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Behavioral and Demographic Responses of Mule Deer to Energy Development on Winter Range

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ABSTRACT Anthropogenic habitat modification is a major driver of global biodiversity loss. In North America, one of the primary sources of habitat modification over the last 2 decades has been exploration for and production of oil and natural gas (hydrocarbon development), which has led to demographic and behavioral impacts to numerous wildlife species. Developing effective

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measures to mitigate these impacts has become a critical task for wildlife managers and conservation practitioners. However, this task has been hindered by the difficulties involved in identifying and isolating factors driving population responses. Current research on responses of wildlife to development predominantly quantifies behavior, but it is not always clear how these responses scale to demography and population dynamics. Concomitant assessments of behavior and population-level processes are needed to gain the mechanistic understanding required to develop effective mitigation approaches. We simultaneously assessed the demographic and behavioral responses of a mule deer population to natural gas development on winter range in the Piceance Basin of Colorado, USA, from 2008 to 2015. Notably, this was the period when development declined from high levels of active drilling to only production phase activity (i.e., no drilling). We focused our data collection on 2 contiguous mule deer winter range study areas that experienced starkly different levels of hydrocarbon development within the Piceance Basin.

We assessed mule deer behavioral responses to a range of development features with varying levels of associated human activity by examining habitat selection patterns of nearly 400 individual adult female mule deer. Concurrently, we assessed the demographic and physiological effects of natural gas development by comparing annual adult female and overwinter fawn (6-month-old animals) survival, December fawn mass, adult female late and early winter body fat, age, pregnancy rates, fetal counts, and lactation rates in December between the 2 study areas. Strong differences in habitat selection between the 2 study areas were apparent. Deer in the less-developed study area avoided development during the day and night, and selected habitat presumed to be used for foraging. Deer in the heavily developed study area selected habitat presumed to be used for thermal and security cover to a greater degree. Deer faced with higher densities of development avoided areas with more well pads during the day and responded

neutrally or selected for these areas at night. Deer in both study areas showed a strong reduction in use of areas around well pads that were being drilled, which is the phase of energy development associated with the greatest amount of human presence, vehicle traffic, noise, and artificial light. Despite divergent habitat selection patterns, we found no effects of development on individual condition or reproduction and found no differences in any of the physiological or vital rate parameters measured at the population level. However, deer density and annual increases in density were higher in the low-development area. Thus, the recorded behavioral alterations did not appear to be associated with demographic or physiological costs measured at the individual level, possibly because populations are below winter range carrying capacity. Differences in population density between the 2 areas may be a result of a population decline prior to our study (when development was initiated) or area-specific differences in habitat quality, juvenile dispersal, or neonatal or juvenile survival; however, we lack the required data to contrast evidence for these mechanisms.

Given our results, it appears that deer can adjust to relatively high densities of well pads in the production phase (the period with markedly lower human activity on the landscape), provided there is sufficient vegetative and topographic cover afforded to them and populations are below carrying capacity. The strong reaction to wells in the drilling phase of development suggests mitigation efforts should focus on this activity and stage of development. Many of the wells in this area were directionally drilled from multiple-well pads, leading to a reduced footprint of disturbance, but were still related to strong behavioral responses. Our results also indicate the likely value of mitigation efforts focusing on reducing human activity (i.e., vehicle traffic, light, and noise). In combination, these findings indicate that attention should be paid to the spatial configuration of the final development footprint to ensure adequate cover. In our

study system, minimizing the road network through landscape-level development planning would be valuable (i.e., exploring a maximum road density criteria). Lastly, our study highlights the importance of concomitant assessments of behavior and demography to provide a comprehensive understanding of how wildlife respond to habitat modification.

KEY WORDS Bayesian hierarchical model, Colorado, global positioning system radio-collar, mark-resight, natural gas development, *Odocoileus hemionus*, resource selection function, risk-disturbance hypothesis, spatial ecology, survival.

RÈSUMÈN

Les modifications anthropogéniques de l’habitat sont une source majeure de la perte de biodiversité. En Amérique du Nord, l’une des sources importantes de modification de l’habitat durant les deux dernières décennies est reliée à l’exploration et à la production d’huile et de gaz naturel (développements reliés aux hydrocarbures). Ces développements ont causé des impacts démographiques et comportementaux pour de nombreuses espèces fauniques. Développer des mesures efficaces afin de réduire ces impacts est devenu une tâche importante des gestionnaires de la faune et des conservationnistes. Cependant, cette tâche a été compliquée par les difficultés associées à l’identification des facteurs influençant les réponses de la population aux développements. Les recherches portant sur les réponses de la faune aux développements quantifient principalement le comportement, mais il n’est pas toujours facile de comprendre comment ces réponses sont reliées à la démographie et à la dynamique des populations. Une évaluation concomitante du comportement et des processus de la population sont requis afin d’obtenir une compréhension mécanistique permettant de développer des mesures de mitigation appropriées. Nous avons évalué simultanément les réponses démographiques et comportementales d’une population de cerf mulet sur leur aire d’hivernage, associées au développement relié au gaz

naturel dans le bassin Piceance du Colorado, USA, entre 2008 et 2015. Ceci correspondait à la période où le niveau de développement a fluctué de façon importante, entre une phase de forage active et une phase de production (sans forage). Nous avons concentré notre collection de données sur deux aires d'hivernage adjacentes qui ont subi des niveaux différents de développement reliés aux hydrocarbures à l'intérieur du bassin Piceance.

Nous avons évalué la réponse comportementale des cerfs mulets aux attributs reliés au développement avec des niveaux variés d'activités humaines en examinant la sélection d'habitat de près de 400 femelles cerfs mulets. Nous avons aussi évalué l'effet des développements reliés au gaz naturel sur la démographie et la physiologie en comparant la survie annuelle des femelles adultes et la survie hivernale des faons (âgés de 6 mois), les réserves de gras des femelles au début et à la fin de l'hiver, l'âge, le taux de gestation et le taux de lactation en décembre entre les deux aires d'études. Des différences majeures au niveau de la sélection d'habitat ont été observées entre les deux aires d'études. Les cerfs habitant l'aire d'étude moins développée évitaient les zones développées durant le jour et la nuit et sélectionnaient des habitats afin de s'alimenter. Les cerfs habitant l'aire d'étude plus développée sélectionnaient plus fortement des habitats à des fins de sécurité et de couvert thermal. Les cerfs faisant face à une plus grande densité de développement évitaient les endroits avec une plus grande densité de puits durant le jour alors qu'ils n'évitaient pas ou sélectionnaient ces endroits durant la nuit. Les cerfs habitant les deux aires d'études montraient une réduction importante de l'utilisation des puits durant leur forage, ce qui correspondait à la phase de développement avec la plus grande présence humaine, circulation automobile, bruit, et lumière artificielle. Malgré des patrons de sélection d'habitat divergents, nous n'avons pas détecté un effet des développements sur la condition ou la reproduction et nous n'avons pas trouvé de différence chez les taux vitaux ou physiologiques mesurés au niveau de la population. Cependant, la densité de cerfs et le taux de changement annuel dans la densité étaient supérieurs dans l'aire d'étude moins développée. Les changements comportementaux mesurés ne semblaient donc pas être associés avec des coûts démographiques ou physiologiques au niveau individuel, possiblement parce que les populations étaient sous la capacité biotique de l'aire d'hivernage. Les différences entre les densités de population entre les deux aires d'études sont peut-être dû à un déclin de la population précédant notre étude (lorsque le développement démarrait) ou à des différences au niveau de la qualité de l'habitat, du dispersement ou de la survie des nouveau-nés ou des juvéniles. Cependant, nous manquons les données requises pour contraster ces mécanismes.

Selon nos résultats, il apparait que les cerfs mulets peuvent s'adapter à une densité élevée de puits durant la phase de production (la période avec moins d'activités humaines) si la quantité de protection offerte par la végétation et la topographie est suffisante et si la population est sous la capacité biotique. La forte réponse aux puits durant la période de forage indique que les mesures de mitigation devraient prioriser ces activités et ce stade de développement. Plusieurs des puits de la région étaient percés directionnellement à partir d'un même endroit, entraînant une réduction de l'emprise, mais ils entrainaient néanmoins une réponse comportementale des cerfs. Nos résultats démontrent aussi l'importance potentielle de mesures de mitigation tentant de réduire le niveau d'activité humaine (i.e.la circulation automobile, la lumière et le bruit). Nos résultats soulignent l'importance de porter attention à la configuration spatiale du développement afin d'assurer un niveau de couvert suffisant. Dans notre système, minimiser le réseau des routes en utilisant une planification au niveau du paysage pourrait être utile (i.e. explorer un critère maximum pour la densité de route). Dernièrement, notre étude a démontré l'importance d'évaluer en même temps le comportement et la démographie afin de procurer une compréhension globale de la réponse de la faune aux modifications de l'habitat.

Contents

INTRODUCTION

Land-use change and associated human activities have profound effects on ecological processes (Vitousek et al. 1997, Foley et al. 2005, Haberl et al. 2007). These effects include disrupting long-distance animal migrations (Harris et al. 2009), altering animal behavior (Tuomainen and Candolin 2011), facilitating the introduction of nonnative species (Hansen and Clevenger 2005), and driving declines of local populations and global biodiversity (Wilcove et al. 1998, Sala et al. 2000, Gibson et al. 2013). In the coming decades, land-use change will continue to alter natural systems, modifying thousands of square kilometers of land (Li et al. 2017) with negative consequences for some species and ecosystems (Lawler et al. 2014), including the decline and possible extirpation of hundreds of species (Powers and Jetz 2019). Assessment of the ecological consequences of land-use change is critical for species management and conservation and is fundamental for understanding ecological processes under contemporary environmental conditions where human disturbance is a dominant feature.

The most fundamental ecological effects of land-use change result from conversion, fragmentation and alteration of habitat (habitat modification). The pervasiveness of habitat modification has led to it becoming one of the primary foci of wildlife ecology and management. Because habitat modification removes or alters fundamental components of ecosystems that species rely on, demographic effects are expected (e.g., reduced survival and population declines; Wittmer et al. 2007, Dzialak et al. 2011*b*, Webb et al. 2011*d*). Indeed, habitat modification associated with land-use has contributed to global declines in wildlife populations across numerous taxa (Wilcove et al. 1998, Sala et al. 2000), and substantial losses of biodiversity (Newbold et al. 2016). Studies assessing the demographic effects of habitat modification provide direct inference to the processes of primary interest to conservation and management. However, subtle demographic responses are difficult to detect, and these studies often are costly and time consuming (i.e., responses often can only be assessed after many years of study). Furthermore, if adverse effects are documented, demographic studies typically provide only enough information for coarse management or conservation measures (i.e., cessation of habitat modification in general) instead of more targeted measures (e.g., development-free buffers around sensitive habitat [Doherty et al. 2008] or seismic exploration line width specifications [Tigner et al. 2015]).

Because assessing demographic responses to habitat modification is difficult, most studies examining effects on wildlife focus on behavior. Behavioral responses to habitat modification can be assessed over shorter time scales and often require smaller sample sizes than demographic studies to achieve sufficient statistical power to evaluate meaningful effect sizes. Behavior also provides the mechanistic link from individual to populations through effects on fitness (Berger-Tal et al. 2011, Greggor et al. 2016). Behavioral shifts in response to disturbance can include abandonment of areas important for critical life-history stages (Kuck et al. 1985, Amar et al. 2015), switching daily activity patterns (Gaynor et al. 2018), and altered space use behavior (Faille et al. 2010), habitat selection (Hebblewhite and Merrill 2008), or foraging activity (Ciuti et al. 2012). Implicit in approaches focused on behavior, is the assumption that behavioral shifts affect individual fitness or populations (but see Gill et al. 2001). However, such shifts can be indicative of adaptive plasticity, which allows individuals to mitigate potential effects (Huey et al. 2003, Ghalambor et al. 2007, Tuomainen and Candolin 2011). Notably, behavior often is the primary means by which species can adjust to habitat disturbance in the short term (Berger-Tal et al. 2011, Greggor et al. 2016). Thus, in the absence of data on demography or fitness proxies, behavioral studies can have limited utility for understanding the implications of habitat modification on broader ecological process (Wilson et al. 2020), which often are more robust metrics for decision making in wildlife management and conservation.

Addressing behavior and demography simultaneously offers a comprehensive understanding of species responses to habitat modification. Such an approach allows quantification of fitness or demographic changes and identification of behavioral adjustments that can help diagnose the drivers of these changes. Such work can provide powerful insight to the contexts under which species can adapt to habitat modification, which is critical for effective management and conservation decision-making (Buchholz 2007, Caro 2007). However, whether behavioral responses to habitat modification can successfully buffer individuals from fitness effects is context-dependent. If species are displaced from limiting habitat (e.g., nesting or calving grounds), then it is likely that behavioral responses will result in reduced individual fitness and subsequent population declines. The ability to alter behavior (i.e., behavioral plasticity) can be adaptive (Ghalambor et al. 2007, 2010) but requires that environmental changes produce cues that are both recognizable and reliable (Sih et al. 2011, Sih 2013) and that habitat has not been modified in such a way to significantly reduce carrying capacity. If cues are not reliable, this can lead to the formation of ecological or evolutionary traps (Robertson et al. 2013). However, even if habitat is not limiting, or changes do not increase risk to species, behavioral responses to human disturbance can result in significant opportunity cost akin to the non-consumptive effects of predation risk (Frid and Dill 2002).

In North America, energy development has become an important driver of land-use change and habitat modification (McDonald et al. 2009). Energy development is projected to continue to alter landscapes at a continental scale for at least the next 2 decades (U.S. Energy Information Administration [EIA] 2020), and likely over a much longer period. Among the domestic energy sectors in North America, oil and natural gas (hydrocarbon) development have shown particularly rapid growth, driven largely by unconventional hydrocarbon resources (e.g., oil sands or shale natural gas; EIA 2012). These resources are widespread globally (EIA 2013), and despite recent downturns, their development is expected to continue (EIA 2020).

The habitat modification from hydrocarbon development has various effects on wildlife behavior and demography (Northrup and Wittemyer 2013). Specifically, hydrocarbon development alters a number of behaviors that are linked to fitness. The literature on wildlife responses to hydrocarbon development has documented shifts in habitat selection by mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), greater sage grouse (*Centrocercus urophasianus*), and grizzly bears (*Ursus arctos*; Sawyer et al. 2006, Carpenter et al. 2010, Dzialak et al. 2011*b*, Laberee et al. 2014, Northrup et al. 2015), altered home range patterns in mule deer and elk (Webb et al. 2011*a*, Northrup et al. 2016*b*), effects on circadian patterns in entire wildlife communities (Lendrum et al. 2017), and changes in song characteristics in songbirds (Francis et al. 2011). Likewise, a number of studies have documented demographic responses to hydrocarbon development, such as decreased survival in elk and greater sage grouse (Holloran et al. 2010, Dzialak et al. 2011*b*, Webb et al. 2011*d*) and reduced recruitment, or proxies of recruitment, in greater sage grouse and mule deer (Holloran et al. 2010, Johnson et al. 2016). Further, hydrocarbon development increased nest predation on several songbird species (Hethcoat and Chalfoun 2015) and there is some evidence that this habitat modification can lead to population declines for caribou (*Rangifer tarandus*) and sage grouse (Sorensen et al. 2008, Wasser et al. 2011, Green et al. 2017). Despite a large and growing literature documenting effects, the preponderance of research focuses on behavior, with a paucity of demographic analyses (Northrup and Wittemyer 2013). Understanding if behavioral responses to energy development are leading to reduced fitness and subsequent declines in demographic parameters is critical as natural resource managers actively work to mitigate the negative effects of development (Kiesecker et al. 2009, Sochi and Kiesecker 2016).

In the western United States, much of the recent hydrocarbon development has been on public lands that encompass habitat for ungulate populations that are the primary focus of wildlife management agencies. Specifically, considerable development has occurred on the winter ranges of mule deer, which historically have experienced large-scale population fluctuations across their distribution (Unsworth et al. 1999). Winter is a critical time for mule deer because they can experience large die offs (White and Bartmann 1998) likely linked to limited access to sufficient high-quality forage (Wallmo et al. 1977, Parker et al. 1984, Bishop et al. 2009). Any substantive human activity on deer winter range is of concern to wildlife managers because it could lead to decreased habitat, reductions in foraging time, reduced access to forage, or increased energy expense through movement. Such effects are particularly costly on winter range, which is geographically limited, where deer are nutritionally constrained (Wallmo et al. 1977, Bishop et al. 2009) and snow dramatically increases the costs of locomotion (Parker et al. 1984).

Hydrocarbon development involves a variety of infrastructure types that modify the landscape in different ways. Well pads, facilities (including compressor stations, refining plants, and personnel camps), roads, and pipelines all directly remove wildlife habitat. Accompanying increases in human activity, including traffic, artificial light, and noise associated with drilling can further lead to indirect habitat loss (Sawyer et al. 2009, Northrup et al. 2015). In addition, development can facilitate the invasion of non-native plant species (Bergquist et al. 2007) and can be accompanied by reseeding of disturbed areas, potentially leading to permanent vegetation shifts or reduced plant diversity. These landscape changes are potentially concerning for mule deer because the species is known to be sensitive to habitat modification and the associated increases in human activity. Mule deer avoid developed areas (Nicholson et al. 1997), including roads during certain times of the year (Marshal et al. 2006; Webb et al. 2011*c*, 2013; Lendrum et al. 2012) and human activity in different forms causes mule deer to shift activity patterns and move more or migrate faster (Freddy et al. 1986, Stephenson et al. 1996, Boroski and Mossman 1998, Lendrum et al. 2013). Deer also are displaced to varying degrees from the areas around hydrocarbon development and related infrastructure (Sawyer et al. 2006, 2017; Webb et al. 2011*c*; Northrup et al. 2015), and the associated levels of human activities at development sites can largely influence displacement, with greater avoidance of sites with more people and machinery (Sawyer et al. 2009, Northrup et al. 2015).

Hydrocarbon development also can influence several other ecological and behavioral processes in mule deer. Home range dynamics of mule deer are affected by development, with the presence of some infrastructure types eliciting reduced year-to-year overlap in ranges (Northrup et al. 2016*b*). However, habitat heterogeneity appears to be an important predictor of mule deer space use (Kie et al. 2002), and they have been shown to potentially use areas near well pads and other development infrastructure because of the increased availability of forage (Webb et al. 2011*c*), or during certain times of the year when habitat might be more limiting (Marshal et al. 2006, Lendrum et al. 2012). Further, human activity can displace predators of mule deer (Ripple and Beschta 2008) and energy development appears to influence the spatial patterns of mule deer predation (Lendrum et al. 2018). Thus, habitat modifications from energy development can have mixed effects on the species.

In Colorado, USA, substantial research has been conducted on mule deer responses to predator reductions and habitat improvements on winter range. Collectively, this work shows that the species is highly constrained by available forage (Wallmo et al. 1977) during winter. As such, enhanced nutrition during winter through *ad libitum* feeding with pellets (Bishop et al. 2009) or reducing overstory trees to promote growth of palatable understory shrubs (Bergman et al. 2014) has elicited positive demographic responses, including increased overwinter survival. Further, predation of mule deer on winter range has been shown to be entirely compensatory in Colorado (Bartmann et al. 1992, White and Bartmann 1998), and largely compensatory in other parts of the Intermountain West (Hurley et al. 2011), indicating populations often are at or above carrying capacity on winter range. Mule deer in Colorado also have seen a protracted decline over the last 30 years (Bergman et al. 2015). These factors raise concerns that if development causes behavioral shifts for mule deer, it could exacerbate the already difficult nutritional conditions on winter range (Bishop et al. 2009, Monteith et al. 2013), and contribute to continued population declines or slowed population growth or recovery. These concerns are amplified by recent work in Wyoming, USA, by Sawyer et al. (2017) that showed strong and consistent avoidance of the areas around natural gas development and a 36% decline in abundance over a 15-year period. These results suggest that the strong behavioral responses of mule deer to natural gas development that have been documented elsewhere also could be associated with declines in deer populations. Thus, there is a need to improve our understanding of the demographic consequences of documented behavioral responses of deer to hydrocarbon development.

Our objective was to test hypotheses about whether and how habitat modification from hydrocarbon development influenced mule deer behavior and demography. We leveraged a unique opportunity, whereby 2 halves of a contiguous mule deer winter range area were exposed to vastly different levels of hydrocarbon development, providing a pseudo-experimental design (i.e., one area with heavy modification and one area with light modification; Fig. 1). Over a 7-year period, we assessed the effect of hydrocarbon development on mule deer (hereafter deer unless otherwise indicated) behavior by examining habitat selection relative to development features and environmental factors related to cover and forage. We also examined a suite of demographic parameters measured at the individual or study area scale, including early and late winter body fat and mass, pregnancy rates, fetal counts, survival of fawns (from 6 months of age onwards), survival of adult females, lactation rates, and winter range population density. Recent studies in this broader study region have investigated different aspects of mule deer habitat selection, finding a variety of behavioral responses to development (Lendrum et al. 2012, 2013; Northrup et al. 2015, 2016*a*). Thus, we assumed that we would see differences in behavior of mule deer in the 2 study areas. However, there has been no assessment of whether such behavioral responses have influenced fitness or population-level demographic processes. To address this gap, we tested the following alternative hypotheses and subsequent predictions:

Hypothesis A proposed that habitat modification elicits behavioral responses and these responses lead to reductions in individual fitness and therefore reduced population size and demographic rates. Under this hypothesis, we predicted that deer in the 2 study areas would show different responses to cover- and forage-related covariates. Because of the large differences in hydrocarbon development infrastructure between areas, we assumed differences in response to development would be pervasive. Subsequently, we predicted that deer in the more heavily developed area would be in worse condition and have lower survival and lower density. We did not predict that we would see significant differences in pregnancy rates or fetal counts because these metrics are largely invariant until deer are at or above carrying capacity.

Hypothesis B proposed that habitat modification elicits behavioral responses, with no subsequent effect on individual fitness, population size, or demographic rates, suggesting behavior effectively mitigates the demographic impacts of development. Under this hypothesis, we predicted that deer in the 2 study areas would show different responses to cover- and forage-related covariates, but there would be no differences in any demographic parameters at the individual or study area level and density would be similar between these areas.

STUDY AREA

The study took place between January 2008 and March 2015. The study area was the Magnolia mule deer winter range in the Piceance Basin of northwestern Colorado (39.954^{0}N, 108.356^{0}W; Fig. 1), which encompasses an area of 184 km^2. Average elevation in the area was 2,045 m. The climate was characterized by cold winters (mean Dec–Mar temp 2008–2015 in Meeker, CO = −3.8° C, range = −37.2–22.8° C) and warm dry summers (mean Jun–Sep temp 2008–2015 in Meeker, CO = 17.5° C, range: −2.2–35.6° C) with monsoonal precipitation in late summer. The area was topographically variable with the dominant vegetation consisting of big sagebrush (*Artemisia tridentata*) and a pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus ostesperma*) shrubland complex. Other dominant shrubs included Utah serviceberry (*Amalenchier utahensis*), mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentata*), and mountain snowberry (*Symphoricarpos oreophilus*). For a more detailed description of the vegetation of the area see Bartmann and Steinert (1981) and Bartmann et al. (1992). Natural predators of mule deer in this area included coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*; Lendrum et al. 2018). Elk and feral horses (*Equus ferus*) also inhabited the area. This area was popular for hunting during the fall with an annual average of 511 deer harvested in the wildlife management unit (Game Management Unit 22), which encompassed the entire study area (Table 1). Chronic wasting disease occurred within the mule deer population in this area at low levels (2.4% prevalence in adult males in the most recent assessment; *n* = 255, 95% CI = 0.9–5.1%; https://cpw.state.co.us/Documents/Research/CWD/CWDprevalence_GMU-DAU_deer.pdf, accessed 02 Oct. 2020). There is active cattle ranging in the area and it also contains vast hydrocarbon resources that have seen active development since the 1970s. Starting in the mid-2000s, natural gas development increased sharply but declined rapidly since 2012 (Fig. 2).

Mule deer in this area are migratory, moving between low-elevation winter range and high-elevation summer range, where they birth fawns. Deer typically occupy their winter range between October and April of each year (Lendrum et al. 2014, Northrup et al. 2014*b*) and migrate to several different summer range areas (Lendrum et al. 2014). Summer range varied in elevation between 2,000 m and 2,800 m and vegetation consisted of Gambel oak (*Quercus gambelii*), quaking aspen (*Populus tremuloides*), pinyon pine, Utah juniper, Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) with mixed mountain shrublands consisting of mountain mahogany, bitterbrush, big sagebrush, mountain snowberry, rubber rabbitbrush (*Ericameria nauseosa*), and Utah serviceberry. Natural gas development density varied across summer range, with some areas being free from development and other areas having 0.04–0.06 well pads/km^2. In this area, and across the Intermountain West, mule deer populations have had substantial fluctuations and large declines over the last 30–50 years, with the ultimate causes remaining ambiguous (White and Bartmann 1998, Unsworth et al. 1999, Bergman et al. 2015).

METHODS

Mule Deer Captures

Between January 2008 and March 2015, we captured mule deer using helicopter net gunning (Krausman et al. 1985, Webb et al. 2008, Jacques et al. 2009, Northrup et al. 2014*a*; Table 2). All of the below procedures were approved by the Colorado Parks and Wildlife Institutional Animal Care and Use Committee (protocol numbers 17-2008 and 01-2012) and followed the guidelines of the American Society of Mammalogists (Sikes 2016). Upon capture of adult female deer (>1 year old; hereafter does), we administered 0.5 mg/kg of midazolam and 0.25 mg/kg of Azaperone (Wildlife Pharmaceuticals, Windsor, CO, USA) and transferred them to a central processing site via helicopter (49% of captures ferried <3.25 km, 51% ferried 3.25–6.5 km). At the processing site, we weighed deer, drew blood, measured chest girth and hind foot length, and estimated their age using tooth replacement and wear (Severinghaus 1949, Robinette et al. 1957, Hamlin et al. 2000). We also obtained a body condition score by palpating the rump, and measured the thickness of subcutaneous rump fat and the depth of the longissimus dorsi muscle using ultrasound (Stephenson et al. 1998, 2002; Cook et al. 2001, 2007, 2010). We used the body condition score and ultrasound measurements to estimate the percent ingesta-free body fat of each deer (Cook et al. 2007, 2010; hereafter fat). Between December 2013 and December 2015, we determined whether each deer was lactating during December through visual examination. Lastly, we fit each deer with a global positioning system (GPS) radio-collar (G2110D Advanced Telemetry Systems, Isanti, MN, USA) set to attempt a relocation once every 5 hours and equipped with a mechanism programmed to release in 16 months after the date of capture. Collars also were equipped with a mortality beacon that was activated if the collar was immobile for ≥8 hours. We attached placards to each collar with unique color and symbol combinations to allow for field-based individual identification. We monitored the deer's temperature throughout processing and released them at the processing site.

During most years, we captured the same individuals during early (Dec) and late (Mar) winter. However, there were some exceptions to this procedure during the first years of the study: 1) we did not capture any deer in March 2008, 2) we did not capture any does in December 2009, and 3) we captured new individuals in March 2010. Starting in December 2010, we captured the same individuals in early and late winter and only captured new individuals in late winter to replace any deer that died since the previous December. During late-winter captures, we assessed pregnancy using ultrasound and for does for which we did not detect a fetus, we confirmed pregnancy status using pregnancy-specific protein B from blood samples. Starting in 2011, we determined the number of fetuses each deer was carrying in late-winter using ultrasound (Stephenson et al. 1995). At the onset of the study, we captured deer across the entire Magnolia winter range assuming they were one contiguous group. However, GPS radio-collar data from the first year of the study indicated that individuals were split between the northern and southern half of the winter range, with most individuals from the 2 groups migrating to different summer ranges. Thus, we split our study area into north Magnolia and south Magnolia (Fig. 1). We assigned deer to an area based on where they spent the majority of the winter using the proportion of GPS radio-collar locations in each area (Table A1, available online in Supporting Information). In addition to having different summer ranges, deer in the 2 areas were exposed to substantially different densities of features related to natural gas development, with south Magnolia having greater road densities (1.9 km/km^2 in south Magnolia, 1.2 km/km^2 in north Magnolia), pipeline densities (1.2 km/km^2 in south Magnolia, 0.5 km/km^2 in north Magnolia), industrial facilities (0.1 facilities/km^2 in south Magnolia, 0.01 facilities/km^2 in north Magnolia), and well pads (0.62–0.78 pads/km^2 in south Magnolia, 0.01–0.06 pads/km^2 in north Magnolia; Figs. 1–2). Hereafter, we refer to the more heavily developed south Magnolia study area as the high-development area and the north Magnolia study area as the low-development area. Making valid inference to the effect of development at the study area level on deer behavior and demography requires that deer are largely contained within one study area or the other. To assess fidelity of the deer assigned to each study area, we conducted 2 analyses. First, we estimated utilization distributions (UDs) by fitting kernel density estimators for each deer and winter season (31 October through 1 May of the following year) using the ctmm package in the R statistical software (Calabrese et al. 2016) assuming locations were independent and identically distributed, which equates to a conventional kernel density estimator (Calabrese et al. 2016). We then calculated the proportion of the UD that overlapped with each of the outlined study area boundaries in each year the animal was collared to assess if there were any changes in study area use across years and to examine how often deer overlapped with a different study area than the one to which it was assigned. Next, we calculated individual animal UD overlap between years for each deer collared in >1 year to assess finer-scale fidelity of individuals to their specific range area. We calculated overlap following Winner et al. (2018).

We captured mule deer fawns (deer born the previous June) using helicopter net gunning December 2008–2015 (Table 3). As with does, we originally captured fawns across both study areas, but then captured them separately in the low- and high-development areas beginning in December 2009. We weighed and sexed fawns, fit them with a very high frequency (VHF; Advanced Telemetry Systems, Isanti MN, USA) radio-collar, and released them at the capture location. Fawn collars were spliced and fit with rubber surgical tubing to allow for neck growth. The tubing deteriorated over time, allowing for the collar to drop off, typically on summer range. As with doe collars, fawn collars were fit with placards to allow for individual identification. Fawn collars were also equipped with a mortality beacon that was activated if the collar was immobile for ≥8 hours.

Statistical Analysis of Habitat Selection

We examined habitat selection using the GPS data collected from radio-collared does. To guard against the potential behavioral effects of helicopter capture, we censored the first 4 days of data following capture as suggested by Northrup et al. (2014*a*). In addition, we censored all data with a dilution of precision >10 (<1% of all data; D'eon and Delparte 2005, Lewis et al. 2007). Because deer are migratory in this area, and migration times vary by year and individual

(Lendrum et al. 2013, Northrup et al. 2014*b*), we defined winter range as the time between 31 October and 1 May to maintain a temporally consistent sample across years. We censored any data falling outside this period and any locations off of winter range during this period. We examined the GPS radio-collar datasets of each individual deer and censored any apparently erroneous locations (indicated by large movements induced by single outlier locations) and any locations falling outside the study area boundaries (Fig. 1); we did not censor locations falling to the east of the study area boundaries because this was the only boundary not delineated using topographic features. The total number of censored locations equated to <3% of all locations. Lastly, we categorized each location by the winter season during which it occurred (e.g., winter 2013 for data between Nov 2012 and Apr 2013) and whether it occurred during the night or day, with night defined as the time between sunset and sunrise (http://www.esrl.noaa.gov/gmd/grad/solcalc/, accessed 02 Oct. 2020).

We estimated resource selection functions (RSFs; Manly et al. 2002, Johnson et al. 2006) for each winter and study area. Resource selection functions provide estimates of the relative probability of selection of resource units based on the habitat characteristics of those resource units. We estimated RSFs for day and night separately using hierarchical conditional logistic regression (Duchesne et al. 2010) fit in a Bayesian framework where all parameters were allowed to vary by individual, resulting in population-level parameter estimates that robustly incorporated individual variability (see Northrup et al. 2015 for more details and below model statement for explicit distributional assumptions). Although mule deer are typically most active at dusk and dawn, our fix schedule (1 fix every 5 hours) resulted in relatively few crepuscular locations. Further, other research in nearby study areas has previously shown strong contrasts in behavior between night and day (Northrup et al. 2015), and our interest was in examining if there were differences between the study areas in these behaviors. Thus, we did not fit a model to data during crepuscular time periods. Resource selection functions require the designation of an area assumed available for selection by animals (often called the availability distribution). We estimated the availability distribution using the predictor distribution (see below) from a continuous-time correlated random walk model (Hooten et al. 2014). Using this approach, the availability distribution is dynamic and varies for every used location, which accounts for local behavior of the animal and autocorrelation in the availability distribution.

We fit continuous-time correlated random walk models for each individual and year combination using the crawl package in the R statistical software (Johnson et al. 2008) and following the approach of Hooten et al. (2014) to extract the predictor distribution for each location. Predictor distributions are a continuously distributed prediction of where the animal is expected to be at some later point in time (in our case 1 fix, or 5 hours, after a used location of interest) using data from all prior movements. This distribution can be visualized as a bivariate normal distribution, with the mean of the distribution being the most likely location of the animal. The continuous-time correlated random walk model includes an autocorrelation term, which weights movements near in time to a greater degree than previous movements and thus produces estimates of availability that are dynamic in space and time. Using the mean and variance of these predictor distributions, we randomly generated coordinates for the sample of available locations. This approach is similar to a step-selection function (Fortin et al. 2005) but provides a continuous distribution of available locations as opposed to the discrete distribution that comes from using empirical turn angle and step length distributions in the originally described version of this approach. Further, the traditional step selection function uses a constant empirical distribution for turn angle and step length, but our approach allows for a more continuously dynamic definition of availability. Such an approach is intuitive because it serves to shrink the availability distribution when the animal is stationary and expand it when they are mobile. For each individual, we conducted a sensitivity analysis of the parameter estimates relative to the size of the availability sample (Northrup et al. 2013). Once we determined a sufficient sample size, we standardized all continuous covariates ($\frac{x_i - \bar{x}}{\mathrm{SD}(\boldsymbol{x})}$, where x_i is the *i*th data point; see below for description of covariates) and tested for pairwise correlations among covariates using |*r*| < 0.7 as a cutoff above which we did not include correlated covariates in the same model (Dormann et al. 2013). We standardized covariates using values combined across both study areas, all winter seasons, years, and day and night so that all coefficient estimates would be directly comparable across models. Next, we assessed multicollinearity using condition numbers, as described by Lazaridis (2007; values >5.4 are indicative of an ill-conditioned model). This method is used prior to model fitting to assess multicollinearity. We fit the hierarchical models using a Markov chain Monte Carlo (MCMC) algorithm written in the R statistical language. Our model took the following form:

$$[y_{tn}|\boldsymbol{\beta_n}] = \frac{e^{\boldsymbol{x}'_{\boldsymbol{y_{tn}}}\boldsymbol{\beta_n}}}{\sum_{j=1}^{J} e^{\boldsymbol{x}'_{\boldsymbol{j_{tn}}}\boldsymbol{\beta_n}}}$$

$$\boldsymbol{\beta_n} \sim \mathrm{Normal}(\boldsymbol{\mu_\beta}, \boldsymbol{\sigma^2_\beta}\mathbf{I})$$

$$\boldsymbol{\mu_\beta} \sim \mathrm{Normal}(\mathbf{0}, 2\mathbf{I})$$

$$\log\left(\sigma^2_{\beta_k}\right) \sim \mathrm{Normal}(0, 1),$$

where y_{tn} is a resource unit represented by habitat covariates $\boldsymbol{x_{y_{tn}}}$ that is chosen by animal n at time t from a set of available resource units $\boldsymbol{J}$, represented by habitat covariates $\boldsymbol{x_{j_{tn}}}$. $\boldsymbol{\beta_n}$ are the set of coefficients related to the k habitat covariates for individual n, and $\boldsymbol{\mu_\beta}$ and $\boldsymbol{\sigma^2_\beta}$ are the population-level mean and variance of the coefficients, with $\mathbf{I}$ as an identity matrix. We fit this model to data from the night and day periods separately for each winter season–study area combination for a total of 28 models. We combined data from 2008 and 2009 because sample sizes were small at the outset of the study. Although environmental and development conditions varied between these years, the temporally specific definition of availability partially accounts for this variation. We ran the MCMC algorithm for a variable number of iterations because of differences in the number needed for convergence (Table B1, available online in Supporting Information), thinning chains to every twentieth iteration, and assessed convergence by examining the trace plots of all parameters to ensure proper mixing. We drew inference based on a combination of the coefficient magnitudes and the proportion of the posterior distributions overlapping 0. Because all covariates were standardized across years and models, the magnitudes are directly comparable, and thus provide inference on whether selection or avoidance of a particular covariate was greater or lesser in one year or study area compared to another. However, coefficient magnitude alone is not sufficient to draw robust ecological inference because there can be substantial uncertainty in an effect despite a large magnitude coefficient. Thus, we also made inference based on the proportion a posterior distribution that fell to either side of 0; we considered a posterior probability of an effect >90% to provide strong evidence of an effect, between 80% and 90% moderate evidence of an effect, and <80% weak evidence for an effect.

To visualize the habitat selection patterns of deer, we mapped the mean predicted population-level RSF values in each study area and year for the corresponding model (i.e., we predicted habitat selection in the low-development area using the model fit to deer from the low-development area) and binned predictions into 10 quantiles. To visualize differences in habitat selection between the high- and low-development area, we then mapped the habitat selection patterns of deer in each study area to the landscape in the opposite study area; that is, for each year, we mapped the mean population-level RSF values from the model fit to deer from the low-development area to the landscape of the high-development area and vice versa. This exercise provided a visualization of how deer in the low-development area would select habitat in a heavily developed area if they showed no changes to their behavior. To quantify differences in mean predicted habitat selection, we calculated the proportion of each study area that had a higher RSF value, using unbinned values, for the model fit to deer from that study area compared to the model fit to deer from the other study area.

Lastly, we assessed the area of land in each study area that was avoided by deer, according to the RSF results. Because the predictions of relative probability of selection from an RSF for a given year are not relative to other years, temporal comparisons of RSF values are not meaningful. However, it is possible to calculate the proportion of area in each year avoided relative to availability as the proportion of area where selection at the population level is less than 1. Thus, for each year and study area, we calculated the proportion of land where the predicted RSF value was less than 1. Further, as our results indicated a consistent avoidance of drilling well pads, we calculated the proportion of the landscape within the high-development area that was within 1 km of a drilling pad.

Spatial Predictor Variables of Habitat Selection

We chose a set of predictor variables that were related to 1) cover and forage, and 2) anthropogenic features (Table 4). Cover- and forage-related variables included a terrain ruggedness index (the mean difference between the elevation in a cell and that of the 8 neighboring cells, representing topographic cover) calculated from a United States Geological Survey digital elevation model with a 30-m resolution, and daily depth of snow (representing availability of vegetation during the winter) obtained from a distributed snow evolution model (Liston and Elder 2006). We validated predictions from the snow model using weather stations that we deployed within the study area (Northrup et al. 2016*b*). Further, we assessed selection of a suite of land cover-related variables. We obtained a spatial land cover layer from the Colorado Vegetation Classification Project (https://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c), which classified the vegetation of our study area into 69 categories. We aggregated these categories into 4 vegetation communities associated with security and thermal cover (represented by pinyon pine, juniper, and interspersed pinyon and juniper communities), forage (represented by sagebrush, sagebrush grassland mix, and mountain shrub communities), combined cover and forage (represented by mixed-vegetation land cover types: sagebrush and mountain shrub communities mixed with either pinyon pine, juniper, or both), and sparsely vegetated areas (represented by bare ground, rock, and sparsely vegetated areas). Lastly, we calculated the distance to any edges representing the transition from treed land cover to non-treed land cover as a measure of distance to cover. To assess variation in conditions over time on the two study areas, we qualitatively compared all of the cover and forage covariates assessed for each year between the study areas. We also quantified the average normalized difference vegetation index (NDVI), which is a coarse metric of plant biomass, from May through September for each year and study area simply to assess study area wide variation in this parameter over years. We obtained NDVI spatial layers as 7-day composites at a resolution of 1 km^2 and downloaded layers from the United States Geological Survey earth explorer (earthexplorer.usgs.gov, accessed 08 Aug 2020).

Anthropogenic covariates included the distance to the nearest road (and a quadratic term for distance to road) obtained from a spatial layer for roads created by digitizing aerial imagery from the National Agricultural Imagery Program (NAIP); the distance to natural gas pipelines using data obtained from the White River Bureau of Land Management office and validated using the NAIP imagery; the distance to natural gas facilities (e.g., compressor stations and gas plants) obtained by digitizing NAIP imagery and validating the majority of facilities on the ground; and a suite of covariates representing the spatial density of hydrocarbon well pads. We included a quadratic effect for roads because Northrup et al. (2015) reported this form of nonlinearity in past work on mule deer in this area. In contrast, we assumed that deer would display linear avoidance or selection of pipelines and facilities relative to availability. Facilities represent a major disturbance and thus we assumed a large-scale avoidance would occur relative to availability, which in our case was drawn from a relatively small spatial extent around each point. Pipelines have relatively limited human activity associated with them and thus we did not expect a nonlinear response relative to our scale of availability. We were interested in assessing the cumulative impacts of well-pad development and thus assessed the response of deer to the number of well pads within exclusive 200-m concentric rings (hereafter buffers) to a distance of 1,000 m (i.e., the number of pads within 200 m of a deer or available location, the number of pads between 200 m and 400 m, etc.). This allows for implicit assessment of cumulative effects by examining predicted responses across different numbers of well pads in different buffers (e.g., the number of pads being actively drilled within 400 m and the number of pads being actively drilled 400–600 m from locations).

Early in the study, when active drilling was occurring, the development landscape was highly dynamic, with the number of wells in different phases of production often varying from day to day (Fig. 2). To capture these dynamics, we obtained detailed information on the status of hydrocarbon wells from the Colorado Oil and Gas Conservation Commission (COGCC; cogcc.state.co.us, accessed 24 Jun 2015). The COGCC maintains a daily-updated database of the status and location of every well (but not well pad) throughout Colorado. We downloaded this database on 24 June 2015 and censored all wells that did not fall within 2 km of a mule deer GPS location. Next, we grouped wells onto well pads by digitizing all well pads in the study area using NAIP imagery. We grouped wells onto pads if they fell within the same digitized pad or in close proximity (generally <50 m). Using these grouped data, we created a time series of well pad spatial layers, accurate to the day, indicating the status of each well pad. The lifespan of a well pad can be dynamic, and we expected that the different phases of this lifespan would elicit different responses from deer. We categorized well pad status as abandoned, actively being drilled (drilling), or producing. The most active phase is expected to be the drilling phase, which is associated with large volumes of traffic, noise, artificial light, and human activity that can be constant and last several weeks. The production phase, when natural gas is being actively extracted, is typically associated with lower levels of human activity and can last for many years. We classified well pads as drilling if there was at least 1 well that was being actively drilled. We extended the drilling dates for 2 weeks before and after the start (spud) and end (test) dates to account for activity associated with moving equipment onto and off of the well pad. We classified well pads as producing if there were no wells being drilled and at least 1 well was classified as an injection well, shut-in, or producing. Injection wells are those used for pumping water or gas back underground, whereas shut-in wells are those that have been drilled but for which no natural gas is being actively extracted (https://cogcc.state.co.us/documents/about/COGIS_Help/glossary.htm, accessed 01 Jan. 2017).

Further, we included wells in this category that were in the completion process, which entails the installation of the permanent equipment used for producing natural gas. A detailed examination of the status dates of the wells in this study area indicated that the time between when a well was drilled and when it was completed ranged from weeks to years. The completion process is expected to last only a few weeks, so we included pads in the completion phase in the producing status. Although we included wells in this classification that were not actually producing natural gas, the vast majority of wells in this classification were actively producing natural gas, indicating the response of deer to this covariate largely represents the response to the production phase. There were too few wells in the other statuses (e.g., shut-in) to separate into their own classification. We classified pads as abandoned if all wells were listed as abandoned and thus, presumed to not be functioning or maintained. Lastly, many wells in the study area were not associated with well pads (i.e., they likely had been permitted but never constructed); thus, we excluded these wells. We visited the location of many of these permitted wells and they were never associated with active development. We created 10 development-related covariates from these data representing the number of pads of different statuses in the concentric buffers discussed above. We measured distances to the edges of pads.

We could not estimate RSF coefficients for the following covariates because of insufficient development or deer locations: for the high-development area, the number of well pads with active drilling within 200 m or between 200 m and 400 m during winter 2009, the number of well pads with active drilling within 200 m during winter 2010 and all drilling covariates after 2010. For the low-development area, we could not estimate coefficients for any drilling covariates for any years (Fig. 2). Likewise, we could not estimate coefficients for the number of producing well pads within 200 m in the low-development area for any year. For most individuals, there were no used locations within these buffer distances. As such, a finite coefficient cannot be estimated, and models fail to converge. Thus, we combined buffers to achieve model convergence. For example, in the low-development area, we estimated coefficients for the number of producing pads within 400 m and then within 200-m concentric buffers out to 1,000 m.

Field and Statistical Methods for Demographic Analyses

We monitored the survival of doe and fawn mule deer using radio-telemetry daily from the ground and bi-weekly from the air from a fixed-wing aircraft. Upon detection of a mortality signal, we located deer on the ground and performed a necropsy to determine the cause of death. During late March of each year, we conducted 3–5 mark-resight surveys in the 2 study areas via helicopter to estimate deer abundance. We delineated helicopter flight paths within the 2 study areas following topographic contours (e.g., drainages and ridges) using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, CA, USA), such that the distances between flight paths were approximately 500–600 m and the entirety of each study area was covered. Two observers and a pilot flew the flight paths, navigating using a GPS unit, and they recorded every deer that they saw as either marked with the unique identifier recorded, unmarked, or marked and unidentifiable. During the mark-resight surveys, we simultaneously conducted 2 telemetry surveys from a fixed-wing aircraft to determine if each marked individual was within or outside of the study area boundaries. For does, we plotted the GPS locations of each individual following collar recovery to evaluate whether they were within or outside of the study area boundaries during surveys. Deer were seldom outside of the study area boundaries (9 of 181 in 2010, 2 of 163 in 2011, 8 of 191 in 2012, 9 of 208 in 2013, 10 of 220 in 2014, and 10 of 220 in 2015).

We examined if there were any differences in deer body condition (early and late winter fat), age, pregnancy rates, fetal counts, lactation status, and fawn mass between study areas. Our objective was to test for an effect of development at the study area level on each metric over time. Thus, for each metric, except body fat, we fit a single linear or generalized linear model, with year and study area as categorical covariates. Further, we included an interaction between year and study area. This approach allowed us to directly test for differences in each metric between study areas and years in a single model as opposed to conducting multiple comparisons for each year and study area combination as might be done with a *t*-test. For body fat, we fit 2 separate generalized linear models for beta-distributed data. The first model included the entire time series of data and the second included only data from deer captured on or after December 2013 when we began collecting information on lactation status. In the second model, we included lactation status as a covariate to control for this likely important effect on individual doe condition. For age, we fit a linear model to log transformed values. For pregnancy and lactation status, we fit generalized linear models for Bernoulli-distributed data. For fetal counts, we fit a generalized linear model for Poisson-distributed data. For fawn mass, we fit a generalized linear model for gamma-distributed data. For all models we used a Type I error rate of 0.05 on the coefficients to indicate statistical significance. We fit all models in the R statistical software (R Core Team 2016).

We used the VHF and GPS collar monitoring data to assess survival separately for fawns and does using the known-fate survival model in the statistical software program MARK (White and Burnham 1999). We fit separate models because although we monitored adult females continuously, fawn collars were designed to fall off before the following fall (in some years, most collars fell off in late spring). Thus, we did not have matching temporal coverage of fawn and doe data, which necessitated different models. For does, we fit a set of candidate models to evaluate the hypothesis that survival varied across study areas and over time. We used different model structures to evaluate the temporal resolution at which survival varied (months, years, and seasons). Because winter is known to be a limiting time for mule deer in Colorado, and because mortality can vary by year (White et al. 1987, Bartmann et al. 1992, Bergman et al. 2014), we allowed survival to vary by time (year plus season or month) in every model. Thus, in our most highly parameterized (global) model, survival varied monthly between study areas, whereas in the model with the fewest parameters, survival varied by season across years. We assessed 2 different season covariates; the first covariate allowed survival to vary among summer (June – September), winter (November – April), and migration (May and October), with survival during fall and spring migration being equal, and the second allowed survival to differ between fall and spring migration. We compared models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) and made inference based on AIC_c weights and model-averaged survival estimates (Burnham and Anderson 2002). We assumed that any individuals that died within 10 days of capture (does and fawns) had suffered a capture-related mortality and we censored these animals from the survival analysis.

For fawns, we fit a set of candidate models to evaluate alternative hypotheses about whether survival varied across time (months or winter season [Dec. – April]) and between study areas. Because many fawn collars dropped off in late spring or early summer, we did not have sufficient sample sizes to fit summer models; thus, we assessed fawn survival for the winter season only. We compared models using AIC_c and made inference based on AIC_c weights and model-averaged survival estimates (Burnham and Anderson 2002). In the most highly parameterized model, survival varied monthly across years and between study areas, whereas in the simplest model survival varied by year and was constant between study areas. As with does, we expected annual variation in fawn survival and thus never fit a model excluding year.

We estimated abundance for both study areas, separately, between 2009 and 2015 using the immigration-emigration logit-normal mixed effects mark-resight model (McClintock et al. 2009, McClintock and White 2012) in MARK. This model allows for estimation of parameters for the mean resighting probability across years and surveys, individual heterogeneity in resighting probability within years, and differences in the population size within the survey areas and the super population using the survey area (i.e., whether there was any immigration or emigration). We fit models with varying combinations of these parameters in MARK and assessed model parsimony using $\mathrm{AIC}_{c.}$ We converted abundance estimates to density estimates by dividing by the survey area (i.e., the capture area boundaries). To assess the annual rate of change in population size between the 2 study areas, we refit the resulting top model to study area, including a random effect for annual population size, with a mean specified as a linear trend over time. We fit this model using variance components estimation, allowing for a quantification of population change over time (Burnham and White 2002, Burnham 2013). Because the 2 study areas had different initial abundances, the resulting estimates of realized growth were not directly comparable. Thus, we converted these estimates to a proportional change over time, by dividing by the intercept (i.e., abundance in year 0) and compared between study areas. We refit models, as opposed to including random effects in initial models, because our primary objective was in examining differences in the density estimate between study areas in each year, not growth rates. The inclusion of the random effects can result in shrinkage of annual abundance estimates towards the linear trend thus potentially obscuring between study area differences in some years.

Although the outputs of models from MARK revealed if the 95% confidence intervals for models of abundance (converted to density) overlapped, we were interested in assessing the degree of confidence interval overlap between the estimates from each study area in each year. Using the mean and standard error of the abundance estimates, we assumed a log normal distribution and conducted a Monte Carlo simulation to assess overlap. We drew 10,000 random samples for each study area for each year representing the suite of possible true underlying values of abundance. We converted these to density by dividing by the area of each study area and then calculated the overlap between the 2 resulting distributions by dividing the sum of the intersection of the distributions by the sum of their union.

RESULTS

Habitat Selection

After accounting for occasional collar malfunction, mortality, or failure to recover collars, our final GPS radio-collar dataset included 528 deer-years of data (Table 2). Fix success of GPS radio-collars averaged >90% for the entire study. Deer displayed high fidelity to study areas (Tables A1 and A2, available online in Supporting Information). Although deer occasionally used parts of both study areas and traveled outside of both, on average there was 90% UD overlap for deer assigned to the high-development area and 83% UD overlap for deer assigned to the low-development area (Table A1). Further, deer assigned to the low-development area showed only 2% UD overlap with the high-development area and deer assigned to the high-development area showed only 3% UD overlap with the low-development area. Further, only 6 deer moved their winter range areas between years such that there was greater UD overlap in the opposite study area from prior years (Tables 2, A1, A2). In addition, deer displayed high fidelity to their specific winter ranges, with an average of 81% year-to-year UD overlap in the low-development area and 84% year-to-year UD overlap in the high-development area (Table A2).

In the low-development area, we were unable to estimate coefficients for the response to well pads with active drilling because we rarely recorded deer within 1 km of such pads. In the high-development area, where drilling activity had declined to low levels after 2010 (Fig. 2), we estimated coefficients in 2008–2009 and 2010, but we combined the closest buffer distances (within either 400 m or 600 m) in both years because of few locations within that distance. These estimates indicated that deer in the high-development area showed stronger relative avoidance of areas with more well pads that were being actively drilled in close proximity (Fig. 3; Tables C2 & C3).

We found strong differences between the 2 study areas in the response to producing well pads (Fig. 4; Tables C1-C4). Although there was annual variation, in general, deer in the low-development area avoided the areas with more producing well pads in close proximity during both night and day, with relative avoidance increasing at closer distance buffers (Fig. 4; Tables C1 & C2). There were not enough locations within 200 m of producing well pads in any year to estimate a coefficient for this buffer distance for night or day in the low-development area, indicating strong avoidance of these areas. Deer in the high-development area displayed a weaker relative avoidance of producing well pads than deer in the low-development area for most year and distance buffer combinations, with coefficient magnitudes almost always smaller than corresponding estimates for the low-development area (Fig. 4; Tables C1-C4). Further, these deer appeared to display differences in selection between night and day relative to well pads. In several years, deer avoided areas with more producing well pads in close proximity during the day, with null response or selection of areas with more pads in close proximity during the night (Fig. 4; Tables C3 & C4). Deer in the low-development area showed some similar temporal patterning during some years, but this pattern was inconsistent and generally weaker than that of the high-development deer. Examining responses to well pads falling within multiple buffers simultaneously indicated a strong cumulative effect of development, with stronger avoidance of areas that had both drilling and producing well pads, or many drilling well pads falling within multiple buffer distance (Fig. 3 & 4; Fig. 5, Tables C1-C4).

In both study areas, deer displayed differences between night and day in their response to human features other than well pads. In the low-development area, deer generally avoided areas closer to natural gas facilities during the day, but selected areas closer to these features at night, though with high uncertainty in all years and time periods (Fig. 6; Tables C1 & C2). Also, in the low-development area, deer showed a moderate difference in responses to roads at night, with deer generally selecting areas closer to roads during the night relative to day (Fig. 7; Tables C1 & C2). Deer displayed a relatively consistent selection of areas closer to pipelines in the low-development area, but this selection was stronger and more consistent during the night (Fig. 8; Tables C1 & C2). In the high-development area, deer displayed a somewhat similar temporal pattern of habitat selection relative to roads, pipelines, and facilities, though there was substantially less uncertainty in the response to facilities (Figs. 6–8; Tables C3 & C4).

Deer also displayed differences between night and day in habitat selection behavior relative to forage and cover in both areas. In the low-development area during the day, deer selected areas of less rugged terrain (Fig. 9), closer to edges (Fig. 10), and in land cover classes related to cover (Fig. 11) and showed little consistent selection or avoidance of areas in response to snow depth (Fig. 12; Tables C1 & C2). In contrast, during the night, deer did not consistently select habitat in relation to terrain ruggedness or habitat edges (Figs. 9, 10) and selected areas with deeper snow (Fig. 12) and land cover types related to forage (reference category in Fig. 11; Tables C3 & C4). Deer in both the high-development and low-development areas selected habitat similarly in relation to terrain ruggedness but showed substantially different responses to the other cover and forage covariates (Figs. 9–12; Tables C-C4). In the high-development area, deer always selected areas closer to edges (Fig. 10) and displayed no consistent responses to snow depth (Fig. 12; Tables C3 & 4). In addition, deer in the high-development area displayed a similar temporal pattern of habitat selection relative to land cover types but more strongly and consistently selected cover habitat during the day than in the low-development area and did not display as strong a selection for forage during the night (Fig. 11; Tables C1-C4). Cumulatively, these responses resulted in strong differences in the spatial behavior of mule deer between the 2 study areas that also varied between night and day (Fig. 13).

Average measures of all covariates related to forage and cover were similar between the two study areas across all years (Tables 5-6). Further, NDVI values were similar between the study areas in all years (Table 7). Mapping of the RSF values showed the substantial differences in habitat selection patterns between the 2 study areas (Fig. 13 & 14). When using the models fit to deer from the low-development area to predict habitat selection to the high-development area, in all years >80% of the landscape had a lower RSF value than predicted when using the model fit to deer from the high-development area (Fig. 14). Reflecting changes in human activity throughout the study, approximately 30% of the high-development area fell within 1 km of well pads with active drilling in 2009, 22% in 2010, 9% in 2011, 5% in 2010, and 0% afterwards. However, our calculation of the proportion of each study area that was avoided relative to availability in each year was relatively consistent for the high-development area (Table 8).

Demography

Across the 8 years of the study, we captured 371 unique does on multiple occasions, for a total of 653 captures (Table 2). We also captured 766 unique fawns during this time (371 males and 395 females; Table 3). Despite occasional differences in mean values of age, doe body fat, pregnancy metrics, and lactation status, there were no noticeable trends over time, and no consistent differences between study areas (Figs. 15–17; Tables 9–10; Tables D1-D6). There were no statistical differences during any winter season between the 2 study areas in early winter doe body fat either when accounting for lactation status or not (Fig. 16; Table 10). Although controlling for lactation status did not influence the effect of study area on body fat, deer that were lactating had significantly lower body fat than those that were not ($\bar{x}$ body fat proportion of lactating does = 0.09 (SD = 0.023), $\bar{x}$ body fat proportion of non-lactating does = 0.12 (SD = 0.034); Table 10). There were no statistical differences during any winter season between the 2 study areas in late winter doe fat, change in doe fat over winter, or fetal counts (Figs. 16–17; Tables 9–10; Tables D1-D6). Raw lactation rates differed moderately between study areas (2013 low development $\bar{x} = 0.45, \mathrm{SD} = 0.51$; 2013 high development $\bar{x} = 0.33, \mathrm{SD} = 0.48$; 2014 low development $\bar{x}$ = 0.59, SD = 0.50; 2014 high development $\bar{x} = 0.46, SD = 0.51$), but generalized linear models indicated that these differences were not significant (Table 9). Pregnancy rates also did not appear to differ between areas (Fig. 17), though pregnancy rates were 100% in some years, making it impossible to fit a model to these data assessing differences in years. A generalized linear model fit to all data combined across years with only a covariate for study area indicated no significant difference in pregnancy rates between the high- and low-development areas (β for effect of high-development study area = 0.55, P = 0.23). There were several significant terms for the age model, but age only differed significantly between the study areas in a single year, with older does in the high-development area in 2010 (Fig. 15; Table 9). In addition, fawn mass varied significantly across years (Fig. 18), with the highest values in December 2009 and significantly lighter fawns in all other years except 2013 and 2015 (Tables D7-D9). However, these differences were consistent across study areas and sexes, with no statistically significant differences between areas in any years and for either sex (Table 11; Tables D7-D9). Males were significantly heavier than females on average (Fig. 18; Table 11).

Few does died in any year of the study and there was no apparent pattern between study areas (Table 2; Table E1; Figs. F1-F9). The top model for does indicated that survival varied between study areas and across seasons and years, with seasons split into summer, winter, and a single transition season (i.e., survival in the spring and fall transition periods were equal; Table 12; Fig. 19). Mean doe survival was marginally higher in the high-development area than the low-development area (Fig. 19; coefficient for the effect of being in the low-development area = −0.42 ± 0.50 [SE]). Excluding study area differences resulted in a model with nearly identical weight to the top model (Table 13; Table E1). Seasonal doe survival was generally high (mean monthly survival across study areas = 0.987, range = 0.85–1.0) but varied by season, with winter and summer being nearly identical, and transition-season being lower (Fig. 19). Models in which survival varied by month were not among the more parsimonious, with such models having zero AIC_c weight (Table 13).

Raw fawn mortality counts varied substantially from year to year (Table 3). The top fawn model indicated that survival varied by year only (Table 14) and had nearly twice the weight of the next best model (Table 15; Table E2-E6; Figs. F10-F17). Despite the second-best model suggesting evidence for study area differences, annual and monthly variation was substantially stronger (Fig. 20; effect size for study area = −0.41, whereas average absolute value of effect size for year = 1.00). Further, the 95% confidence intervals for the coefficient for study area in this model overlapped zero (Table E2, available online in Supporting Information).

In the low-development area, the mark-resight model with resighting probability varying by individual and survey, and no immigration or emigration, was the most parsimonious among the candidate models (Table 16). In the high-development area, the model with resighting probability varying by survey, but not individual, and no immigration or emigration was the most parsimonious (Table 16). Deer density was higher in the low-development area during each year, but confidence intervals overlapped in all but 2 years (2011 and 2015; Fig. 21). Monte Carlo simulations indicated that confidence interval overlap was 47% in 2010, 0% in 2011, 13% in 2012, 8% in 2013, 21% in 2014, and 0% in 2015, suggesting that in most years there was evidence for greater density in the low-development area. The *post hoc* model assessing change over time in abundance indicated that deer abundance increased significantly over time in both study areas. Abundance increased at a greater rate in the low-development study area than the high-development study area, but confidence intervals for the rate of increase overlapped (mean annual increase for low- and high-development areas were 0.057 [95% CI = 0.021–0.78] and 0.045 [95% CI = 0.021–0.087], respectively; Fig. 21).

DISCUSSION

We contrasted behavior and demography of mule deer between areas of heavy and light natural gas development to test alternative hypotheses about how habitat modification influences the species on their winter range. As expected, based on previous work in this area and others (Northrup et al. 2015, Sawyer et al. 2017), we saw behavioral responses to development with strong contrasts between the 2 study areas. Deer avoided infrastructure in the lightly developed area where they had sufficient space to do so and selected for variables assumed to relate to forage. In the more heavily developed area, where deer did not have the space to avoid infrastructure wholesale, they selected for areas with greater cover and patterned their habitat selection to use areas near well pads at night. In accordance with hypothesis B, these behavioral differences did not manifest as demographic effects, with no differences in any measured metric, except density, between the 2 study areas. These findings indicate that deer can show remarkable behavioral plasticity in relation to habitat modification, which can potentially buffer them against demographic effects, at least under the development and deer densities in our study area. However, deer density was lower with greater development, which suggests a demographic difference between the deer in these study areas that was not captured by our design. Below we discuss possible reasons for this difference.

The behavioral responses of deer we observed corroborate the findings of past studies on the species that have shown altered habitat selection in response to hydrocarbon development (Sawyer et al. 2006, 2009, 2017; Webb et al. 2011*c*; Northrup et al. 2015, 2016*b*). Further, studies on other species have found similar behavioral responses to energy development and related infrastructure, with elk (Webb et al. 2011*b*), sage grouse (Holloran et al. 2010), and chestnut-collared longspurs (*Calcarius ornatus*; Ng et al. 2019) among the numerous species exhibiting altered behavior. Behavioral alterations in response to habitat modification are expected, as they are the initial means by which species can cope with disturbance (Berger-Tal et al. 2011, Greggor et al. 2016). These alterations are typically assumed to reduce individual fitness, and subsequently to affect population dynamics. Habitat selection, specifically, is a behavior that is expected to influence individual fitness (Morris 1989), and variation in this behavior can drive population dynamics (Matthiopoulos et al. 2015, 2019). Thus, several researchers have inferred detrimental effects on species from altered habitat selection in areas disturbed by hydrocarbon development (Carpenter et al. 2010, Beckmann et al. 2012, Northrup et al. 2015). Our behavioral results would, at first, seem to suggest substantial effects on individual fitness through altered habitat selection in the more heavily developed area.

Despite the strong behavioral differences between study areas noted above, we did not document a concomitant effect of natural gas development on most demographic measures, supporting hypothesis B. We developed hypothesis A, whereby we predicted altered behavior leading to demographic differences between the 2 areas, based on the prediction that altered habitat selection would lead to reduced access to high quality forage and thus lower condition and survival. However, this hypothesis was clearly refuted, with deer showing nearly identical measures of all condition and demographic metrics other than density. These results stand in stark contrast to the only other study that has conjointly assessed behavioral and demographic effects of natural gas development on mule deer. Sawyer et al. (2017), working in a sagebrush ecosystem in the Pinedale area of Wyoming before and during development, examined mule deer abundance and the average distance between individuals and well pads over 15 years of ongoing activity (compared to approximately 10 years of activity in our study area as of 2015). This study found that mule deer were farther from natural gas development on their winter range in years after development began. During this time, the population declined by 36%. Mule deer in the Wyoming study system appeared to avoid development more strongly than in our study area, a pattern that persisted after active drilling stopped. However, the authors did not measure deer body condition, reproductive parameters, or monitor fawns, making it difficult to draw mechanistic links between behavioral responses and abundance. In contrast to Sawyer et al. (2017), deer in our study in northwest Colorado that were subject to similarly high densities of development (i.e., deer in the high-development study area) avoided well pads during the drilling phase and used all but the closest areas around well pads that were in the production phase as available. Further, deer in our study appeared to increase their use of cover in the more developed area. We believe that strong differences in the habitat of the 2 study systems drove these contrasting findings. The Wyoming study did not conduct a formal assessment of habitat selection, so it is impossible to directly compare results, but the Pinedale area consists mostly of sagebrush and has limited topography, whereas our study area had substantial available tree cover and complex topography. We suggest that these characteristics have allowed deer to adjust behaviorally, using areas closer to well pads and other infrastructure with greater cover, whereas they were displaced from large areas around development in the flatter and more open Wyoming system. Our results are more similar to the response of pronghorn in the same Wyoming system (Beckmann et al. 2012, 2016). Beckmann et al. (2012) examined the habitat selection patterns of pronghorn in response to natural gas development over 5 years. They found that development influenced pronghorn habitat selection but with no consistent direction of effect. Despite some behavioral responses, Beckmann et al. (2016) found that pronghorn survival, mass, fecal corticosteroids, and progesterone were nearly identical between developed and undeveloped areas. However, Sawyer et al. (2019), working on pronghorn over a 15-year period in an overlapping study area, documented an increase in the number of individuals abandoning their ranges, which complicates interpretation of the results of Beckmann et al. (2012, 2016). These congruent and contrasting findings across regions and species have implications for regulations aimed at reducing impacts of hydrocarbon development on wildlife. For example, it could have been potentially misleading to use the mule deer results of Sawyer et al. (2017) to assume negative responses of natural gas development on pronghorn in the same area or to mule deer in our study area. This suggests that, if analyses from a similar ecological context are lacking, development and mitigation plans might need to be custom fit to the species and area of interest to ensure effectiveness.

Mule Deer Behavior and Natural Gas Development

Deer in our 2 study areas displayed markedly different patterns of habitat selection. We interpret these results as the manifestation of different behavioral tactics from a species that is known to be highly philopatric (Robinette 1966, Garrott et al. 1987, Northrup et al. 2016*b*), and from individuals who displayed remarkable fidelity. In the low-development area, deer could simply move to areas of their home ranges far from development while likely maintaining their typical habitat selection patterns. Such a tactic was possible because of the low density of development, and thus relatively larger amount of undeveloped habitat within their ranges to which they could be displaced. Deer in the high-development area did not have undeveloped areas within their winter ranges to which they could move and thus modified their behavior at a finer scale, focusing on access to cover over access to forage. Similar patterns of reduced direct interaction with development without large-scale abandonment of ranges has been seen in previous studies of elk and mule deer in areas with active natural gas development (Webb et al. 2011*a*, *b*). However, other studies offer contrasting findings, with pronghorn and mule deer in Wyoming displaying potential abandonment or large-scale avoidance of developed winter range areas (Sawyer et al. 2017, 2019) and sage grouse showing reduced lek attendance near well pads (Walker et al. 2007). All of these species typically display philopatry, so these findings suggest that abandonment occurs where alternative habitats, within an animals range, offering cover from the disturbance are not available.

Although the above differences in habitat selection of deer might seem nuanced, they represent strong contrasts in spatial behavior between the 2 areas, which can have important implications for conservation planning (Harju et al. 2011). The mapping of habitat selection patterns of deer from the low-development area to the landscape in the high-development area indicated compromised behavior assuming consistent habitat selection patterns (Fig. 14). However, deer in the high-development area regularly used habitat that naïve deer would avoid. Our condition measures did not support a link between these behavioral shifts and physiological costs, possibly because of the generally low forage quality on mule deer winter range (Wallmo et al. 1977). Notably, all deer were in a net negative energy balance on their winter range, regardless of density of development or forage availability in the area. This contradictory finding is likely because the major decline in condition that deer experience over the winter supersedes benefits that use of areas with more forage may provide during this period (Monteith et al. 2013).

If low forage quality is the reason for the lack of any documented demographic response, then it is possible that greater attention should be paid to management and mitigation options during the late winter and early spring when green-up begins. This period likely is particularly important for deer to begin to recoup condition losses over the winter, and behavioral responses to development likely are more impactful. Furthermore, given the importance of the summer range for critical stages of reproduction and net energy balance gains that carry deer through winter, summer disturbance could be more important than previously considered. Indeed, the timing of development relative to important life-history stages is likely critical to understanding how different species might respond to development during different times of the year. As mentioned above, our results are similar to those found for pronghorn on their winter range in Wyoming, whereby no physiological costs were associated with altered habitat selection around energy development infrastructure. Beckmann et al. (2016) posited that because pronghorn already experience substantial condition declines over winter, any effect of habitat loss from energy development was masked. These results contrast with those from avian studies that have examined the effect of energy development during the breeding season. Ng et al. (2019) documented reduced parental care in chestnut-collared longspurs closer to development infrastructure, leading to fewer offspring fledged in these areas. Likewise, Walker et al. (2007) documented declines in male sage grouse attendance at leks when they were located closer to energy development. However, even for avian species during the critical nesting period, these results are not always consistent; Ludlow and Davis (2018) found a range of effects (both positive and negative) of hydrocarbon wells on waterfowl and shorebird nest site selection but no effect on daily nest survival. Considering these contrasting findings, close attention should be paid to the timing of development activities relative to life-history stages. Indeed, for mule deer, behavioral responses during the fawning period could have greater demographic consequences than what we show in this study and thus further research into this potential is warranted.

Mule Deer Demography and Natural Gas Development

Our demographic results indicate that at the current development and deer population densities, natural gas well pads in the production phase on winter range are not affecting the measured individual demographic and physiological parameters in our study area. Our sample sizes were large and thus we had the power to detect relatively small differences between study areas and years. For example, the probability of detecting a difference in fawn survival between 0.95 and 0.85 (0.95 was approximately the average monthly survival for the less developed area) was 0.45. Estimated differences in survival were usually smaller than 0.1, and deer in the high-development area had marginally higher survival than in the low-development area in general. For does, differences between study areas were always small (the mean of the absolute value of differences in monthly survival between areas was 0.015) and would require annual sample sizes approaching 1,000 collared does to see statistically significant differences if survival truly varied by that small amount. Thus, the lack of differences in demographic parameters (particularly survival) is a robust finding.

The demographic parameters we measured were indicative of a population below carrying capacity. In particular, survival of fawns in this study was high (average of overwinter model-averaged survival estimates for the low-development area = 0.77 and for the high-development area = 0.78; Fig. 20). Forrester and Wittmer (2013) reviewed survival rates of mule deer throughout their range, and the survival estimates for fawns from our study exceed nearly every study reviewed. Further, these survival rates were higher than comparable studies conducted in this study area or in similar habitat that experimentally removed predators (Bartmann et al. 1992, Hurley et al. 2011), assessed habitat improvements (Bergman et al. 2014), or reduced deer density (White and Bartmann 1998). During certain years, fawn survival in our study was similar to those reported by Bishop et al. (2009) who fed deer pellets *ad libitum* during winter to intentionally raise the carrying capacity in their study system, though on average their estimates were higher than ours. Doe survival was on par with estimates from other studies (mean model-averaged annual survival estimate for low-development area = 0.82 and for the high-development area = 0.85). For large ungulates, adult survival is the most sensitive vital rate but typically varies little, with population dynamics often driven by recruitment (Gaillard et al. 1998). Thus, the comparatively high fawn survival in our study further strengthens our impression that these populations were below carrying capacity. Other demographic and physiological parameters that we measured were similar or exceeded those in other studies. Specifically, early and late winter doe body fat was the same or higher in our study than in similar studies (Bishop et al. 2009; Monteith et al. 2013, 2014; Bergman et al. 2018). Only does receiving supplemental feed *ad libitum* in Bishop et al. (2009) had higher body fat than those in our study. Pregnancy rates in our study also were on par or higher than those in other studies (Bishop et al. 2009, Freeman et al. 2014, Monteith et al. 2014), and fawn mass was comparable to Hurley et al. (2011) and substantially higher than during the 1980s in the same ecosystem as our study (Bartmann et al. 1992). These comparisons indicate that in both study areas, deer were not strongly limited by habitat availability as might be expected under substantial habitat modification.

Mule deer in the Piceance Basin declined substantially in the 1990s (White and Bartmann 1998, Unsworth et al. 1999). Although this past work did not overlap spatially with our current study, they took place in the same ecosystem. During those studies, winter range deer densities were 5–6 times higher than in our study (White and Bartmann 1998). Thus, the current demographic rates likely represent a rebounding population that is below carrying capacity, where winter range habitat is not strongly limiting. Under these conditions, our results indicate that the current density of development in the producing phase is not actively affecting these populations, despite the strong behavioral differences between the 2 study areas. However, habitat modification from natural gas development could induce negative demographic consequences that occurred prior to our work (potentially accounting for the differences in densities observed; see discussion below) or could not be detected in our study. First, because deer appear to be well below carrying capacity, we are unable to determine if habitat modification has permanently altered the density of deer that this landscape is able to support. Thus, if deer densities continue to increase, we may observe differences in demographic responses manifest as a function of different carrying capacities or observe density-dependent effects sooner on the more heavily developed area. Likewise, most of the winters during our study were mild (i.e., little snow and relatively mild temperatures, with snow melting in early spring), except for the first and fourth winters. Mule deer populations have traditionally been limited by winter range forage availability (Wallmo et al. 1977, Parker et al. 1984, Bishop et al. 2009) and thus we would expect some interaction between the high level of habitat modification and winter severity, whereby deer in the high-development area might have particularly depressed demographic rates during harsh winters. Because winters were relatively mild during our study, we were unable to test this interaction. Long-term declines in winter severity associated with climate change may further reduce the chances of such a scenario.

Critically, our study began after natural gas development had peaked. In fact, intensive drilling and associated activity levels declined through the duration of the study, thereby relaxing displacement of deer most strongly associated with the drilling phase of development. Sawyer et al. (2006, 2017) examined deer responses to natural gas development in a before-during study design and found large-scale displacement of deer after initiation, associated with reductions in abundance. Thus, we are uncertain if there were similar responses in our population, which might account for observed differences in density, and if the remaining deer that were studied are those less prone to negative effects from development (e.g., habituated to development). Strong demographic effects in response to the initial habitat modification before our study would explain the documented differences in deer density, but we lack the information required to make this inference. In addition, although this study primarily assessed the response of deer to well pads in the later stages of development (i.e., production), the responses to drilling were strong and the area affected by this activity was large, particularly in the first year of the study. Drilling appears to have shifted deer activity to other areas of their home ranges as evidenced by the high fidelity to winter use areas and the relatively consistent proportion of the high-development area where deer selection was reduced. The subsequent reduction of drilling activity then increased the relative selection of areas where wells were previously being drilled. If drilling activity increases above previous levels in coming years, we are uncertain of how this will affect deer behavior and demography, particularly now that deer density is higher than during the more active drilling phase. At very high densities of drilling activity, deer could display habituation similar to responses to production activity, or alternatively, the avoidance that we documented could produce demographic effects. Further, because drilling activity is associated with substantial noise, it might also affect the ability of deer to avoid predators if they did habituate to drilling activity at higher densities. There is likely some level above which deer or pad densities are high enough to affect demography and population dynamics, but conditions during our study were apparently below this threshold. Identifying these thresholds will be complicated because it is likely a function of the species, habitat, weather, climate, and timing of development. For example, Sawyer et al. (2017) found larger-scale avoidance by naïve (i.e., not previously exposed) mule deer and Sawyer et al. (2019) found substantial increases in the number of naïve pronghorn completely abandoning their study areas. Although our study did not include naïve deer, comparisons to our results suggest deer can persist at higher densities in proximity to development in our study area with more vegetative and topographic cover. Likewise, life-history stage is important when considering thresholds; Sawyer et al. (2020), working with mule deer during migration, found deer use during migration strongly declined at surface disturbance levels of around 3%. However, they did not assess any demographic consequences of these responses. In our heavily developed study area, around 4% of the landscape is disturbed by well pads, facilities, and roads. Deer still use these areas, albeit in an altered manner, but we documented no large-scale avoidance as in the study by Sawyer et al. (2020).

In addition to the potential for demographic effects under the different scenarios discussed above, despite nearly identical demographic and physiological measures between the 2 study areas, there was, potentially, a lower rate of population growth in the high-development area and consistently higher point estimates of density in the low-development area (though confidence intervals overlapped for linear trends in density and for annual density estimates in most years). Four possible processes could cause differences in density, although we do not currently have the data to directly address which of these is most likely. First, habitat quality could be different between the 2 areas and thus carrying capacity could be lower in the more heavily developed area. However, remotely sensed covariates linked to habitat quality (e.g., NDVI, snow cover) were similar between the 2 study areas. Further if habitat quality was different, we would expect to see differences in overwinter change in body fat. As such, we assume this is unlikely. Second, it is possible fawns in the high-development area lost more mass during the winter than those in the low-development area, but these differences did not manifest themselves over winter. Given summer is the time when deer gain energy (Monteith et al. 2013), this seems unlikely. Recapture of individual fawns in late winter would be needed to address this hypothesis.

The third possible explanation is that the onset of development reduced deer density in the more heavily developed area. This reduction could have occurred from deer abandoning their winter ranges, or from a reduction in carrying capacity due to larger-scale avoidance of well pads during the construction and drilling phases. Either process could have led to lower density compared to the low-development area. Given deer are highly philopatric even in the presence of substantial development (Robinette 1966, Garrott et al. 1987, Northrup et al. 2016*b*), and our fidelity analysis exemplified this behavior in over 400 individuals in this study, we do not find evidence that deer are currently abandoning their winter ranges to a greater degree in the high-development area. Sawyer et al. (2006) and Sawyer et al. (2019) found deer and pronghorn, respectively, to be strongly displaced at the onset of development. Thus, density differences could result from displacement of sensitive individuals before initiation of our study, or the emigration of juveniles, which we did not follow for multiple years. If density was reduced in the high-development area at the onset of development, regardless of the mechanism, then the apparent population growth that we documented would be a result of low density relative to carrying capacity.

The last explanation for potential differences in population trends and density in the 2 study areas is that neonatal or fetal survival could be different between the 2 areas because of differences in predator abundance or habitat quality on summer range, which would lead to lower overall recruitment rates despite similar overwinter fawn survival. Lower recruitment rates would explain differences in population growth rates despite all other demographic parameters being nearly identical. Because neonatal fawn mortality tends to be high in mule deer generally (Pojar and Bowden 2004, Lomas and Bender 2007), as confirmed in this study area (Peterson 2016, Peterson et al. 2017), any differences in survival of this age class could be an important driver of population dynamics. Further, if there were differences in habitat quality between the summer ranges, then lower recruitment in one area could lead to the documented consistency in other demographic parameters. That is, if recruitment is low in the high-development area, it could lead to similar overwinter fawn survival and similar condition metrics between the 2 areas, despite differences in available habitat because of the subsequent reductions in density. However, our data do not support this possibility because doe body fat in both March (prior to departure for summer range) and December (after arrival back on winter range) were consistent between study areas across all years. The similar body fat values indicate that, on average, deer were recovering similar fat stores on both summer ranges. Similarly, for the few years that we collected lactation status information, we saw no differences between the study areas in body fat after controlling for lactation, suggesting differences in recruitment (which affect female body condition) were not a factor. Deer that are still lactating in December likely still have fawns at heel, and thus the similar fat values for lactating deer in both study areas suggests minimal differences in habitat quality between the summer ranges. This finding would suggest that recruitment rates are either not different between the study areas or only the fattest does in the high-development study area were rearing fawns (an unlikely condition given deer reproductive strategies). It is also possible that recruitment differed, but these differences were too small to affect study area-level differences in body fat. Such small differences in survival from birth to 6 months of age probably could affect differences in population growth, and thus cannot be discounted as a driver of potential differences in density. A congruent study being conducted in this area on deer reproduction found some potential evidence for lower birth rates (i.e., more stillbirths) on the summer range of the high-development area, compared to the summer range of the low-development area (Peterson 2016, Peterson et al. 2017). However, differences were not consistent across time and additional study areas were sampled to provide sufficient power, thus providing weak evidence that neonatal survival or birth rates were influencing patterns of density in our current study. The only other measure of recruitment we had was lactation rates in December, which did indicate potential, but non-significant, differences in recruitment on the 2 study areas.

In light of the above discussion, our inability to estimate recruitment is a clear limitation of this study. We had only 2 years of data on lactation rates, which, based on the negative relationship with doe body condition that we documented, is likely to represent some index of recruitment. More detailed information on recruitment rates would greatly clarify our results. Specifically, study area-level estimates would allow us to better resolve the differences in population dynamics. Currently, our results only show that density and, to a lesser extent, population growth appeared higher in the low-development area, but the mechanism is unclear. For example, all of the following are reasonable explanations for lower density on the more developed area: lower recruitment, lower initial density, abandonment of ranges upon initiation of development, reduced carrying capacity due to habitat loss from development, or innate differences in habitat quality.

Understanding the degree to which development affects further population growth will require continued examination under higher densities of well pads and deer, assessments of responses on summer range, and monitoring fawns through the entirety of their first year of life. We focused on winter range because deer in these areas inhabit summer ranges that are far apart and differ strongly in development activity and forage quality (Lendrum et al. 2012, 2013, 2014; Northrup et al. 2014*b*). Furthermore, mule deer management in Colorado and the rest of the Intermountain West has traditionally focused on winter range because deer face limited access to forage (Wallmo et al. 1977, Parker et al. 1984, Bishop et al. 2009) and can experience pronounced mortality during this period (White and Bartmann 1998). Thus, winter range assessments have the strongest implications for current management practices. In light of our findings, and reduced winter severity from climate change, increased attention should be focused on deer on their summer range.

The Use of Habitat Selection Analyses to Assess Effects of Human Disturbance

Habitat selection has long been used to assess wildlife responses to human activity and foundational ecological theory provides a pathway for inference to population and demographic responses through individual fitness (Fretwell and Lucas 1969, Charnov 1976, Frid and Dill 2002). Further, recent work has directly quantified links between habitat selection and population dynamics (Matthiopoulos et al. 2019). The numerous challenges involved in obtaining detailed demographic information (i.e., large numbers of marked individuals needed for long time periods) result in many studies requiring inferential leaps between behavioral responses, individual fitness, and population consequences. Our results highlight the need for caution when inferring population consequences from habitat selection analyses (see also Wilson et al. 2020), and indicate that some behavioral responses may be indicative of adaptive phenotypic plasticity (Ghalambor et al. 2007, Tuomainen and Candolin 2011) and not result in negative population-level consequences. This is particularly true for species that are adaptable to disturbance and where the disturbance is relatively short lived (i.e., less than the lifespan of an individual).

Our study focused on habitat selection of a relatively adaptable species on winter range where forage resources are typically limiting (Bishop et al. 2009). Thus, as mentioned above, it might be that nutrition is so limiting during this time that any behavioral response to development does not further restrict access to forage given the little nutritional value during winter. Further, the manner in which animals respond to disturbance is likely impossible to intuit from demographic data alone. Combining behavioral and demographic studies, as we have done here, provides a mechanistic understanding of how animals respond to human disturbance, which is subsequently crucial for developing effective mitigation measures (Dzialak et al. 2011*a*). For example, in our study, deer used areas closer to development by shifting use of these areas to the night time and increasing their use of cover habitat. This finding provides strong support for mitigation measures aimed at maintaining such cover habitat (discussed below) and reducing the human footprint during the drilling phase. Although pairing detailed demographic and behavioral studies will continue to be difficult, because of the need for sustained long-term funding and diverse expertise, pressing management issues warrant such work to obtain a more complete understanding of human-modified systems and potential mitigation measures.

Limitations

Despite the large sample sizes of individuals in our study, we had a few key limitations that could be improved upon in future research. Although a concurrent study measured neonatal fawn (i.e., birth through 6 months of age) survival (Peterson 2016, Peterson et al. 2017), this study did not directly match our design either spatially or temporally, thus limiting our ability to infer effects on population dynamics from their results; concurrent information on neonatal survival across our entire study period would have been valuable to help clarify differences in density between our 2 study areas. However, this type of data is costly and difficult to collect, particularly in our study area where fawning areas on summer range were often >100 km apart and dispersed. Likewise, the results of our study highlight the potential need to more closely monitor the condition of fawns throughout the entire first year of life. Although we saw no differences in early winter fawn mass, fawns in the more heavily developed study area possibly lost more mass over winter, leading to potentially lower survival during migration and over the summer. If we had collected this information, we might have been better able to assess the differences in density between the 2 study areas. Again, collecting these data would be costly, requiring recapture of >100 fawns or improved technology allowing annual survival estimates. Perhaps most critically, a clear limitation of our study was that we began research after the initiation of natural gas development. Sawyer et al. (2017) documented a strong response by mule deer to the initiation of natural gas development, providing a strong argument for procuring data before, during, and after development activity when possible. In addition to these limitations, that deer in our study migrated to different summer ranges adds complexity to the inference. Although we were able to account for potential differences in nutrition along migratory routes and over summer by measuring early winter fawn mass and doe condition (all of which were statistically indistinguishable between the 2 study areas), a better study design would include deer with shared summer ranges.

In addition to the above limitations, our combined behavioral and demographic analyses could be improved upon in future work. An ideal design would quantitatively integrate the behavioral and demographic data. For example, RSF coefficients might be used as covariates in survival models to directly assess whether behavior influenced survival, or the effect of metrics such as body fat on habitat selection behavior might be examined. In our study, we were limited by a few factors that made such an analysis impractical or uninformative. First, our RSF analyses included a large number of parameters, making direct integration complex. That is, to include RSF coefficients as covariates in a survival model would require >15 parameters in some years. Likewise, we were unable to estimate some coefficients in some years (e.g., for drilling well pads), again complicating analyses. Further, survival of does was so high that our models could not support a large number of covariates. Recent advances in habitat selection modeling provide a roadmap for designing future studies that can better integrate demography and RSFs (Matthiopoulos et al. 2015, 2019), but our design did not allow for following these examples. Lastly, aside from density, there were no documented differences in demographic metrics between the 2 study areas. Thus, had we been able to better integrate these datasets, it is unclear what inference such analyses would have provided.

MANAGEMENT IMPLICATIONS

Our findings support focusing mitigation efforts on reducing impacts during the construction and drilling phases of hydrocarbon development and limiting human activity and noise during the longer production phase. Such measures should include strategic spatial configuration of infrastructure that reduces road networks or minimizes construction of new roads, encourages multi-well pads and directional drilling (where possible) to reduce the footprint, noise (and artificial light) reducing retaining walls, and remote liquid-gathering systems (Sawyer et al. 2009). Most of the wells in our study area are directionally drilled from pads with multiple wells, which substantially reduced development density and resulted in a spatial configuration that allowed deer to respond behaviorally.

Our results in combination with those of other studies on mule deer (Sawyer et al. 2017, 2020) support maintaining cover habitat and refuge areas free from development so that deer can adapt their behavior without being displaced wholesale from their ranges. Landscape planning to ensure the minimization of the industrial footprint (e.g., roads, pipeline, processing stations) is critical for the maintenance of such cover habitat. More dispersed development, provided it does not lead to a significantly larger road network, might be more effective at minimizing impacts to deer and is supported by the surface disturbance thresholds documented by Sawyer et al. (2020). Although focusing mitigation on the drilling phase of development seems intuitive, our results offer some optimism that natural gas impacts might be more short-lived than previously thought and provides for feasible options for mule deer conservation in development planning considerations.

Our modeling framework also provides results that can be used to infer development density thresholds and the subsequent behavioral responses. By focusing on the number of development features within different buffers, we were able to assess the cumulative impact of development on deer behavior (e.g., Fig. 5). This information could be used by developers and land and wildlife managers in conjunction to identify potential development scenarios that minimize the behavioral effects of development on deer. For example, spacing infrastructure such that areas with multiple well pads in buffers that were avoided by deer should be limited. However, under similar ecological contexts as in our system (i.e., rugged terrain and ample vegetative cover) and similar deer and development densities, these behavioral responses are unlikely to elicit demographic effects. As such, we suggest that the development densities during our study could be used as a starting point for further work assessing the potential existence of thresholds of development above which demographic effects might occur, and future development planning could maintain similar thresholds to minimize population-level impacts in areas with similar habitat characteristics (i.e., ≤ 0.8 pads/km^2 on pinyon–juniper-dominated winter range in generally rugged terrain). In areas similar to our study area in land cover and topography, the RSF models for the high-development study area could be used to assess how deer would be anticipated to respond under different scenarios. Maps that show predictions from the high-development RSF model to the low-development area (Fig. 14) indicate how deer might respond behaviorally if the low-development area saw increased industrial activity. Such maps could be augmented with proposed development plans to further assess behavioral responses of deer and identify a strategy to extract natural gas with the least behavioral effect on deer. However, deer do not exist in these landscapes in isolation, and development strategies that are beneficial for them might affect more sensitive species, such as greater sage grouse. Thus, multiple species will need to be considered in development plans.

Currently, many areas of the western United States place restrictions on drilling activity on winter ranges. Our results do not provide strong evidence for or against these restrictions because of the limited amount of drilling during our study (i.e., initiated as drilling declined on the landscape). It might be tempting to interpret the lack of demographic response to the production phase as evidence for removing drilling restrictions and speeding the transition to production, but this could be misguided. If the density differences recorded in this study were a function of an initial response by deer to drilling, removing restrictions could elicit local population declines through larger-scale avoidance as seen in mule deer and pronghorn in Wyoming (Sawyer et al. 2019, 2020). Thus, we propose that planning be based on conditions present on proposed development areas until further research focused on scenarios with more active drilling over longer periods of time can be conducted. Ultimately, the variability evident in our results when compared to stronger responses of deer and pronghorn from other systems, suggests development planners should acknowledge the dynamics involved in wildlife-energy development interactions. Considerations of topographic and vegetative diversity and whether or not there is evidence that animals are habitat limited should be incorporated into development planning options. This approach may ultimately foster a collaborative and likely more successful planning process.

It remains to be seen whether the development in our area will limit mule deer populations at higher densities. The direct habitat conversion caused by roads, well pads, and facilities will at some threshold have demographic consequence for these populations. Thus, concerned managers should focus late-stage mitigation on recontouring and revegetating well pads, and reducing the overall road network and reclaiming roads or restricting public access thereon.

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Figure 1. Location of study area for assessment of effects of natural gas development on mule deer, 2008–2015, including study-area outlines, roads, natural gas well pads, and facilities in the north and south Magnolia winter range study areas in the Piceance Basin, Colorado, USA. North Magnolia is the northern polygon with low development and south Magnolia is the southern polygon with high development. Black arrows in the top right panel show the general migration directions of deer in the 2 study areas.

Figure 2. Number of natural gas well pads classified as producing natural gas (A) or actively being drilled (B) between January 2008 and May 2015 in the high- and low-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 3. Posterior distributions of population-level coefficients corresponding to the number of well pads within different buffers around deer global positioning system (GPS) locations where active drilling was ongoing. Estimates are for models fit to data from the high-development study area for night and day for the 2008–2009 and 2010 winters. We estimated coefficients using resource selection functions fit to GPS radio-collar data from doe mule deer on winter range in the Piceance Basin, Colorado, USA. Note that the range of *y*-axis values differs by plot.

Figure 4. Posterior distributions of population-level coefficients corresponding to the number of well pads within different distance buffers around deer global positioning system (GPS) locations that were producing natural gas. We obtained estimates using resource selection functions fit to GPS radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for

each year, daytime and nighttime, and for the low- and high-development study areas. Where estimates are missing (i.e., 200 m for the low-development area), we did not include covariates in models because too few data points fell within the distance buffer.

Figure 5. Predicted relative probability of selection as a function of the number of producing well pads within 200 m and the number of drilling well pads within 400 m (A) and the number of drilling well pads within 400 m and within 400–600 m (B). We generated estimates using population-level coefficients from resource selection functions fit to global positioning system radio-collar data from doe mule deer during the day during the 2010 winter season in the high-development winter range study area in the Piceance Basin, Colorado, USA. Note that only 1 year is shown as representative examples for simplicity.

Figure 6. Predicted relative probability of selection relative to the distance to natural gas facilities from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates.

Figure 7. Predicted relative probability of selection relative to the distance to roads from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and

for the low- and high-development study areas. We show only median estimates. Note that the range of *y*-axis values differs by plot.

Figure 8. Predicted relative probability of selection relative to the distance to pipelines from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates.

Figure 9. Predicted relative probability of selection relative to a terrain ruggedness index from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates. Note that the range of *y*-axis values differs by plot.

Figure 10. Predicted relative probability of selection relative to the distance to treed edges from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates. Note that the range of *y*-axis values differs by plot.

Figure 11. Coefficient estimates for covariates related to land cover classification from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates. In all models, the reference category was the land cover class defined as forage.

Figure 12. Predicted relative probability of selection relative to snow depth from population-level resource selection functions fit to global positioning system radio-collar data from doe mule deer during winter in the Piceance Basin, Colorado, USA, from winter 2008 and 2009 through winter 2015. We fit models separately for each year, daytime and nighttime, and for the low- and high-development study areas. We show only median estimates. Note that the range of *y*-axis values differs by plot.

Figure 13. Maps of predicted median relative probability of selection calculated from population-level coefficients estimated using resource selection functions (RSF) fit to global positioning system radio-collar data from doe mule deer. We fit models separately for each winter from 2008–2009 through 2015 for nighttime and daytime in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA. We combined data from 2008 and 2009 because of low sample sizes but produced maps for each year separately. We averaged dynamic covariates (i.e., snow depth and development infrastructure locations) across the entire winter season for mapping purposes. Lighter colors indicate higher relative probability of selection. Predicted RSF values have been binned into 10 bins based on quantiles for display purposes

only. The study area boundaries are shown in white, with the northern study area relating to the low-development area and the southern area the high-development area. The *x* and *y* axes represent the X and Y coordinates in meters for North American Datum of 1983 (NAD83) Universal Transverse Mercator zone 12.

Figure 14. Maps of predicted median relative probability of selection calculated from population-level coefficients estimated using resource selection functions (RSF) fit to global positioning system radio-collar data from doe mule deer. We fit models separately for each winter from 2008–2009 through 2015 for nighttime and daytime in the high- and low-development winter range study areas in the Piceance Basin, Colorado, USA. We created maps by predicting relative probability of selection across study areas. For each year, we predicted relative probability of selection in the low-development area using the corresponding high-development area model and vice versa, providing an assessment of what habitat selection patterns would look like if deer were moved to the opposite study area and showed invariant behavior. We combined data from 2008 and 2009 because of low sample sizes but produced maps for each year separately. We averaged dynamic covariates (i.e., snow depth and development infrastructure locations) across the entire winter season for mapping purposes. Lighter collars indicate higher relative probability of selection. Predicted RSF values have been binned into 10 bins based on quantiles. The study area boundaries are shown in white, with the northern study area relating to the low-development area and the southern area the high-development area. The *x* and *y* axes represent the X and Y coordinates in meters for North American Datum of 1983 (NAD83) Universal Transverse Mercator zone 12.

Figure 15. Median and interquartile range of age of doe mule deer, determined using patterns of tooth eruption and wear between the 2010 and 2015 winter seasons in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 16. Mean ± standard deviation percent ingesta-free body fat determined using ultrasonography and palpation of the rump for doe mule deer captured in December (A) and March (B) between March 2009 and December 2015 in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA. Panel C shows mean ± standard deviation of December to March change in percent ingesta-free body fat.

Figure 17. Mean ± standard deviation of pregnancy rate determined using pregnancy-specific protein B (A) and fetal counts determined using ultrasonography (B) for doe mule deer captured in March between 2009 and 2015 in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 18. Mean ± standard deviation of male (left panel) and female (right panel) mass for mule deer fawns captured in December between 2009 and 2015 in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 19. Mean and 95% confidence limits for model-averaged doe mule deer monthly survival between March 2009 and April 2015, in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 20. Mean and 95% confidence limits for model-averaged fawn mule deer monthly survival between March 2009 and April 2015, in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA.

Figure 21. Mean and 95% confidence limits of mule deer population density estimated from the most parsimonious model according to Akaike's Information Criterion (A) and the *post hoc* model fit with a random effect on population size (B), with the mean size specified as a linear trend for the 2010 through 2015 winter seasons in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA. For panel B, estimated mean and 95% confidence intervals of the trend are shown as solid and dashed lines respectively.

Table 1. Harvest statistics for the study period for Game Management Unit 22, which encompasses the Piceance Basin of Colorado, USA. Statistics include estimated number of adult male (buck), adult female (doe) and fawn mule deer harvested, and total days hunted by hunters. We obtained data from https://cpw.state.co.us/thingstodo/Pages/Statistics-Deer.aspx (accessed 01 Jan 2016). All hunting took place in the fall of each year.

Year	Bucks harvested	Does harvested	Fawns harvested	Total hunter days
2015	404	14	0	3,258
2014	413	88	10	3,521
2013	436	102	4	3,343
2012	358	110	5	2,998
2011	457	115	10	3,732
2010	404	76	6	3,563
2009	390	74	4	3,910
2008	401	113	0	4,488

Table 2. Sample sizes of mule deer captured, determined to have died, used in resource selection functions (RSF), and switching between study areas for each winter season and study area (low development [dev] or high development) in the Piceance Basin of Colorado, USA. Also reported are the mean and range of global positioning system locations for individuals used in RSF models in each year. Mortalities are reported as total mortalities from early winter capture through to next year's early winter capture (typically Dec–Dec). We calculated number of deer switching study areas as those that previously had the majority of their kernel density utilization distribution overlapping with one study and in subsequent years had the majority of their kernel density utilization distribution overlapping with the other study area.

Winter season	Low dev captures early winter / late winter (recaptures)	High dev captures early winter / late winter (recaptures)	Mortalities low dev	Mortalities high dev	Number used in RSF low dev	Number used in RSF high dev	Number switching study areas	Mean number of relocations (range) low dev	Mean number of relocations (range) high dev
2007–2008	8 (0) / 0	7 (0) / 0	0	0	7	7	0	439 (219–512)	423 (215–508)
2008–2009	0 / 16 (1)	0 / 14 (1)	0	0	15	13	0	356 (262–540)	340 (238–538)

2009–2010	21 (0) / 11 (0)	19 (0) / 25 (16)	4	1	33	31	0	361 (162–735)	308 (198–710)
2010–2011	20 (0) / 20 (9)	20 (2) / 20 (10)	13	8	45	48	0	572(129–748)	565 (127–818)
2011–2012	31 (2) / 30 (29)	33 (4) / 28 (28)	8	6	44	50	1	605 (22–826)	586 (137–803)
2012–2013	29 (2) / 29 (29)	33 (7) / 31 (29)	3	7	51	55	2	670 (143–836)	656 (107–825)
2013–2014	32 (2) / 30 (29)	30 (3) / 30 (27)	8	3	48	46	1	593 (79–771)	608 (159–753)
2014–2015	29 (1) / 28 (26)	27 (1) / 32 (26)	2	2	21	14	1	705 (606–758)	617 (151–747)

Table 3. Winter season of capture, number of individuals per study area (low development [dev] area or high development) overall and by sex, and number of animals dying between capture and the following June for mule deer fawns captured during December on winter range in the Piceance Basin, Colorado, USA.

Winter season	Number captured low dev (male, female)	Number captured high dev (male, female)	Mortalities low dev	Mortalities high dev
2008–2009	60 (30, 30)	60 (42, 18)	6	7
2009–2010	64 (32, 32)	59 (19, 40)	4	3
2010–2011	60 (24, 36)	61 (32, 29)	30	22
2011–2012	59 (29, 30)	53 (27, 26)	16	12
2012–2013	58 (24, 34)	60 (30, 30)	9	10
2013–2014	61 (28, 33)	61 (30, 31)	6	4
2014–2015	60 (34, 26)	61 (31, 30)	3	4

Table 4. Variables used in resource selection function modeling for adult female mule deer in the Piceance Basin, Colorado, USA, process that we hypothesized they represented (cover, forage, or anthropogenic), description of variable, and the source.

Variable	Category	Description	Source
Terrain ruggedness index	Cover	The mean difference between the elevation in a cell and that of the 8 neighboring cells, representing topographic cover	https://earthexplorer.usgs.gov/
Snow depth	Forage	Daily snow depth derived from a distributed snow evolution model	(Liston and Elder 2006, Northrup et al. 2016*b*)
Land cover	Cover and forage	Categorical variable with land cover classified as cover, forage, cover and forage, or sparse	https://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c
Distance to edge	Cover	Distance to any edges representing the transition from treed land cover to non-treed land cover	https://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c
Distance to road	Anthropogenic	Distance to roads	Digitized from aerial imagery obtained from the National Agricultural Imagery Program https://earthexplorer.usgs.gov/
Distance to pipeline	Anthropogenic	Distance to pipelines	White River Bureau of Land Management office and supplemented from aerial imagery obtained from the National Agricultural Imagery Program https://earthexplorer.usgs.gov/
Distance to facilities	Anthropogenic	Distance to natural gas facilities	Digitized from aerial imagery obtained from the National Agricultural Imagery Program https://earthexplorer.usgs.gov/ and validated on the ground

Drilling pads xxx	Anthropogenic	Number of well pads classified as drilling within a given buffer distance	cogcc.state.co.us
Production pads xxx	Anthropogenic	Number of well pads classified as producing within a given buffer distance	cogcc.state.co.us

Table 5. Average (SD) of covariates used in resource selection function modeling representing cover and mule deer forage for the low- and high-development study areas in the Piceance Basin, Colorado, USA. Forage, cover, cover and forage, and sparse are categorical covariates and we present the proportion of each study area composed of these categories.

Covariate	Low development	High development
Terrain ruggedness index	4.95 (3.05)	5.00 (3.2)
Elevation (m)	2,040 (115)	2,055 (112)
Distance to edge (m)	57.5 (49.35)	60.6 (56.54)
Forage	0.33	0.35
Cover	0.23	0.22
Cover and forage	0.36	0.33
Sparse	0.08	0.09

Table 6. Average (SD) of daily snow depth layers (m) used in resource selection function modeling for each winter season of the study for the low- and high-development study areas in the Piceance Basin, Colorado, USA.

Winter season	Low development	High development
2007–2008	0.32 (0.10)	0.31 (0.10)
2008–2009	0.09 (0.05)	0.08 (0.05)
2009–2010	0.18 (0.06)	0.17 (0.06)
2010–2011	0.22 (0.08)	0.18 (0.09)
2011–2012	0.12 (0.04)	0.11 (0.05)
2012–2013	0.14 (0.07)	0.11 (0.07)
2013–2014	0.10 (0.03)	0.09 (0.04)
2014–2015	0.05 (0.04)	0.04 (0.04)

Table 7. Average (SD) of weekly normalized difference vegetation index layers for May–September of the summer preceding each winter season of the study for the low- and high-development study areas in the Piceance Basin, Colorado, USA.

Winter season	Low development	High development
2007–2008	97.18 (51.94)	97.07 (51.89)
2008–2009	97.28 (56.15)	96.73 (55.61)
2009–2010	96.20 (55.78)	95.15 (54.99)
2010–2011	96.30 (53.84)	95.44 (53.22)
2011–2012	97.35 (54.92)	96.44 (54.35)
2012–2013	92.42 (52.65)	91.82 (52.37)
2013–2014	93.29 (52.67)	92.92 (52.32)
2014–2015	96.30 (52.83)	95.61 (52.82)

Table 8. Proportion of each of the high-development (dev) and low-development study areas predicted to be avoided, relative to availability during the day and night for winters 2009 through 2015 from population-level resource selection function models fit to global positioning system radio-collar data from mule deer does in the Piceance Basin, Colorado, USA. Any value < 1 indicated selection less than available (avoidance).

Winter season	Low dev day	Low dev night	High dev day	High dev night
2009	0.72	0.88	0.77	0.55
2010	0.64	0.83	0.68	0.77
2011	0.31	0.73	0.60	0.49
2012	0.46	0.92	0.76	0.49
2013	0.29	0.91	0.75	0.72
2014	0.29	0.95	0.72	0.71
2015	0.30	0.95	0.78	0.69

Table 9. Parameters and coefficient estimates for regression models fit to demographic data for mule deer does captured in the Piceance Basin, Colorado, USA between 2009 and 2015. Coefficients followed by an asterisk (*) indicate 95% confidence intervals that did not overlap 0. We used linear regression for log transformed values of age, Poisson regression for number of fetuses, and logistic regression for lactation status.

Covariate	Age[a]	Number of fetuses[b]	Lactation status[c]
Intercept	1.27*	−0.02	−0.19
2011	0.31*		
2012	0.20		
2013	0.16	−0.11	
2014	0.25	−0.09	0.54
2015	0.11	−0.17	
High development	0.34*	0.09	−0.50
2011 × high development	−0.30		
2012 × high development	−0.25		
2013 × high development	−0.14	0.19	
2014 × high development	−0.20	0.21	−0.003
2015 × high development	−0.35	−0.02	

[a] Reference category (i.e., the effect represented by the intercept) was the low-development area in 2010.

[b] Reference category was the low-development area in 2012.

[c] Reference category the low-development area in 2013.

Table 10. Covariates and coefficient estimates for regression models fit to condition data for mule deer does captured in the Piceance Basin, Colorado, USA between 2009 and 2015. Coefficients followed by an asterisk (*) indicate 95% confidence intervals that did not overlap 0. We used beta regression models in all cases except for overwinter change in fat, where we used a linear regression.

Covariate	Early winter fat[a]	Early winter fat lactation model[b]	Late winter fat[a]	Overwinter change in fat[c]
Intercept	−1.99*	−1.97*	−2.58*	−5.65*
2010	−0.17		0.07	
2011	−0.11		−0.05	0.30
2012	−0.08		0.09	−0.60
2013	−0.11		−0.02	0.11
2014	−0.08	0.14	0.04	−0.09
2015			0.07	
High development	−0.05	−0.02	−0.07	0.28
2010 × high development	0.15		0.00	
2011 × high development	0.01		−0.05	0.79
2012 × high development	−0.03		−0.02	0.32

2013 × high development	0.15		0.13	−0.59
2014 × high development	0.13	0.05	0.15	−0.82
2015 × high development			0.08	
Lactating		−0.34*		
High development lactating		0.19		
Lactating 2014		−0.10		
High development lactating 2014		−0.21		
Amount of fat in Dec				0.87*

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[a] Reference category (i.e., the effect represented by the intercept) was the low-development area in 2009.

[b] Reference category was the low-development area in 2013.

[c] Reference category was the low-development area in 2015.

Table 11. Covariates, coefficient estimates, standard errors, and lower and upper 95% confidence intervals for a gamma regression model fit to mass of fawns captured in December in the Piceance Basin, Colorado, USA, between 2010 and 2015. The reference category (i.e., the effect represented by the intercept) was females in the low-development area in 2015.

Covariate	Estimate	SE	Lower CI	Upper CI
Intercept	3.59	0.02	3.5508	3.6292
High development	−0.04	0.03	−0.0988	0.0188
Male	0.08	0.03	0.0212	0.1388
2010	−0.06	0.03	−0.1188	−0.0012
2011	−0.07	0.03	−0.1288	−0.0112
2012	−0.11	0.03	−0.1688	−0.0512
2013	−0.01	0.03	−0.0688	0.0488
2014	−0.13	0.03	−0.1888	−0.0712
High development × male	0.01	0.04	−0.0684	0.0884
High development × 2010	0.02	0.04	−0.0584	0.0984
High development × 2011	−0.005	0.04	−0.0834	0.0734
High development × 2012	0.03	0.04	−0.0484	0.1084
High development × 2013	0.02	0.04	−0.0584	0.0984

High development × 2014	0.07	0.04	−0.0084	0.1484
Male × 2010	0.02	0.04	−0.0584	0.0984
Male × 2011	0.001	0.04	−0.0774	0.0794
Male × 2012	0.001	0.04	−0.0774	0.0794
Male × 2013	−0.02	0.04	−0.0984	0.0584
Male × 2014	0.03	0.04	−0.0484	0.1084
High development × male × 2010	0.02	0.06	−0.0976	0.1376
High development × male × 2011	0.01	0.06	−0.1076	0.1276
High development × male × 2012	−0.03	0.06	−0.1476	0.0876
High development × male × 2013	0.02	0.06	−0.0976	0.1376
High development × male × 2014	−0.06	0.06	−0.1776	0.0576

Table 12. Covariates, coefficient estimates, standard errors, and lower and upper 95% confidence intervals for the top known-fate survival model fit to data from mule deer does in the Piceance Basin, Colorado, USA from 2009–2015 according to Akaike's Information Criterion corrected for small sample sizes. In this model survival varied by year and season, with an additive effect of study area. Seasons were characterized as winter, summer, and transition, with equivalent survival during fall and spring transition seasons. The reference category was winter 2014–2015 in the high-development area.

Parameter	Estimate	SE	Lower CI	Upper CI
Intercept	5.24	0.53	4.21	6.27
Low development	−0.41	0.26	−0.92	0.09
Winter 2009	14.87	0.00	14.87	14.87
Transition 2009	14.87	0.00	14.87	14.87
Summer 2009	18.12	0.00	18.12	18.12
Winter 2009–2010	16.95	0.00	16.95	16.95
Transition 2010	−1.62	0.77	−3.13	−0.11
Summer 2010	−0.52	0.87	−2.22	1.19
Winter 2010–2011	−0.49	0.67	−1.81	0.83
Transition 2011	−2.59	0.62	−3.82	−1.37
Summer 2011	−1.41	0.68	−2.74	−0.08
Winter 2011–2012	−0.88	0.62	−2.09	0.32
Transition 2012	−0.23	1.12	−2.43	1.97
Summer 2012	−1.33	0.65	−2.61	−0.06
Winter 2012–2013	−0.04	0.71	−1.43	1.35
Transition 2013	−1.68	0.71	−3.08	−0.28
Summer 2013	0.41	1.12	−1.79	2.60
Winter 2013–2014	−0.74	0.62	−1.95	0.47
Transition 2014	−1.70	0.72	−3.10	−0.29
Summer 2014	0.40	1.12	−1.79	2.60

Table 13. Model structure, Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c values from top model (ΔAIC_c), AIC_c weights, and number of parameters (K) for known-fate survival models fit to data from doe mule deer in 2 study areas in the Piceance Basin of Colorado, USA, between 2008 and 2015. Season1 indicates models for which survival during fall and spring migration were equal, and season2 indicates models for which survival varied between fall and spring migration.

Model structure	AIC_c	ΔAIC_c	AIC_c weight	K
Season1 × year + study[a]	669.27	0.00	0.57	20
Season1 × year	669.89	0.62	0.42	19
Season1 ×year × study	678.27	9.00	0.01	26
Season2 × year + study	678.66	9.39	0.01	38
Season2 × year	679.29	10.02	0.00	25
Season2 × year × study	692.90	23.63	0.00	50
Year × month + study	735.90	66.63	0.00	75
Year × month	736.54	67.27	0.00	74
Year × month × study	835.93	166.66	0.00	148

[a] Study indicates a binary parameter distinguishing the 2 study areas.

Table 14. Parameters, coefficient estimates, standard errors, and lower and upper 95% confidence intervals for a known-fate survival model fit to data from mule deer fawns in the Piceance Basin, Colorado, USA, from 2009–2015. In this model survival varied by year. The reference category was 2015.

Parameter	Estimate	SE	Lower CI	Upper CI
Intercept	4.26	0.38	3.51	5.00
2009	−1.86	0.48	−2.79	−0.92
2010	−0.08	0.54	−1.14	0.98
2011	−2.41	0.41	−3.21	−1.60
2012	−1.60	0.43	−2.44	−0.76
2013	−1.14	0.45	−2.02	−0.27
2014	−0.34	0.50	−1.31	0.64

Table 15. Model structure, Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c values from top model (ΔAIC_c), AIC_c weights, and number of parameters (K) for known-fate survival models fit to data from fawn mule deer in 2 study areas in the Piceance Basin of Colorado, USA, between 2008 and 2015.

Model structure	AIC_c	ΔAIC_c	AIC_c weight	K
Year	1,035.46	0.00	0.45	7
Year + study[a]	1,036.87	1.41	0.22	8
Year × month	1,037.44	1.98	0.17	35
Year × month + study	1,038.86	3.39	0.08	36
Year + month	1,039.21	3.75	0.07	11
Year × study	1,045.69	10.23	0.00	14
Year × month × study	1,074.23	38.77	0.00	70
Month	1,121.28	85.82	0.00	5

[a] Study indicates a binary parameter distinguishing the 2 study areas.

Table 16. Model structures, Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c from top model (ΔAIC_c), AIC_c weights, and number of parameters (*K*) for immigration-emigration logit-normal mixed effects mark-resight models fit to doe mule deer winter range data in the Piceance Basin, Colorado, USA. Models include mean resight probability (*p*), which was allowed to vary by year and survey or kept constant (.), individual heterogeneity in resighting probability (σ), and the difference between the population size within the study area and the super population size using the study area (α).

Model structure	*K*	AIC_c	ΔAIC_c	AIC_c weights
Low development				
p(year × survey), $\sigma \neq 0$, $\alpha = 0$	49	2,809	0.0	0.997
p(year × survey), $\sigma = 0$, $\alpha = 0$	43	2,821	11.9	0.003
p(year × survey), $\sigma \neq 0$, $\alpha \neq 0$	62	2,835	25.9	0.000
p(year × survey), $\sigma = 0$, $\alpha \neq 0$	56	2,847	37.7	0.000
p(.), $\sigma \neq 0$, $\alpha = 0$	30	3,121	311.8	0.000
p(.), $\sigma = 0$, $\alpha = 0$	24	3,134	324.8	0.000
High development				
p(year × survey), $\sigma = 0$, $\alpha = 0$	43	2,883	0.0	0.967

p(year × survey), $\sigma \neq 0$, $\alpha = 0$	49	2,890	6.7	0.033
p(year × survey), $\sigma = 0$, $\alpha \neq 0$	56	2,907	24.6	0.000
p(year × survey), $\sigma \neq 0$, $\alpha \neq 0$	62	2,914	31.5	0.000
$p(.)$, $\sigma = 0$, $\alpha = 0$	24	3,135	252.6	0.000
$p(.)$, $\sigma \neq 0$, $\alpha = 0$	30	3,142	258.9	0.000

SUMMARY OF CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Adult female mule deer showed substantial behavioral plasticity in the face of natural gas development, with no apparent demographic consequences. Topographically diverse winter range with adequate vegetation providing sufficient food and cover allow deer to alter behavior in an adaptive manner, and similar features should be considered in future development planning.