological Applications*, **15**, 1893–1905.
- Harju SM, Dzialak MR, Taylor RC, Hayden-Wing LD, Winstead JB (2010) Thresholds and time lags in effects of energy development on greater sage-grouse populations. *Journal of Wildlife Management*, **74**, 437–448.
- Harris NC, Kauffman MJ, Mills LS (2008) Inferences about ungulate population dynamics derived from age ratios. *Journal of Wildlife Management*, **72**, 1143–1151.
- Hebblewhite M, Merrill EH (2011) Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos*, **120**, 1860–1870.
- Heffelfinger JR, Messmer TA (2003) Introduction. In: *Mule Deer Conservation: Issues and Management Strategies* (eds de Vos JC Jr, Conover MR, Headrick NE), pp. 1–11. Berryman Institute Press, Utah State University, Logan, Utah.
- Holloran MJ, Kaiser RC, Hubert WA (2010) Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management*, **74**, 65–72.
- Hurley MA, Unsworth JW, Zaiger P *et al.* (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs*, **178**, 1–33.
- Hurley MA, Hebblewhite M, Gaillard J-M *et al.* (2014) Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philosophical Transactions of the Royal Society Series B*, **369**, 20130196.
- Idaho Department of Fish and Game (1999) *White-Tailed Deer, Mule Deer, and elk Management Plan*. Idaho Department of Fish and Game, Boise, Idaho.
- International Energy Agency (2015). *World Energy Outlook 2015*. Available at: <http://www.worldenergyoutlook.org/weo2015/> (accessed 21 June 2016).
- Krausman PR, Smith SM, Derbridge J, Merkle J (2011) The cumulative effects of suburban and exurban influences on wildlife. In: *Cumulative Effects in Wildlife Management: Impact Mitigation* (eds Krausman PR, Harris LK), pp. 135–192. CRC Press, Boca Raton, Florida.
- Leinwand IIF, Theobald DM, Mitchell J, Knight RL (2010) Landscape dynamics at the public-private interface: a case study in Colorado. *Landscape and Urban Planning*, **97**, 182–193.
- Leu M, Hanser SE, Knick ST (2008) The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications*, **18**, 1119–1139.
- McClure RA (2009) Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landscape Ecology*, **24**, 483–493.
- McClure MF, Bissonette JA, Conover MR (2005) Migratory strategies, fawn recruitment, and winter habitat use by urban and rural mule deer (*Odocoileus hemionus*). *European Journal of Wildlife Research*, **51**, 170–177.
- McKee JK, Sciulli PW, Foose CD, Waite TA (2004) Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, **115**, 161–164.
- McMichael AJ (2000) The urban environment and health in a world of increasing globalization: issues for developing countries. *Bulletin of the World Health Organization*, **78**, 1117–1126.
- Middleton AD, Kauffman MJ, McWhirter DE *et al.* (2013) Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, **94**, 1245–1256.
- Miller JR, Groom M, Hess GR *et al.* (2008) Biodiversity conservation in local planning. *Conservation Biology*, **23**, 53–63.
- Monteith KL, Stephenson TR, Bleich VC, Conner MM, Pierce BM, Bowyer RT (2013) Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology*, **82**, 377–388.
- Monteith KL, Bleich VC, Stephenson TR, Pierce BM, Conner MM, Kie JG, Bowyer RT (2014) Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs*, **186**, 1–50.
- Monteith KL, Klaver RW, Hersey KR, Holland AA, Thomas TP, Kauffman MJ (2015) Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia*, **178**, 1137–1148.
- Nellemann C, Stoen O-G, Kindberg J *et al.* (2007) Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, **138**, 157–165.
- Northrup JM, Wittemyer G (2013) Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, **16**, 112–125.
- Northrup JM, Anderson CR Jr, Wittemyer G (2015) Identifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology*, **21**, 3961–3970.
- Parker KL, Barboza PS, Gillingham PM (2009) Nutritional integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.
- Pejchar L, Reed SE, Bixler P, Ex L, Mockrin MH (2015) Consequences of residential development for biodiversity and human well-being. *Frontiers in Ecology and in the Environment*, **13**, 146–153.
- Pinheiro J, Bates DM (2000) *Mixed Effects Models in S and S-Plus*. Springer-Verlag, New York, NY.
- Polfus JL, Krausman PR (2012) Impacts of residential development on ungulates in the Rocky Mountain west. *Wildlife Society Bulletin*, **36**, 647–657.
- Porter WF, Underwood HB, Woodard JL (2004) Movement behavior, dispersal, and the potential for localized management of deer in a suburban environment. *Journal of Wildlife Management*, **68**, 247–256.
- Pruetz R, Standridge N (2008) What makes transfer of development rights work?: Success factors from research and practice. *Journal of the American Planning Association*, **75**, 78–87.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.
- Raithel JD, Kauffman MJ, Pletscher DH (2007) Impact of spatial and temporal variation in calf survival on the growth of elk populations. *Journal of Wildlife Management*, **71**, 795–803.
- Ramallo CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. *Trends in Ecology and Evolution*, **27**, 179–188.
- Ray AJ, Barsugli JJ, Averyt KB *et al.* (2008) *Climate change in Colorado: a synthesis to support water resources management and adaptation*. CU-NOAA Western Water Assessment.
- Reed SE, Hilty JA, Theobald DM (2014) Guidelines and incentives for conservation development in local land-use regulations. *Conservation Biology*, **28**, 258–268.
- Robinson BG, Hebblewhite M, Merrill EH (2010) Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia*, **164**, 265–275.
- Sawyer H, Nielson RM, Lindzey F, McDonald LL (2006) Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management*, **70**, 396–403.
- Sawyer H, Kauffman MJ, Nielson RM (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052–1061.
- Sawyer H, Kauffman MJ, Middleton AD, Morrison TA, Nielson RM, Wyckoff TB (2013) A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology*, **50**, 68–78.
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.
- Seto KC, Büneralp B, Hutya LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, **109**, 16083–16088.
- Shallow JRT, Hurley MA, Monteith KL, Bowyer RT (2015) Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. *Journal of Mammalogy*, **96**, 194–205.
- Sorensen T, McLoughlin PD, Hervieux D, Dzus E, Nolan J, Wynes B, Boutin S (2008) Determining sustainable levels of cumulative effects for boreal caribou. *Journal of Wildlife Management*, **72**, 900–905.
- Theobald DM (2005) Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecology and Society*, **10**, 32.
- Theobald DM, Romme WH (2007) Expansion of the US wildland-urban interface. *Landscape and Urban Planning*, **83**, 340–354.
- Theobald DM, Miller JR, Hobbs NT (1997) Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning*, **39**, 25–36.

- Tuomainen U, Candolin U (2011) Behavioral responses to human-induced environmental change. *Biological Reviews*, **86**, 640–657.
- Vias AC, Carruthers JI (2005) Regional development and land use change in the Rocky Mountain West 1982–1997. *Growth and Change*, **36**, 244–272.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science*, **277**, 494–499.
- Vogel WO (1989) Response of deer to density and distribution of housing in Montana. *Wildlife Society Bulletin*, **17**, 406–413.
- Walston LJ, Cantwell BL, Krummel JR (2009) Quantifying spatiotemporal changes in a sagebrush ecosystem in relation to energy development. *Ecography*, **32**, 943–952.
- Wong BBM, Candolin U (2015) Behavioral responses to changing environments. *Behavioral Ecology*, **26**, 665–673.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Results from univariate linear mixed models correlating different habitat variables with mule deer fawn ratios.

Table S2. Model selection results from testing all subsets of habitat variables with mule deer fawn ratios.