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

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

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20

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

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

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

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

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

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

75

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

79

80 **RÉSUMÉ**

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

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

100 Nous avons évalué la réponse comportementale des cerfs muets aux attributs reliés au
101 développement avec des niveaux variés d'activités humaines en examinant la sélection d'habitat de près
102 de 400 femelles cerfs muets. Nous avons aussi évalué l'effet des développements reliés au gaz naturel
103 sur la démographie et la physiologie en comparant la survie annuelle des femelles adultes et la survie
104 hivernale des faons (âgés de 6 mois), les réserves de gras des femelles au début et à la fin de l'hiver,
105 l'âge, le taux de gestation et le taux de lactation en décembre entre les deux aires d'études. Des
106 différences majeures au niveau de la sélection d'habitat ont été observées entre les deux aires d'études.
107 Les cerfs habitant l'aire d'étude moins développée évitaient les zones développées durant le jour et la
108 nuit et sélectionnaient des habitats afin de s'alimenter. Les cerfs habitant l'aire d'étude plus développée
109 sélectionnaient plus fortement des habitats à des fins de sécurité et de couvert thermal. Les cerfs faisant
110 face à une plus grande densité de développement évitaient les endroits avec une plus grande densité de
111 puits durant le jour alors qu'ils n'évitaient pas ou sélectionnaient ces endroits durant la nuit. Les cerfs
112 habitant les deux aires d'études montraient une réduction importante de l'utilisation des puits durant
113 leur forage, ce qui correspondait à la phase de développement avec la plus grande présence humaine,
114 circulation automobile, bruit, et lumière artificielle. Malgré des patrons de sélection d'habitat
115 divergents, nous n'avons pas détecté un effet des développements sur la condition ou la reproduction et
116 nous n'avons pas trouvé de différence chez les taux vitaux ou physiologiques mesurés au niveau de la
117 population. Cependant, la densité de cerfs et le taux de changement annuel dans la densité étaient
118 supérieurs dans l'aire d'étude moins développée. Les changements comportementaux mesurés ne

119 semblaient donc pas être associés avec des coûts démographiques ou physiologiques au niveau
120 individuel, possiblement parce que les populations étaient sous la capacité biotique de l'aire
121 d'hivernage. Les différences entre les densités de population entre les deux aires d'études sont peut-
122 être dû à un déclin de la population précédant notre étude (lorsque le développement démarrait) ou à
123 des différences au niveau de la qualité de l'habitat, du dispersement ou de la survie des nouveau-nés ou
124 des juvéniles. Cependant, nous manquons les données requises pour contraster ces mécanismes.

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

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Contents

144	INTRODUCTION	5
145	STUDY AREA	14
146	METHODS	16
147	Mule Deer Captures	16
148	Statistical Analysis of Habitat Selection.....	19
149	Spatial Predictor Variables of Habitat Selection.....	24
150	Field and Statistical Methods for Demographic Analyses.....	28
151	RESULTS	32
152	Habitat Selection.....	32
153	Demography.....	36
154	DISCUSSION.....	39
155	Mule Deer Behavior and Natural Gas Development	42
156	Mule Deer Demography and Natural Gas Development	45
157	The Use of Habitat Selection Analyses to Assess Effects of Human Disturbance	53
158	Limitations	55
159	MANAGEMENT IMPLICATIONS.....	56
160	ACKNOWLEDGMENTS	59
161	LITERATURE CITED	60
162		

163 INTRODUCTION

164 Land-use change and associated human activities have profound effects on ecological processes
165 (Vitousek et al. 1997, Foley et al. 2005, Haberl et al. 2007). These effects include disrupting
166 long-distance animal migrations (Harris et al. 2009), altering animal behavior (Tuomainen and
167 Candolin 2011), facilitating the introduction of nonnative species (Hansen and Clevenger 2005),
168 and driving declines of local populations and global biodiversity (Wilcove et al. 1998, Sala et al.
169 2000, Gibson et al. 2013). In the coming decades, land-use change will continue to alter natural

170 systems, modifying thousands of square kilometers of land (Li et al. 2017) with negative
171 consequences for some species and ecosystems (Lawler et al. 2014), including the decline and
172 possible extirpation of hundreds of species (Powers and Jetz 2019). Assessment of the ecological
173 consequences of land-use change is critical for species management and conservation and is
174 fundamental for understanding ecological processes under contemporary environmental
175 conditions where human disturbance is a dominant feature.

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

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

211 Addressing behavior and demography simultaneously offers a comprehensive
212 understanding of species responses to habitat modification. Such an approach allows
213 quantification of fitness or demographic changes and identification of behavioral adjustments
214 that can help diagnose the drivers of these changes. Such work can provide powerful insight to
215 the contexts under which species can adapt to habitat modification, which is critical for effective

216 management and conservation decision-making (Buchholz 2007, Caro 2007). However, whether
217 behavioral responses to habitat modification can successfully buffer individuals from fitness
218 effects is context-dependent. If species are displaced from limiting habitat (e.g., nesting or
219 calving grounds), then it is likely that behavioral responses will result in reduced individual
220 fitness and subsequent population declines. The ability to alter behavior (i.e., behavioral
221 plasticity) can be adaptive (Ghalambor et al. 2007, 2010) but requires that environmental
222 changes produce cues that are both recognizable and reliable (Sih et al. 2011, Sih 2013) and that
223 habitat has not been modified in such a way to significantly reduce carrying capacity. If cues are
224 not reliable, this can lead to the formation of ecological or evolutionary traps (Robertson et al.
225 2013). However, even if habitat is not limiting, or changes do not increase risk to species,
226 behavioral responses to human disturbance can result in significant opportunity cost akin to the
227 non-consumptive effects of predation risk (Frid and Dill 2002).

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

236 The habitat modification from hydrocarbon development has various effects on wildlife
237 behavior and demography (Northrup and Wittemyer 2013). Specifically, hydrocarbon
238 development alters a number of behaviors that are linked to fitness. The literature on wildlife

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

258 In the western United States, much of the recent hydrocarbon development has been on
259 public lands that encompass habitat for ungulate populations that are the primary focus of
260 wildlife management agencies. Specifically, considerable development has occurred on the
261 winter ranges of mule deer, which historically have experienced large-scale population

262 fluctuations across their distribution (Unsworth et al. 1999). Winter is a critical time for mule
263 deer because they can experience large die offs (White and Bartmann 1998) likely linked to
264 limited access to sufficient high-quality forage (Wallmo et al. 1977, Parker et al. 1984, Bishop et
265 al. 2009). Any substantive human activity on deer winter range is of concern to wildlife
266 managers because it could lead to decreased habitat, reductions in foraging time, reduced access
267 to forage, or increased energy expense through movement. Such effects are particularly costly on
268 winter range, which is geographically limited, where deer are nutritionally constrained (Wallmo
269 et al. 1977, Bishop et al. 2009) and snow dramatically increases the costs of locomotion (Parker
270 et al. 1984).

271 Hydrocarbon development involves a variety of infrastructure types that modify the
272 landscape in different ways. Well pads, facilities (including compressor stations, refining plants,
273 and personnel camps), roads, and pipelines all directly remove wildlife habitat. Accompanying
274 increases in human activity, including traffic, artificial light, and noise associated with drilling
275 can further lead to indirect habitat loss (Sawyer et al. 2009, Northrup et al. 2015). In addition,
276 development can facilitate the invasion of non-native plant species (Bergquist et al. 2007) and
277 can be accompanied by reseeding of disturbed areas, potentially leading to permanent vegetation
278 shifts or reduced plant diversity. These landscape changes are potentially concerning for mule
279 deer because the species is known to be sensitive to habitat modification and the associated
280 increases in human activity. Mule deer avoid developed areas (Nicholson et al. 1997), including
281 roads during certain times of the year (Marshal et al. 2006; Webb et al. 2011c, 2013; Lendrum et
282 al. 2012) and human activity in different forms causes mule deer to shift activity patterns and
283 move more or migrate faster (Freddy et al. 1986, Stephenson et al. 1996, Boroski and Mossman
284 1998, Lendrum et al. 2013). Deer also are displaced to varying degrees from the areas around

285 hydrocarbon development and related infrastructure (Sawyer et al. 2006, 2017; Webb et al.
286 2011c; Northrup et al. 2015), and the associated levels of human activities at development sites
287 can largely influence displacement, with greater avoidance of sites with more people and
288 machinery (Sawyer et al. 2009, Northrup et al. 2015).

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

300 In Colorado, USA, substantial research has been conducted on mule deer responses to
301 predator reductions and habitat improvements on winter range. Collectively, this work shows
302 that the species is highly constrained by available forage (Wallmo et al. 1977) during winter. As
303 such, enhanced nutrition during winter through *ad libitum* feeding with pellets (Bishop et al.
304 2009) or reducing overstory trees to promote growth of palatable understory shrubs (Bergman et
305 al. 2014) has elicited positive demographic responses, including increased overwinter survival.
306 Further, predation of mule deer on winter range has been shown to be entirely compensatory in
307 Colorado (Bartmann et al. 1992, White and Bartmann 1998), and largely compensatory in other

308 parts of the Intermountain West (Hurley et al. 2011), indicating populations often are at or above
309 carrying capacity on winter range. Mule deer in Colorado also have seen a protracted decline
310 over the last 30 years (Bergman et al. 2015). These factors raise concerns that if development
311 causes behavioral shifts for mule deer, it could exacerbate the already difficult nutritional
312 conditions on winter range (Bishop et al. 2009, Monteith et al. 2013), and contribute to continued
313 population declines or slowed population growth or recovery. These concerns are amplified by
314 recent work in Wyoming, USA, by Sawyer et al. (2017) that showed strong and consistent
315 avoidance of the areas around natural gas development and a 36% decline in abundance over a
316 15-year period. These results suggest that the strong behavioral responses of mule deer to natural
317 gas development that have been documented elsewhere also could be associated with declines in
318 deer populations. Thus, there is a need to improve our understanding of the demographic
319 consequences of documented behavioral responses of deer to hydrocarbon development.

320 Our objective was to test hypotheses about whether and how habitat modification from
321 hydrocarbon development influenced mule deer behavior and demography. We leveraged a
322 unique opportunity, whereby 2 halves of a contiguous mule deer winter range area were exposed
323 to vastly different levels of hydrocarbon development, providing a pseudo-experimental design
324 (i.e., one area with heavy modification and one area with light modification; Fig. 1). Over a 7-
325 year period, we assessed the effect of hydrocarbon development on mule deer (hereafter deer
326 unless otherwise indicated) behavior by examining habitat selection relative to development
327 features and environmental factors related to cover and forage. We also examined a suite of
328 demographic parameters measured at the individual or study area scale, including early and late
329 winter body fat and mass, pregnancy rates, fetal counts, survival of fawns (from 6 months of age
330 onwards), survival of adult females, lactation rates, and winter range population density. Recent

331 studies in this broader study region have investigated different aspects of mule deer habitat
332 selection, finding a variety of behavioral responses to development (Lendrum et al. 2012, 2013;
333 Northrup et al. 2015, 2016a). Thus, we assumed that we would see differences in behavior of
334 mule deer in the 2 study areas. However, there has been no assessment of whether such
335 behavioral responses have influenced fitness or population-level demographic processes. To
336 address this gap, we tested the following alternative hypotheses and subsequent predictions:

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

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

352 **STUDY AREA**

353 The study took place between January 2008 and March 2015. The study area was the Magnolia
354 mule deer winter range in the Piceance Basin of northwestern Colorado (39.954°N, 108.356°W;
355 Fig. 1), which encompasses an area of 184 km². Average elevation in the area was 2,045 m. The
356 climate was characterized by cold winters (mean Dec–Mar temp 2008–2015 in Meeker, CO =
357 –3.8° C, range = –37.2–22.8° C) and warm dry summers (mean Jun–Sep temp 2008–2015 in
358 Meeker, CO = 17.5° C, range: –2.2–35.6° C) with monsoonal precipitation in late summer. The
359 area was topographically variable with the dominant vegetation consisting of big sagebrush
360 (*Artemisia tridentata*) and a pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*)
361 shrubland complex. Other dominant shrubs included Utah serviceberry (*Amelanchier utahensis*),
362 mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentata*), and mountain
363 snowberry (*Symphoricarpos oreophilus*). For a more detailed description of the vegetation of the
364 area see Bartmann and Steinert (1981) and Bartmann et al. (1992). Natural predators of mule
365 deer in this area included coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx*
366 *rufus*), and black bears (*Ursus americanus*; Lendrum et al. 2018). Elk and feral horses (*Equus*
367 *ferus*) also inhabited the area. This area was popular for hunting during the fall with an annual
368 average of 511 deer harvested in the wildlife management unit (Game Management Unit 22),
369 which encompassed the entire study area (Table 1). Chronic wasting disease occurred within the
370 mule deer population in this area at low levels (2.4% prevalence in adult males in the most recent
371 assessment; $n = 255$, 95% CI = 0.9–5.1%;
372 https://cpw.state.co.us/Documents/Research/CWD/CWDprevalence_GMU-DAU_deer.pdf,
373 accessed 02 Oct. 2020). There is active cattle ranging in the area and it also contains vast
374 hydrocarbon resources that have seen active development since the 1970s. Starting in the mid-
375 2000s, natural gas development increased sharply but declined rapidly since 2012 (Fig. 2).

376 Mule deer in this area are migratory, moving between low-elevation winter range and
377 high-elevation summer range, where they birth fawns. Deer typically occupy their winter range
378 between October and April of each year (Lendrum et al. 2014, Northrup et al. 2014b) and
379 migrate to several different summer range areas (Lendrum et al. 2014). Summer range varied in
380 elevation between 2,000 m and 2,800 m and vegetation consisted of Gambel oak (*Quercus*
381 *gambelii*), quaking aspen (*Populus tremuloides*), pinyon pine, Utah juniper, Douglas-fir
382 (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies*
383 *lasiocarpa*) with mixed mountain shrublands consisting of mountain mahogany, bitterbrush, big
384 sagebrush, mountain snowberry, rubber rabbitbrush (*Ericameria nauseosa*), and Utah
385 serviceberry. Natural gas development density varied across summer range, with some areas
386 being free from development and other areas having 0.04–0.06 well pads/km². In this area, and
387 across the Intermountain West, mule deer populations have had substantial fluctuations and large
388 declines over the last 30–50 years, with the ultimate causes remaining ambiguous (White and
389 Bartmann 1998, Unsworth et al. 1999, Bergman et al. 2015).

390 **METHODS**

391 **Mule Deer Captures**

392 Between January 2008 and March 2015, we captured mule deer using helicopter net gunning
393 (Krausman et al. 1985, Webb et al. 2008, Jacques et al. 2009, Northrup et al. 2014a; Table 2).
394 All of the below procedures were approved by the Colorado Parks and Wildlife Institutional
395 Animal Care and Use Committee (protocol numbers 17-2008 and 01-2012) and followed the
396 guidelines of the American Society of Mammalogists (Sikes 2016). Upon capture of adult female
397 deer (>1 year old; hereafter does), we administered 0.5 mg/kg of midazolam and 0.25 mg/kg of
398 Azaperone (Wildlife Pharmaceuticals, Windsor, CO, USA) and transferred them to a central

399 processing site via helicopter (49% of captures ferried <3.25 km, 51% ferried 3.25–6.5 km). At
400 the processing site, we weighed deer, drew blood, measured chest girth and hind foot length, and
401 estimated their age using tooth replacement and wear (Severinghaus 1949, Robinette et al. 1957,
402 Hamlin et al. 2000). We also obtained a body condition score by palpating the rump, and
403 measured the thickness of subcutaneous rump fat and the depth of the longissimus dorsi muscle
404 using ultrasound (Stephenson et al. 1998, 2002; Cook et al. 2001, 2007, 2010). We used the body
405 condition score and ultrasound measurements to estimate the percent ingesta-free body fat of
406 each deer (Cook et al. 2007, 2010; hereafter fat). Between December 2013 and December 2015,
407 we determined whether each deer was lactating during December through visual examination.
408 Lastly, we fit each deer with a global positioning system (GPS) radio-collar (G2110D Advanced
409 Telemetry Systems, Isanti, MN, USA) set to attempt a relocation once every 5 hours and
410 equipped with a mechanism programmed to release in 16 months after the date of capture.
411 Collars also were equipped with a mortality beacon that was activated if the collar was immobile
412 for ≥ 8 hours. We attached placards to each collar with unique color and symbol combinations to
413 allow for field-based individual identification. We monitored the deer's temperature throughout
414 processing and released them at the processing site.

415 During most years, we captured the same individuals during early (Dec) and late (Mar)
416 winter. However, there were some exceptions to this procedure during the first years of the
417 study: 1) we did not capture any deer in March 2008, 2) we did not capture any does in
418 December 2009, and 3) we captured new individuals in March 2010. Starting in December 2010,
419 we captured the same individuals in early and late winter and only captured new individuals in
420 late winter to replace any deer that died since the previous December. During late-winter
421 captures, we assessed pregnancy using ultrasound and for does for which we did not detect a

422 fetus, we confirmed pregnancy status using pregnancy-specific protein B from blood samples.
423 Starting in 2011, we determined the number of fetuses each deer was carrying in late-winter
424 using ultrasound (Stephenson et al. 1995). At the onset of the study, we captured deer across the
425 entire Magnolia winter range assuming they were one contiguous group. However, GPS radio-
426 collar data from the first year of the study indicated that individuals were split between the
427 northern and southern half of the winter range, with most individuals from the 2 groups
428 migrating to different summer ranges. Thus, we split our study area into north Magnolia and
429 south Magnolia (Fig. 1). We assigned deer to an area based on where they spent the majority of
430 the winter using the proportion of GPS radio-collar locations in each area (Table A1, available
431 online in Supporting Information). In addition to having different summer ranges, deer in the 2
432 areas were exposed to substantially different densities of features related to natural gas
433 development, with south Magnolia having greater road densities (1.9 km/km² in south Magnolia,
434 1.2 km/km² in north Magnolia), pipeline densities (1.2 km/km² in south Magnolia, 0.5 km/km² in
435 north Magnolia), industrial facilities (0.1 facilities/km² in south Magnolia, 0.01 facilities/km² in
436 north Magnolia), and well pads (0.62–0.78 pads/km² in south Magnolia, 0.01–0.06 pads/km² in
437 north Magnolia; Figs. 1–2). Hereafter, we refer to the more heavily developed south Magnolia
438 study area as the high-development area and the north Magnolia study area as the low-
439 development area. Making valid inference to the effect of development at the study area level on
440 deer behavior and demography requires that deer are largely contained within one study area or
441 the other. To assess fidelity of the deer assigned to each study area, we conducted 2 analyses.
442 First, we estimated utilization distributions (UDs) by fitting kernel density estimators for each
443 deer and winter season (31 October through 1 May of the following year) using the ctm
444 package in the R statistical software (Calabrese et al. 2016) assuming locations were independent

445 and identically distributed, which equates to a conventional kernel density estimator (Calabrese
446 et al. 2016). We then calculated the proportion of the UD that overlapped with each of the
447 outlined study area boundaries in each year the animal was collared to assess if there were any
448 changes in study area use across years and to examine how often deer overlapped with a different
449 study area than the one to which it was assigned. Next, we calculated individual animal UD
450 overlap between years for each deer collared in >1 year to assess finer-scale fidelity of
451 individuals to their specific range area. We calculated overlap following Winner et al. (2018).

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

462 **Statistical Analysis of Habitat Selection**

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

468 (Lendrum et al. 2013, Northrup et al. 2014b), we defined winter range as the time between 31
469 October and 1 May to maintain a temporally consistent sample across years. We censored any
470 data falling outside this period and any locations off of winter range during this period. We
471 examined the GPS radio-collar datasets of each individual deer and censored any apparently
472 erroneous locations (indicated by large movements induced by single outlier locations) and any
473 locations falling outside the study area boundaries (Fig. 1); we did not censor locations falling to
474 the east of the study area boundaries because this was the only boundary not delineated using
475 topographic features. The total number of censored locations equated to <3% of all locations.
476 Lastly, we categorized each location by the winter season during which it occurred (e.g., winter
477 2013 for data between Nov 2012 and Apr 2013) and whether it occurred during the night or day,
478 with night defined as the time between sunset and sunrise
479 (<http://www.esrl.noaa.gov/gmd/grad/solcalc/>, accessed 02 Oct. 2020).

480 We estimated resource selection functions (RSFs; Manly et al. 2002, Johnson et al. 2006)
481 for each winter and study area. Resource selection functions provide estimates of the relative
482 probability of selection of resource units based on the habitat characteristics of those resource
483 units. We estimated RSFs for day and night separately using hierarchical conditional logistic
484 regression (Duchesne et al. 2010) fit in a Bayesian framework where all parameters were
485 allowed to vary by individual, resulting in population-level parameter estimates that robustly
486 incorporated individual variability (see Northrup et al. 2015 for more details and below model
487 statement for explicit distributional assumptions). Although mule deer are typically most active
488 at dusk and dawn, our fix schedule (1 fix every 5 hours) resulted in relatively few crepuscular
489 locations. Further, other research in nearby study areas has previously shown strong contrasts in
490 behavior between night and day (Northrup et al. 2015), and our interest was in examining if there

491 were differences between the study areas in these behaviors. Thus, we did not fit a model to data
492 during crepuscular time periods. Resource selection functions require the designation of an area
493 assumed available for selection by animals (often called the availability distribution). We
494 estimated the availability distribution using the predictor distribution (see below) from a
495 continuous-time correlated random walk model (Hooten et al. 2014). Using this approach, the
496 availability distribution is dynamic and varies for every used location, which accounts for local
497 behavior of the animal and autocorrelation in the availability distribution.

498 We fit continuous-time correlated random walk models for each individual and year
499 combination using the *crawl* package in the R statistical software (Johnson et al. 2008) and
500 following the approach of Hooten et al. (2014) to extract the predictor distribution for each
501 location. Predictor distributions are a continuously distributed prediction of where the animal is
502 expected to be at some later point in time (in our case 1 fix, or 5 hours, after a used location of
503 interest) using data from all prior movements. This distribution can be visualized as a bivariate
504 normal distribution, with the mean of the distribution being the most likely location of the
505 animal. The continuous-time correlated random walk model includes an autocorrelation term,
506 which weights movements near in time to a greater degree than previous movements and thus
507 produces estimates of availability that are dynamic in space and time. Using the mean and
508 variance of these predictor distributions, we randomly generated coordinates for the sample of
509 available locations. This approach is similar to a step-selection function (Fortin et al. 2005) but
510 provides a continuous distribution of available locations as opposed to the discrete distribution
511 that comes from using empirical turn angle and step length distributions in the originally
512 described version of this approach. Further, the traditional step selection function uses a constant
513 empirical distribution for turn angle and step length, but our approach allows for a more

514 continuously dynamic definition of availability. Such an approach is intuitive because it serves to
515 shrink the availability distribution when the animal is stationary and expand it when they are
516 mobile. For each individual, we conducted a sensitivity analysis of the parameter estimates
517 relative to the size of the availability sample (Northrup et al. 2013). Once we determined a
518 sufficient sample size, we standardized all continuous covariates ($\frac{x_i - \bar{x}}{SD(x)}$, where x_i is the i th data
519 point; see below for description of covariates) and tested for pairwise correlations among
520 covariates using $|r| < 0.7$ as a cutoff above which we did not include correlated covariates in the
521 same model (Dormann et al. 2013). We standardized covariates using values combined across
522 both study areas, all winter seasons, years, and day and night so that all coefficient estimates
523 would be directly comparable across models. Next, we assessed multicollinearity using condition
524 numbers, as described by Lazaridis (2007; values >5.4 are indicative of an ill-conditioned
525 model). This method is used prior to model fitting to assess multicollinearity. We fit the
526 hierarchical models using a Markov chain Monte Carlo (MCMC) algorithm written in the R
527 statistical language. Our model took the following form:

$$528 \quad [y_{tn} | \boldsymbol{\beta}_n] = \frac{e^{x'_{y_{tn}} \boldsymbol{\beta}_n}}{\sum_{j=1}^J e^{x'_{j_{tn}} \boldsymbol{\beta}_n}}$$

$$529 \quad \boldsymbol{\beta}_n \sim \text{Normal}(\boldsymbol{\mu}_\beta, \boldsymbol{\sigma}_\beta^2 \mathbf{I})$$

$$530 \quad \boldsymbol{\mu}_\beta \sim \text{Normal}(\mathbf{0}, 2\mathbf{I})$$

$$531 \quad \log(\sigma_{\beta_k}^2) \sim \text{Normal}(0, 1),$$

532 where y_{tn} is a resource unit represented by habitat covariates $\mathbf{x}_{y_{tn}}$ that is chosen by animal n at
533 time t from a set of available resource units J , represented by habitat covariates $\mathbf{x}_{j_{tn}}$. $\boldsymbol{\beta}_n$ are the
534 set of coefficients related to the k habitat covariates for individual n , and $\boldsymbol{\mu}_\beta$ and $\boldsymbol{\sigma}_\beta^2$ are the
535 population-level mean and variance of the coefficients, with \mathbf{I} as an identity matrix. We fit this

536 model to data from the night and day periods separately for each winter season–study area
537 combination for a total of 28 models. We combined data from 2008 and 2009 because sample
538 sizes were small at the outset of the study. Although environmental and development conditions
539 varied between these years, the temporally specific definition of availability partially accounts
540 for this variation. We ran the MCMC algorithm for a variable number of iterations because of
541 differences in the number needed for convergence (Table B1, available online in Supporting
542 Information), thinning chains to every twentieth iteration, and assessed convergence by
543 examining the trace plots of all parameters to ensure proper mixing. We drew inference based on
544 a combination of the coefficient magnitudes and the proportion of the posterior distributions
545 overlapping 0. Because all covariates were standardized across years and models, the magnitudes
546 are directly comparable, and thus provide inference on whether selection or avoidance of a
547 particular covariate was greater or lesser in one year or study area compared to another.
548 However, coefficient magnitude alone is not sufficient to draw robust ecological inference
549 because there can be substantial uncertainty in an effect despite a large magnitude coefficient.
550 Thus, we also made inference based on the proportion a posterior distribution that fell to either
551 side of 0; we considered a posterior probability of an effect >90% to provide strong evidence of
552 an effect, between 80% and 90% moderate evidence of an effect, and <80% weak evidence for
553 an effect.

554 To visualize the habitat selection patterns of deer, we mapped the mean predicted
555 population-level RSF values in each study area and year for the corresponding model (i.e., we
556 predicted habitat selection in the low-development area using the model fit to deer from the low-
557 development area) and binned predictions into 10 quantiles. To visualize differences in habitat
558 selection between the high- and low-development area, we then mapped the habitat selection

559 patterns of deer in each study area to the landscape in the opposite study area; that is, for each
560 year, we mapped the mean population-level RSF values from the model fit to deer from the low-
561 development area to the landscape of the high-development area and vice versa. This exercise
562 provided a visualization of how deer in the low-development area would select habitat in a
563 heavily developed area if they showed no changes to their behavior. To quantify differences in
564 mean predicted habitat selection, we calculated the proportion of each study area that had a
565 higher RSF value, using unbinned values, for the model fit to deer from that study area compared
566 to the model fit to deer from the other study area.

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

576 **Spatial Predictor Variables of Habitat Selection**

577 We chose a set of predictor variables that were related to 1) cover and forage, and 2)
578 anthropogenic features (Table 4). Cover- and forage-related variables included a terrain
579 ruggedness index (the mean difference between the elevation in a cell and that of the 8
580 neighboring cells, representing topographic cover) calculated from a United States Geological
581 Survey digital elevation model with a 30-m resolution, and daily depth of snow (representing

582 availability of vegetation during the winter) obtained from a distributed snow evolution model
583 (Liston and Elder 2006). We validated predictions from the snow model using weather stations
584 that we deployed within the study area (Northrup et al. 2016b). Further, we assessed selection of
585 a suite of land cover-related variables. We obtained a spatial land cover layer from the Colorado
586 Vegetation Classification Project
587 (<https://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c>), which
588 classified the vegetation of our study area into 69 categories. We aggregated these categories into
589 4 vegetation communities associated with security and thermal cover (represented by pinyon
590 pine, juniper, and interspersed pinyon and juniper communities), forage (represented by
591 sagebrush, sagebrush grassland mix, and mountain shrub communities), combined cover and
592 forage (represented by mixed-vegetation land cover types: sagebrush and mountain shrub
593 communities mixed with either pinyon pine, juniper, or both), and sparsely vegetated areas
594 (represented by bare ground, rock, and sparsely vegetated areas). Lastly, we calculated the
595 distance to any edges representing the transition from treed land cover to non-treed land cover as
596 a measure of distance to cover. To assess variation in conditions over time on the two study
597 areas, we qualitatively compared all of the cover and forage covariates assessed for each year
598 between the study areas. We also quantified the average normalized difference vegetation index
599 (NDVI), which is a coarse metric of plant biomass, from May through September for each year
600 and study area simply to assess study area wide variation in this parameter over years. We
601 obtained NDVI spatial layers as 7-day composites at a resolution of 1 km² and downloaded
602 layers from the United States Geological Survey earth explorer (earthexplorer.usgs.gov, accessed
603 08 Aug 2020).

604 Anthropogenic covariates included the distance to the nearest road (and a quadratic term
605 for distance to road) obtained from a spatial layer for roads created by digitizing aerial imagery
606 from the National Agricultural Imagery Program (NAIP); the distance to natural gas pipelines
607 using data obtained from the White River Bureau of Land Management office and validated
608 using the NAIP imagery; the distance to natural gas facilities (e.g., compressor stations and gas
609 plants) obtained by digitizing NAIP imagery and validating the majority of facilities on the
610 ground; and a suite of covariates representing the spatial density of hydrocarbon well pads. We
611 included a quadratic effect for roads because Northrup et al. (2015) reported this form of
612 nonlinearity in past work on mule deer in this area. In contrast, we assumed that deer would
613 display linear avoidance or selection of pipelines and facilities relative to availability. Facilities
614 represent a major disturbance and thus we assumed a large-scale avoidance would occur relative
615 to availability, which in our case was drawn from a relatively small spatial extent around each
616 point. Pipelines have relatively limited human activity associated with them and thus we did not
617 expect a nonlinear response relative to our scale of availability. We were interested in assessing
618 the cumulative impacts of well-pad development and thus assessed the response of deer to the
619 number of well pads within exclusive 200-m concentric rings (hereafter buffers) to a distance of
620 1,000 m (i.e., the number of pads within 200 m of a deer or available location, the number of
621 pads between 200 m and 400 m, etc.). This allows for implicit assessment of cumulative effects
622 by examining predicted responses across different numbers of well pads in different buffers (e.g.,
623 the number of pads being actively drilled within 400 m and the number of pads being actively
624 drilled 400–600 m from locations).

625 Early in the study, when active drilling was occurring, the development landscape was
626 highly dynamic, with the number of wells in different phases of production often varying from

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

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

666 We could not estimate RSF coefficients for the following covariates because of
667 insufficient development or deer locations: for the high-development area, the number of well
668 pads with active drilling within 200 m or between 200 m and 400 m during winter 2009, the
669 number of well pads with active drilling within 200 m during winter 2010 and all drilling
670 covariates after 2010. For the low-development area, we could not estimate coefficients for any
671 drilling covariates for any years (Fig. 2). Likewise, we could not estimate coefficients for the
672 number of producing well pads within 200 m in the low-development area for any year. For most

673 individuals, there were no used locations within these buffer distances. As such, a finite
674 coefficient cannot be estimated, and models fail to converge. Thus, we combined buffers to
675 achieve model convergence. For example, in the low-development area, we estimated
676 coefficients for the number of producing pads within 400 m and then within 200-m concentric
677 buffers out to 1,000 m.

678 **Field and Statistical Methods for Demographic Analyses**

679 We monitored the survival of doe and fawn mule deer using radio-telemetry daily from the
680 ground and bi-weekly from the air from a fixed-wing aircraft. Upon detection of a mortality
681 signal, we located deer on the ground and performed a necropsy to determine the cause of death.
682 During late March of each year, we conducted 3–5 mark-resight surveys in the 2 study areas via
683 helicopter to estimate deer abundance. We delineated helicopter flight paths within the 2 study
684 areas following topographic contours (e.g., drainages and ridges) using ArcMap 9.3
685 (Environmental Systems Research Institute, Redlands, CA, USA), such that the distances
686 between flight paths were approximately 500–600 m and the entirety of each study area was
687 covered. Two observers and a pilot flew the flight paths, navigating using a GPS unit, and they
688 recorded every deer that they saw as either marked with the unique identifier recorded,
689 unmarked, or marked and unidentifiable. During the mark-resight surveys, we simultaneously
690 conducted 2 telemetry surveys from a fixed-wing aircraft to determine if each marked individual
691 was within or outside of the study area boundaries. For does, we plotted the GPS locations of
692 each individual following collar recovery to evaluate whether they were within or outside of the
693 study area boundaries during surveys. Deer were seldom outside of the study area boundaries (9
694 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
695 of 220 in 2015).

696 We examined if there were any differences in deer body condition (early and late winter
697 fat), age, pregnancy rates, fetal counts, lactation status, and fawn mass between study areas. Our
698 objective was to test for an effect of development at the study area level on each metric over
699 time. Thus, for each metric, except body fat, we fit a single linear or generalized linear model,
700 with year and study area as categorical covariates. Further, we included an interaction between
701 year and study area. This approach allowed us to directly test for differences in each metric
702 between study areas and years in a single model as opposed to conducting multiple comparisons
703 for each year and study area combination as might be done with a *t*-test. For body fat, we fit 2
704 separate generalized linear models for beta-distributed data. The first model included the entire
705 time series of data and the second included only data from deer captured on or after December
706 2013 when we began collecting information on lactation status. In the second model, we
707 included lactation status as a covariate to control for this likely important effect on individual
708 doe condition. For age, we fit a linear model to log transformed values. For pregnancy and
709 lactation status, we fit generalized linear models for Bernoulli-distributed data. For fetal counts,
710 we fit a generalized linear model for Poisson-distributed data. For fawn mass, we fit a
711 generalized linear model for gamma-distributed data. For all models we used a Type I error rate
712 of 0.05 on the coefficients to indicate statistical significance. We fit all models in the R statistical
713 software (R Core Team 2016).

714 We used the VHF and GPS collar monitoring data to assess survival separately for fawns
715 and does using the known-fate survival model in the statistical software program MARK (White
716 and Burnham 1999). We fit separate models because although we monitored adult females
717 continuously, fawn collars were designed to fall off before the following fall (in some years,
718 most collars fell off in late spring). Thus, we did not have matching temporal coverage of fawn

719 and doe data, which necessitated different models. For does, we fit a set of candidate models to
720 evaluate the hypothesis that survival varied across study areas and over time. We used different
721 model structures to evaluate the temporal resolution at which survival varied (months, years, and
722 seasons). Because winter is known to be a limiting time for mule deer in Colorado, and because
723 mortality can vary by year (White et al. 1987, Bartmann et al. 1992, Bergman et al. 2014), we
724 allowed survival to vary by time (year plus season or month) in every model. Thus, in our most
725 highly parameterized (global) model, survival varied monthly between study areas, whereas in
726 the model with the fewest parameters, survival varied by season across years. We assessed 2
727 different season covariates; the first covariate allowed survival to vary among summer (June –
728 September), winter (November – April), and migration (May and October), with survival during
729 fall and spring migration being equal, and the second allowed survival to differ between fall and
730 spring migration. We compared models using Akaike’s Information Criterion corrected for small
731 sample sizes (AIC_c ; Burnham and Anderson 2002) and made inference based on AIC_c weights
732 and model-averaged survival estimates (Burnham and Anderson 2002). We assumed that any
733 individuals that died within 10 days of capture (does and fawns) had suffered a capture-related
734 mortality and we censored these animals from the survival analysis.

735 For fawns, we fit a set of candidate models to evaluate alternative hypotheses about
736 whether survival varied across time (months or winter season [Dec. – April]) and between study
737 areas. Because many fawn collars dropped off in late spring or early summer, we did not have
738 sufficient sample sizes to fit summer models; thus, we assessed fawn survival for the winter
739 season only. We compared models using AIC_c and made inference based on AIC_c weights and
740 model-averaged survival estimates (Burnham and Anderson 2002). In the most highly
741 parameterized model, survival varied monthly across years and between study areas, whereas in

742 the simplest model survival varied by year and was constant between study areas. As with does,
743 we expected annual variation in fawn survival and thus never fit a model excluding year.

744 We estimated abundance for both study areas, separately, between 2009 and 2015 using
745 the immigration-emigration logit-normal mixed effects mark-resight model (McClintock et al.
746 2009, McClintock and White 2012) in MARK. This model allows for estimation of parameters
747 for the mean resighting probability across years and surveys, individual heterogeneity in
748 resighting probability within years, and differences in the population size within the survey areas
749 and the super population using the survey area (i.e., whether there was any immigration or
750 emigration). We fit models with varying combinations of these parameters in MARK and
751 assessed model parsimony using AIC_c . We converted abundance estimates to density estimates
752 by dividing by the survey area (i.e., the capture area boundaries). To assess the annual rate of
753 change in population size between the 2 study areas, we refit the resulting top model to study
754 area, including a random effect for annual population size, with a mean specified as a linear trend
755 over time. We fit this model using variance components estimation, allowing for a quantification
756 of population change over time (Burnham and White 2002, Burnham 2013). Because the 2 study
757 areas had different initial abundances, the resulting estimates of realized growth were not directly
758 comparable. Thus, we converted these estimates to a proportional change over time, by dividing
759 by the intercept (i.e., abundance in year 0) and compared between study areas. We refit models,
760 as opposed to including random effects in initial models, because our primary objective was in
761 examining differences in the density estimate between study areas in each year, not growth rates.
762 The inclusion of the random effects can result in shrinkage of annual abundance estimates
763 towards the linear trend thus potentially obscuring between study area differences in some years.

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

773 **RESULTS**

774 **Habitat Selection**

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

786 to their specific winter ranges, with an average of 81% year-to-year UD overlap in the low-
787 development area and 84% year-to-year UD overlap in the high-development area (Table A2).

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

796 We found strong differences between the 2 study areas in the response to producing well
797 pads (Fig. 4; Tables C1-C4). Although there was annual variation, in general, deer in the low-
798 development area avoided the areas with more producing well pads in close proximity during
799 both night and day, with relative avoidance increasing at closer distance buffers (Fig. 4; Tables
800 C1 & C2). There were not enough locations within 200 m of producing well pads in any year to
801 estimate a coefficient for this buffer distance for night or day in the low-development area,
802 indicating strong avoidance of these areas. Deer in the high-development area displayed a
803 weaker relative avoidance of producing well pads than deer in the low-development area for
804 most year and distance buffer combinations, with coefficient magnitudes almost always smaller
805 than corresponding estimates for the low-development area (Fig. 4; Tables C1-C4). Further,
806 these deer appeared to display differences in selection between night and day relative to well
807 pads. In several years, deer avoided areas with more producing well pads in close proximity
808 during the day, with null response or selection of areas with more pads in close proximity during

809 the night (Fig. 4; Tables C3 & C4). Deer in the low-development area showed some similar
810 temporal patterning during some years, but this pattern was inconsistent and generally weaker
811 than that of the high-development deer. Examining responses to well pads falling within multiple
812 buffers simultaneously indicated a strong cumulative effect of development, with stronger
813 avoidance of areas that had both drilling and producing well pads, or many drilling well pads
814 falling within multiple buffer distance (Fig. 3 & 4; Fig. 5, Tables C1-C4).

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

826 Deer also displayed differences between night and day in habitat selection behavior
827 relative to forage and cover in both areas. In the low-development area during the day, deer
828 selected areas of less rugged terrain (Fig. 9), closer to edges (Fig. 10), and in land cover classes
829 related to cover (Fig. 11) and showed little consistent selection or avoidance of areas in response
830 to snow depth (Fig. 12; Tables C1 & C2). In contrast, during the night, deer did not consistently
831 select habitat in relation to terrain ruggedness or habitat edges (Figs. 9, 10) and selected areas

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

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

854 **Demography**

855 Across the 8 years of the study, we captured 371 unique does on multiple occasions, for a total of
856 653 captures (Table 2). We also captured 766 unique fawns during this time (371 males and 395
857 females; Table 3). Despite occasional differences in mean values of age, doe body fat, pregnancy
858 metrics, and lactation status, there were no noticeable trends over time, and no consistent
859 differences between study areas (Figs. 15–17; Tables 9–10; Tables D1-D6). There were no
860 statistical differences during any winter season between the 2 study areas in early winter doe
861 body fat either when accounting for lactation status or not (Fig. 16; Table 10). Although
862 controlling for lactation status did not influence the effect of study area on body fat, deer that
863 were lactating had significantly lower body fat than those that were not (\bar{x} body fat proportion of
864 lactating does = 0.09 (SD = 0.023), \bar{x} body fat proportion of non-lactating does = 0.12 (SD =
865 0.034); Table 10). There were no statistical differences during any winter season between the 2
866 study areas in late winter doe fat, change in doe fat over winter, or fetal counts (Figs. 16–17;
867 Tables 9–10; Tables D1-D6). Raw lactation rates differed moderately between study areas (2013
868 low development \bar{x} = 0.45, SD = 0.51; 2013 high development \bar{x} = 0.33, SD = 0.48; 2014 low
869 development \bar{x} = 0.59, SD = 0.50; 2014 high development \bar{x} = 0.46, SD = 0.51), but
870 generalized linear models indicated that these differences were not significant (Table 9).
871 Pregnancy rates also did not appear to differ between areas (Fig. 17), though pregnancy rates
872 were 100% in some years, making it impossible to fit a model to these data assessing differences
873 in years. A generalized linear model fit to all data combined across years with only a covariate
874 for study area indicated no significant difference in pregnancy rates between the high- and low-
875 development areas (β for effect of high-development study area = 0.55, P = 0.23). There were
876 several significant terms for the age model, but age only differed significantly between the study
877 areas in a single year, with older does in the high-development area in 2010 (Fig. 15; Table 9). In

878 addition, fawn mass varied significantly across years (Fig. 18), with the highest values in
879 December 2009 and significantly lighter fawns in all other years except 2013 and 2015 (Tables
880 D7-D9). However, these differences were consistent across study areas and sexes, with no
881 statistically significant differences between areas in any years and for either sex (Table 11;
882 Tables D7-D9). Males were significantly heavier than females on average (Fig. 18; Table 11).

883 Few does died in any year of the study and there was no apparent pattern between study
884 areas (Table 2; Table E1; Figs. F1-F9). The top model for does indicated that survival varied
885 between study areas and across seasons and years, with seasons split into summer, winter, and a
886 single transition season (i.e., survival in the spring and fall transition periods were equal; Table
887 12; Fig. 19). Mean doe survival was marginally higher in the high-development area than the
888 low-development area (Fig. 19; coefficient for the effect of being in the low-development area =
889 -0.42 ± 0.50 [SE]). Excluding study area differences resulted in a model with nearly identical
890 weight to the top model (Table 13; Table E1). Seasonal doe survival was generally high (mean
891 monthly survival across study areas = 0.987, range = 0.85–1.0) but varied by season, with winter
892 and summer being nearly identical, and transition-season being lower (Fig. 19). Models in which
893 survival varied by month were not among the more parsimonious, with such models having zero
894 AIC_c weight (Table 13).

895 Raw fawn mortality counts varied substantially from year to year (Table 3). The top fawn
896 model indicated that survival varied by year only (Table 14) and had nearly twice the weight of
897 the next best model (Table 15; Table E2-E6; Figs. F10-F17). Despite the second-best model
898 suggesting evidence for study area differences, annual and monthly variation was substantially
899 stronger (Fig. 20; effect size for study area = -0.41 , whereas average absolute value of effect size

900 for year = 1.00). Further, the 95% confidence intervals for the coefficient for study area in this
901 model overlapped zero (Table E2, available online in Supporting Information).

902 In the low-development area, the mark-resight model with resighting probability varying
903 by individual and survey, and no immigration or emigration, was the most parsimonious among
904 the candidate models (Table 16). In the high-development area, the model with resighting
905 probability varying by survey, but not individual, and no immigration or emigration was the most
906 parsimonious (Table 16). Deer density was higher in the low-development area during each year,
907 but confidence intervals overlapped in all but 2 years (2011 and 2015; Fig. 21). Monte Carlo
908 simulations indicated that confidence interval overlap was 47% in 2010, 0% in 2011, 13% in
909 2012, 8% in 2013, 21% in 2014, and 0% in 2015, suggesting that in most years there was
910 evidence for greater density in the low-development area. The *post hoc* model assessing change
911 over time in abundance indicated that deer abundance increased significantly over time in both
912 study areas. Abundance increased at a greater rate in the low-development study area than the
913 high-development study area, but confidence intervals for the rate of increase overlapped (mean
914 annual increase for low- and high-development areas were 0.057 [95% CI = 0.021–0.78] and
915 0.045 [95% CI = 0.021–0.087], respectively; Fig. 21).

916 **DISCUSSION**

917 We contrasted behavior and demography of mule deer between areas of heavy and light natural
918 gas development to test alternative hypotheses about how habitat modification influences the
919 species on their winter range. As expected, based on previous work in this area and others
920 (Northrup et al. 2015, Sawyer et al. 2017), we saw behavioral responses to development with
921 strong contrasts between the 2 study areas. Deer avoided infrastructure in the lightly developed
922 area where they had sufficient space to do so and selected for variables assumed to relate to

923 forage. In the more heavily developed area, where deer did not have the space to avoid
924 infrastructure wholesale, they selected for areas with greater cover and patterned their habitat
925 selection to use areas near well pads at night. In accordance with hypothesis B, these behavioral
926 differences did not manifest as demographic effects, with no differences in any measured metric,
927 except density, between the 2 study areas. These findings indicate that deer can show remarkable
928 behavioral plasticity in relation to habitat modification, which can potentially buffer them against
929 demographic effects, at least under the development and deer densities in our study area.
930 However, deer density was lower with greater development, which suggests a demographic
931 difference between the deer in these study areas that was not captured by our design. Below we
932 discuss possible reasons for this difference.

933 The behavioral responses of deer we observed corroborate the findings of past studies on
934 the species that have shown altered habitat selection in response to hydrocarbon development
935 (Sawyer et al. 2006, 2009, 2017; Webb et al. 2011c; Northrup et al. 2015, 2016b). Further,
936 studies on other species have found similar behavioral responses to energy development and
937 related infrastructure, with elk (Webb et al. 2011b), sage grouse (Holloran et al. 2010), and
938 chestnut-collared longspurs (*Calcarius ornatus*; Ng et al. 2019) among the numerous species
939 exhibiting altered behavior. Behavioral alterations in response to habitat modification are
940 expected, as they are the initial means by which species can cope with disturbance (Berger-Tal et
941 al. 2011, Greggor et al. 2016). These alterations are typically assumed to reduce individual
942 fitness, and subsequently to affect population dynamics. Habitat selection, specifically, is a
943 behavior that is expected to influence individual fitness (Morris 1989), and variation in this
944 behavior can drive population dynamics (Matthiopoulos et al. 2015, 2019). Thus, several
945 researchers have inferred detrimental effects on species from altered habitat selection in areas

946 disturbed by hydrocarbon development (Carpenter et al. 2010, Beckmann et al. 2012, Northrup
947 et al. 2015). Our behavioral results would, at first, seem to suggest substantial effects on
948 individual fitness through altered habitat selection in the more heavily developed area.

949 Despite the strong behavioral differences between study areas noted above, we did not
950 document a concomitant effect of natural gas development on most demographic measures,
951 supporting hypothesis B. We developed hypothesis A, whereby we predicted altered behavior
952 leading to demographic differences between the 2 areas, based on the prediction that altered
953 habitat selection would lead to reduced access to high quality forage and thus lower condition
954 and survival. However, this hypothesis was clearly refuted, with deer showing nearly identical
955 measures of all condition and demographic metrics other than density. These results stand in
956 stark contrast to the only other study that has conjointly assessed behavioral and demographic
957 effects of natural gas development on mule deer. Sawyer et al. (2017), working in a sagebrush
958 ecosystem in the Pinedale area of Wyoming before and during development, examined mule deer
959 abundance and the average distance between individuals and well pads over 15 years of ongoing
960 activity (compared to approximately 10 years of activity in our study area as of 2015). This study
961 found that mule deer were farther from natural gas development on their winter range in years
962 after development began. During this time, the population declined by 36%. Mule deer in the
963 Wyoming study system appeared to avoid development more strongly than in our study area, a
964 pattern that persisted after active drilling stopped. However, the authors did not measure deer
965 body condition, reproductive parameters, or monitor fawns, making it difficult to draw
966 mechanistic links between behavioral responses and abundance. In contrast to Sawyer et al.
967 (2017), deer in our study in northwest Colorado that were subject to similarly high densities of
968 development (i.e., deer in the high-development study area) avoided well pads during the drilling

969 phase and used all but the closest areas around well pads that were in the production phase as
970 available. Further, deer in our study appeared to increase their use of cover in the more
971 developed area. We believe that strong differences in the habitat of the 2 study systems drove
972 these contrasting findings. The Wyoming study did not conduct a formal assessment of habitat
973 selection, so it is impossible to directly compare results, but the Pinedale area consists mostly of
974 sagebrush and has limited topography, whereas our study area had substantial available tree
975 cover and complex topography. We suggest that these characteristics have allowed deer to adjust
976 behaviorally, using areas closer to well pads and other infrastructure with greater cover, whereas
977 they were displaced from large areas around development in the flatter and more open Wyoming
978 system. Our results are more similar to the response of pronghorn in the same Wyoming system
979 (Beckmann et al. 2012, 2016). Beckmann et al. (2012) examined the habitat selection patterns of
980 pronghorn in response to natural gas development over 5 years. They found that development
981 influenced pronghorn habitat selection but with no consistent direction of effect. Despite some
982 behavioral responses, Beckmann et al. (2016) found that pronghorn survival, mass, fecal
983 corticosteroids, and progesterone were nearly identical between developed and undeveloped
984 areas. However, Sawyer et al. (2019), working on pronghorn over a 15-year period in an
985 overlapping study area, documented an increase in the number of individuals abandoning their
986 ranges, which complicates interpretation of the results of Beckmann et al. (2012, 2016). These
987 congruent and contrasting findings across regions and species have implications for regulations
988 aimed at reducing impacts of hydrocarbon development on wildlife. For example, it could have
989 been potentially misleading to use the mule deer results of Sawyer et al. (2017) to assume
990 negative responses of natural gas development on pronghorn in the same area or to mule deer in
991 our study area. This suggests that, if analyses from a similar ecological context are lacking,

992 development and mitigation plans might need to be custom fit to the species and area of interest
993 to ensure effectiveness.

994 **Mule Deer Behavior and Natural Gas Development**

995 Deer in our 2 study areas displayed markedly different patterns of habitat selection. We interpret
996 these results as the manifestation of different behavioral tactics from a species that is known to
997 be highly philopatric (Robinette 1966, Garrott et al. 1987, Northrup et al. 2016*b*), and from
998 individuals who displayed remarkable fidelity. In the low-development area, deer could simply
999 move to areas of their home ranges far from development while likely maintaining their typical
1000 habitat selection patterns. Such a tactic was possible because of the low density of development,
1001 and thus relatively larger amount of undeveloped habitat within their ranges to which they could
1002 be displaced. Deer in the high-development area did not have undeveloped areas within their
1003 winter ranges to which they could move and thus modified their behavior at a finer scale,
1004 focusing on access to cover over access to forage. Similar patterns of reduced direct interaction
1005 with development without large-scale abandonment of ranges has been seen in previous studies
1006 of elk and mule deer in areas with active natural gas development (Webb et al. 2011*a, b*).
1007 However, other studies offer contrasting findings, with pronghorn and mule deer in Wyoming
1008 displaying potential abandonment or large-scale avoidance of developed winter range areas
1009 (Sawyer et al. 2017, 2019) and sage grouse showing reduced lek attendance near well pads
1010 (Walker et al. 2007). All of these species typically display philopatry, so these findings suggest
1011 that abandonment occurs where alternative habitats, within an animals range, offering cover from
1012 the disturbance are not available.

1013 Although the above differences in habitat selection of deer might seem nuanced, they
1014 represent strong contrasts in spatial behavior between the 2 areas, which can have important

1015 implications for conservation planning (Harju et al. 2011). The mapping of habitat selection
1016 patterns of deer from the low-development area to the landscape in the high-development area
1017 indicated compromised behavior assuming consistent habitat selection patterns (Fig. 14).
1018 However, deer in the high-development area regularly used habitat that naïve deer would avoid.
1019 Our condition measures did not support a link between these behavioral shifts and physiological
1020 costs, possibly because of the generally low forage quality on mule deer winter range (Wallmo et
1021 al. 1977). Notably, all deer were in a net negative energy balance on their winter range,
1022 regardless of density of development or forage availability in the area. This contradictory finding
1023 is likely because the major decline in condition that deer experience over the winter supersedes
1024 benefits that use of areas with more forage may provide during this period (Monteith et al. 2013).

1025 If low forage quality is the reason for the lack of any documented demographic response,
1026 then it is possible that greater attention should be paid to management and mitigation options
1027 during the late winter and early spring when green-up begins. This period likely is particularly
1028 important for deer to begin to recoup condition losses over the winter, and behavioral responses
1029 to development likely are more impactful. Furthermore, given the importance of the summer
1030 range for critical stages of reproduction and net energy balance gains that carry deer through
1031 winter, summer disturbance could be more important than previously considered. Indeed, the
1032 timing of development relative to important life-history stages is likely critical to understanding
1033 how different species might respond to development during different times of the year. As
1034 mentioned above, our results are similar to those found for pronghorn on their winter range in
1035 Wyoming, whereby no physiological costs were associated with altered habitat selection around
1036 energy development infrastructure. Beckmann et al. (2016) posited that because pronghorn
1037 already experience substantial condition declines over winter, any effect of habitat loss from

1038 energy development was masked. These results contrast with those from avian studies that have
1039 examined the effect of energy development during the breeding season. Ng et al. (2019)
1040 documented reduced parental care in chestnut-collared longspurs closer to development
1041 infrastructure, leading to fewer offspring fledged in these areas. Likewise, Walker et al. (2007)
1042 documented declines in male sage grouse attendance at leks when they were located closer to
1043 energy development. However, even for avian species during the critical nesting period, these
1044 results are not always consistent; Ludlow and Davis (2018) found a range of effects (both
1045 positive and negative) of hydrocarbon wells on waterfowl and shorebird nest site selection but no
1046 effect on daily nest survival. Considering these contrasting findings, close attention should be
1047 paid to the timing of development activities relative to life-history stages. Indeed, for mule deer,
1048 behavioral responses during the fawning period could have greater demographic consequences
1049 than what we show in this study and thus further research into this potential is warranted.

1050 **Mule Deer Demography and Natural Gas Development**

1051 Our demographic results indicate that at the current development and deer population densities,
1052 natural gas well pads in the production phase on winter range are not affecting the measured
1053 individual demographic and physiological parameters in our study area. Our sample sizes were
1054 large and thus we had the power to detect relatively small differences between study areas and
1055 years. For example, the probability of detecting a difference in fawn survival between 0.95 and
1056 0.85 (0.95 was approximately the average monthly survival for the less developed area) was
1057 0.45. Estimated differences in survival were usually smaller than 0.1, and deer in the high-
1058 development area had marginally higher survival than in the low-development area in general.
1059 For does, differences between study areas were always small (the mean of the absolute value of
1060 differences in monthly survival between areas was 0.015) and would require annual sample sizes

1061 approaching 1,000 collared does to see statistically significant differences if survival truly varied
1062 by that small amount. Thus, the lack of differences in demographic parameters (particularly
1063 survival) is a robust finding.

1064 The demographic parameters we measured were indicative of a population below
1065 carrying capacity. In particular, survival of fawns in this study was high (average of overwinter
1066 model-averaged survival estimates for the low-development area = 0.77 and for the high-
1067 development area = 0.78; Fig. 20). Forrester and Wittmer (2013) reviewed survival rates of mule
1068 deer throughout their range, and the survival estimates for fawns from our study exceed nearly
1069 every study reviewed. Further, these survival rates were higher than comparable studies
1070 conducted in this study area or in similar habitat that experimentally removed predators
1071 (Bartmann et al. 1992, Hurley et al. 2011), assessed habitat improvements (Bergman et al. 2014),
1072 or reduced deer density (White and Bartmann 1998). During certain years, fawn survival in our
1073 study was similar to those reported by Bishop et al. (2009) who fed deer pellets *ad libitum* during
1074 winter to intentionally raise the carrying capacity in their study system, though on average their
1075 estimates were higher than ours. Doe survival was on par with estimates from other studies
1076 (mean model-averaged annual survival estimate for low-development area = 0.82 and for the
1077 high-development area = 0.85). For large ungulates, adult survival is the most sensitive vital rate
1078 but typically varies little, with population dynamics often driven by recruitment (Gaillard et al.
1079 1998). Thus, the comparatively high fawn survival in our study further strengthens our
1080 impression that these populations were below carrying capacity. Other demographic and
1081 physiological parameters that we measured were similar or exceeded those in other studies.
1082 Specifically, early and late winter doe body fat was the same or higher in our study than in
1083 similar studies (Bishop et al. 2009; Monteith et al. 2013, 2014; Bergman et al. 2018). Only does

1084 receiving supplemental feed *ad libitum* in Bishop et al. (2009) had higher body fat than those in
1085 our study. Pregnancy rates in our study also were on par or higher than those in other studies
1086 (Bishop et al. 2009, Freeman et al. 2014, Monteith et al. 2014), and fawn mass was comparable
1087 to Hurley et al. (2011) and substantially higher than during the 1980s in the same ecosystem as
1088 our study (Bartmann et al. 1992). These comparisons indicate that in both study areas, deer were
1089 not strongly limited by habitat availability as might be expected under substantial habitat
1090 modification.

1091 Mule deer in the Piceance Basin declined substantially in the 1990s (White and Bartmann
1092 1998, Unsworth et al. 1999). Although this past work did not overlap spatially with our current
1093 study, they took place in the same ecosystem. During those studies, winter range deer densities
1094 were 5–6 times higher than in our study (White and Bartmann 1998). Thus, the current
1095 demographic rates likely represent a rebounding population that is below carrying capacity,
1096 where winter range habitat is not strongly limiting. Under these conditions, our results indicate
1097 that the current density of development in the producing phase is not actively affecting these
1098 populations, despite the strong behavioral differences between the 2 study areas. However,
1099 habitat modification from natural gas development could induce negative demographic
1100 consequences that occurred prior to our work (potentially accounting for the differences in
1101 densities observed; see discussion below) or could not be detected in our study. First, because
1102 deer appear to be well below carrying capacity, we are unable to determine if habitat
1103 modification has permanently altered the density of deer that this landscape is able to support.
1104 Thus, if deer densities continue to increase, we may observe differences in demographic
1105 responses manifest as a function of different carrying capacities or observe density-dependent
1106 effects sooner on the more heavily developed area. Likewise, most of the winters during our

1107 study were mild (i.e., little snow and relatively mild temperatures, with snow melting in early
1108 spring), except for the first and fourth winters. Mule deer populations have traditionally been
1109 limited by winter range forage availability (Wallmo et al. 1977, Parker et al. 1984, Bishop et al.
1110 2009) and thus we would expect some interaction between the high level of habitat modification
1111 and winter severity, whereby deer in the high-development area might have particularly
1112 depressed demographic rates during harsh winters. Because winters were relatively mild during
1113 our study, we were unable to test this interaction. Long-term declines in winter severity
1114 associated with climate change may further reduce the chances of such a scenario.

1115 Critically, our study began after natural gas development had peaked. In fact, intensive
1116 drilling and associated activity levels declined through the duration of the study, thereby relaxing
1117 displacement of deer most strongly associated with the drilling phase of development. Sawyer et
1118 al. (2006, 2017) examined deer responses to natural gas development in a before-during study
1119 design and found large-scale displacement of deer after initiation, associated with reductions in
1120 abundance. Thus, we are uncertain if there were similar responses in our population, which
1121 might account for observed differences in density, and if the remaining deer that were studied are
1122 those less prone to negative effects from development (e.g., habituated to development). Strong
1123 demographic effects in response to the initial habitat modification before our study would
1124 explain the documented differences in deer density, but we lack the information required to make
1125 this inference. In addition, although this study primarily assessed the response of deer to well
1126 pads in the later stages of development (i.e., production), the responses to drilling were strong
1127 and the area affected by this activity was large, particularly in the first year of the study. Drilling
1128 appears to have shifted deer activity to other areas of their home ranges as evidenced by the high
1129 fidelity to winter use areas and the relatively consistent proportion of the high-development area

1130 where deer selection was reduced. The subsequent reduction of drilling activity then increased
1131 the relative selection of areas where wells were previously being drilled. If drilling activity
1132 increases above previous levels in coming years, we are uncertain of how this will affect deer
1133 behavior and demography, particularly now that deer density is higher than during the more
1134 active drilling phase. At very high densities of drilling activity, deer could display habituation
1135 similar to responses to production activity, or alternatively, the avoidance that we documented
1136 could produce demographic effects. Further, because drilling activity is associated with
1137 substantial noise, it might also affect the ability of deer to avoid predators if they did habituate to
1138 drilling activity at higher densities. There is likely some level above which deer or pad densities
1139 are high enough to affect demography and population dynamics, but conditions during our study
1140 were apparently below this threshold. Identifying these thresholds will be complicated because it
1141 is likely a function of the species, habitat, weather, climate, and timing of development. For
1142 example, Sawyer et al. (2017) found larger-scale avoidance by naïve (i.e., not previously
1143 exposed) mule deer and Sawyer et al. (2019) found substantial increases in the number of naïve
1144 pronghorn completely abandoning their study areas. Although our study did not include naïve
1145 deer, comparisons to our results suggest deer can persist at higher densities in proximity to
1146 development in our study area with more vegetative and topographic cover. Likewise, life-
1147 history stage is important when considering thresholds; Sawyer et al. (2020), working with mule
1148 deer during migration, found deer use during migration strongly declined at surface disturbance
1149 levels of around 3%. However, they did not assess any demographic consequences of these
1150 responses. In our heavily developed study area, around 4% of the landscape is disturbed by well
1151 pads, facilities, and roads. Deer still use these areas, albeit in an altered manner, but we
1152 documented no large-scale avoidance as in the study by Sawyer et al. (2020).

1153 In addition to the potential for demographic effects under the different scenarios
1154 discussed above, despite nearly identical demographic and physiological measures between the 2
1155 study areas, there was, potentially, a lower rate of population growth in the high-development
1156 area and consistently higher point estimates of density in the low-development area (though
1157 confidence intervals overlapped for linear trends in density and for annual density estimates in
1158 most years). Four possible processes could cause differences in density, although we do not
1159 currently have the data to directly address which of these is most likely. First, habitat quality
1160 could be different between the 2 areas and thus carrying capacity could be lower in the more
1161 heavily developed area. However, remotely sensed covariates linked to habitat quality (e.g.,
1162 NDVI, snow cover) were similar between the 2 study areas. Further if habitat quality was
1163 different, we would expect to see differences in overwinter change in body fat. As such, we
1164 assume this is unlikely. Second, it is possible fawns in the high-development area lost more mass
1165 during the winter than those in the low-development area, but these differences did not manifest
1166 themselves over winter. Given summer is the time when deer gain energy (Monteith et al. 2013),
1167 this seems unlikely. Recapture of individual fawns in late winter would be needed to address this
1168 hypothesis.

1169 The third possible explanation is that the onset of development reduced deer density in
1170 the more heavily developed area. This reduction could have occurred from deer abandoning their
1171 winter ranges, or from a reduction in carrying capacity due to larger-scale avoidance of well pads
1172 during the construction and drilling phases. Either process could have led to lower density
1173 compared to the low-development area. Given deer are highly philopatric even in the presence of
1174 substantial development (Robinette 1966, Garrott et al. 1987, Northrup et al. 2016b), and our
1175 fidelity analysis exemplified this behavior in over 400 individuals in this study, we do not find

1176 evidence that deer are currently abandoning their winter ranges to a greater degree in the high-
1177 development area. Sawyer et al. (2006) and Sawyer et al. (2019) found deer and pronghorn,
1178 respectively, to be strongly displaced at the onset of development. Thus, density differences
1179 could result from displacement of sensitive individuals before initiation of our study, or the
1180 emigration of juveniles, which we did not follow for multiple years. If density was reduced in the
1181 high-development area at the onset of development, regardless of the mechanism, then the
1182 apparent population growth that we documented would be a result of low density relative to
1183 carrying capacity.

1184 The last explanation for potential differences in population trends and density in the 2
1185 study areas is that neonatal or fetal survival could be different between the 2 areas because of
1186 differences in predator abundance or habitat quality on summer range, which would lead to
1187 lower overall recruitment rates despite similar overwinter fawn survival. Lower recruitment rates
1188 would explain differences in population growth rates despite all other demographic parameters
1189 being nearly identical. Because neonatal fawn mortality tends to be high in mule deer generally
1190 (Pojar and Bowden 2004, Lomas and Bender 2007), as confirmed in this study area (Peterson
1191 2016, Peterson et al. 2017), any differences in survival of this age class could be an important
1192 driver of population dynamics. Further, if there were differences in habitat quality between the
1193 summer ranges, then lower recruitment in one area could lead to the documented consistency in
1194 other demographic parameters. That is, if recruitment is low in the high-development area, it
1195 could lead to similar overwinter fawn survival and similar condition metrics between the 2 areas,
1196 despite differences in available habitat because of the subsequent reductions in density.
1197 However, our data do not support this possibility because doe body fat in both March (prior to
1198 departure for summer range) and December (after arrival back on winter range) were consistent

1199 between study areas across all years. The similar body fat values indicate that, on average, deer
1200 were recovering similar fat stores on both summer ranges. Similarly, for the few years that we
1201 collected lactation status information, we saw no differences between the study areas in body fat
1202 after controlling for lactation, suggesting differences in recruitment (which affect female body
1203 condition) were not a factor. Deer that are still lactating in December likely still have fawns at
1204 heel, and thus the similar fat values for lactating deer in both study areas suggests minimal
1205 differences in habitat quality between the summer ranges. This finding would suggest that
1206 recruitment rates are either not different between the study areas or only the fattest does in the
1207 high-development study area were rearing fawns (an unlikely condition given deer reproductive
1208 strategies). It is also possible that recruitment differed, but these differences were too small to
1209 affect study area-level differences in body fat. Such small differences in survival from birth to 6
1210 months of age probably could affect differences in population growth, and thus cannot be
1211 discounted as a driver of potential differences in density. A congruent study being conducted in
1212 this area on deer reproduction found some potential evidence for lower birth rates (i.e., more
1213 stillbirths) on the summer range of the high-development area, compared to the summer range of
1214 the low-development area (Peterson 2016, Peterson et al. 2017). However, differences were not
1215 consistent across time and additional study areas were sampled to provide sufficient power, thus
1216 providing weak evidence that neonatal survival or birth rates were influencing patterns of density
1217 in our current study. The only other measure of recruitment we had was lactation rates in
1218 December, which did indicate potential, but non-significant, differences in recruitment on the 2
1219 study areas.

1220 In light of the above discussion, our inability to estimate recruitment is a clear limitation
1221 of this study. We had only 2 years of data on lactation rates, which, based on the negative

1222 relationship with doe body condition that we documented, is likely to represent some index of
1223 recruitment. More detailed information on recruitment rates would greatly clarify our results.
1224 Specifically, study area-level estimates would allow us to better resolve the differences in
1225 population dynamics. Currently, our results only show that density and, to a lesser extent,
1226 population growth appeared higher in the low-development area, but the mechanism is unclear.
1227 For example, all of the following are reasonable explanations for lower density on the more
1228 developed area: lower recruitment, lower initial density, abandonment of ranges upon initiation
1229 of development, reduced carrying capacity due to habitat loss from development, or innate
1230 differences in habitat quality.

1231 Understanding the degree to which development affects further population growth will
1232 require continued examination under higher densities of well pads and deer, assessments of
1233 responses on summer range, and monitoring fawns through the entirety of their first year of life.
1234 We focused on winter range because deer in these areas inhabit summer ranges that are far apart
1235 and differ strongly in development activity and forage quality (Lendrum et al. 2012, 2013, 2014;
1236 Northrup et al. 2014*b*). Furthermore, mule deer management in Colorado and the rest of the
1237 Intermountain West has traditionally focused on winter range because deer face limited access to
1238 forage (Wallmo et al. 1977, Parker et al. 1984, Bishop et al. 2009) and can experience
1239 pronounced mortality during this period (White and Bartmann 1998). Thus, winter range
1240 assessments have the strongest implications for current management practices. In light of our
1241 findings, and reduced winter severity from climate change, increased attention should be focused
1242 on deer on their summer range.

1243 **The Use of Habitat Selection Analyses to Assess Effects of Human Disturbance**

1244 Habitat selection has long been used to assess wildlife responses to human activity and
1245 foundational ecological theory provides a pathway for inference to population and demographic
1246 responses through individual fitness (Fretwell and Lucas 1969, Charnov 1976, Frid and Dill
1247 2002). Further, recent work has directly quantified links between habitat selection and population
1248 dynamics (Matthiopoulos et al. 2019). The numerous challenges involved in obtaining detailed
1249 demographic information (i.e., large numbers of marked individuals needed for long time
1250 periods) result in many studies requiring inferential leaps between behavioral responses,
1251 individual fitness, and population consequences. Our results highlight the need for caution when
1252 inferring population consequences from habitat selection analyses (see also Wilson et al. 2020),
1253 and indicate that some behavioral responses may be indicative of adaptive phenotypic plasticity
1254 (Ghalambor et al. 2007, Tuomainen and Candolin 2011) and not result in negative population-
1255 level consequences. This is particularly true for species that are adaptable to disturbance and
1256 where the disturbance is relatively short lived (i.e., less than the lifespan of an individual).

1257 Our study focused on habitat selection of a relatively adaptable species on winter range
1258 where forage resources are typically limiting (Bishop et al. 2009). Thus, as mentioned above, it
1259 might be that nutrition is so limiting during this time that any behavioral response to
1260 development does not further restrict access to forage given the little nutritional value during
1261 winter. Further, the manner in which animals respond to disturbance is likely impossible to intuit
1262 from demographic data alone. Combining behavioral and demographic studies, as we have done
1263 here, provides a mechanistic understanding of how animals respond to human disturbance, which
1264 is subsequently crucial for developing effective mitigation measures (Dzialak et al. 2011a). For
1265 example, in our study, deer used areas closer to development by shifting use of these areas to the
1266 night time and increasing their use of cover habitat. This finding provides strong support for

1267 mitigation measures aimed at maintaining such cover habitat (discussed below) and reducing the
1268 human footprint during the drilling phase. Although pairing detailed demographic and behavioral
1269 studies will continue to be difficult, because of the need for sustained long-term funding and
1270 diverse expertise, pressing management issues warrant such work to obtain a more complete
1271 understanding of human-modified systems and potential mitigation measures.

1272 **Limitations**

1273 Despite the large sample sizes of individuals in our study, we had a few key limitations that
1274 could be improved upon in future research. Although a concurrent study measured neonatal fawn
1275 (i.e., birth through 6 months of age) survival (Peterson 2016, Peterson et al. 2017), this study did
1276 not directly match our design either spatially or temporally, thus limiting our ability to infer
1277 effects on population dynamics from their results; concurrent information on neonatal survival
1278 across our entire study period would have been valuable to help clarify differences in density
1279 between our 2 study areas. However, this type of data is costly and difficult to collect,
1280 particularly in our study area where fawning areas on summer range were often >100 km apart
1281 and dispersed. Likewise, the results of our study highlight the potential need to more closely
1282 monitor the condition of fawns throughout the entire first year of life. Although we saw no
1283 differences in early winter fawn mass, fawns in the more heavily developed study area possibly
1284 lost more mass over winter, leading to potentially lower survival during migration and over the
1285 summer. If we had collected this information, we might have been better able to assess the
1286 differences in density between the 2 study areas. Again, collecting these data would be costly,
1287 requiring recapture of >100 fawns or improved technology allowing annual survival estimates.
1288 Perhaps most critically, a clear limitation of our study was that we began research after the
1289 initiation of natural gas development. Sawyer et al. (2017) documented a strong response by

1290 mule deer to the initiation of natural gas development, providing a strong argument for procuring
1291 data before, during, and after development activity when possible. In addition to these
1292 limitations, that deer in our study migrated to different summer ranges adds complexity to the
1293 inference. Although we were able to account for potential differences in nutrition along
1294 migratory routes and over summer by measuring early winter fawn mass and doe condition (all
1295 of which were statistically indistinguishable between the 2 study areas), a better study design
1296 would include deer with shared summer ranges.

1297 In addition to the above limitations, our combined behavioral and demographic analyses
1298 could be improved upon in future work. An ideal design would quantitatively integrate the
1299 behavioral and demographic data. For example, RSF coefficients might be used as covariates in
1300 survival models to directly assess whether behavior influenced survival, or the effect of metrics
1301 such as body fat on habitat selection behavior might be examined. In our study, we were limited
1302 by a few factors that made such an analysis impractical or uninformative. First, our RSF analyses
1303 included a large number of parameters, making direct integration complex. That is, to include
1304 RSF coefficients as covariates in a survival model would require >15 parameters in some years.
1305 Likewise, we were unable to estimate some coefficients in some years (e.g., for drilling well
1306 pads), again complicating analyses. Further, survival of does was so high that our models could
1307 not support a large number of covariates. Recent advances in habitat selection modeling provide
1308 a roadmap for designing future studies that can better integrate demography and RSFs
1309 (Matthiopoulos et al. 2015, 2019), but our design did not allow for following these examples.
1310 Lastly, aside from density, there were no documented differences in demographic metrics
1311 between the 2 study areas. Thus, had we been able to better integrate these datasets, it is unclear
1312 what inference such analyses would have provided.

1313 **MANAGEMENT IMPLICATIONS**

1314 Our findings support focusing mitigation efforts on reducing impacts during the construction and
1315 drilling phases of hydrocarbon development and limiting human activity and noise during the
1316 longer production phase. Such measures should include strategic spatial configuration of
1317 infrastructure that reduces road networks or minimizes construction of new roads, encourages
1318 multi-well pads and directional drilling (where possible) to reduce the footprint, noise (and
1319 artificial light) reducing retaining walls, and remote liquid-gathering systems (Sawyer et al.
1320 2009). Most of the wells in our study area are directionally drilled from pads with multiple wells,
1321 which substantially reduced development density and resulted in a spatial configuration that
1322 allowed deer to respond behaviorally.

1323 Our results in combination with those of other studies on mule deer (Sawyer et al. 2017,
1324 2020) support maintaining cover habitat and refuge areas free from development so that deer can
1325 adapt their behavior without being displaced wholesale from their ranges. Landscape planning to
1326 ensure the minimization of the industrial footprint (e.g., roads, pipeline, processing stations) is
1327 critical for the maintenance of such cover habitat. More dispersed development, provided it does
1328 not lead to a significantly larger road network, might be more effective at minimizing impacts to
1329 deer and is supported by the surface disturbance thresholds documented by Sawyer et al. (2020).
1330 Although focusing mitigation on the drilling phase of development seems intuitive, our results
1331 offer some optimism that natural gas impacts might be more short-lived than previously thought
1332 and provides for feasible options for mule deer conservation in development planning
1333 considerations.

1334 Our modeling framework also provides results that can be used to infer development
1335 density thresholds and the subsequent behavioral responses. By focusing on the number of

1336 development features within different buffers, we were able to assess the cumulative impact of
1337 development on deer behavior (e.g., Fig. 5). This information could be used by developers and
1338 land and wildlife managers in conjunction to identify potential development scenarios that
1339 minimize the behavioral effects of development on deer. For example, spacing infrastructure
1340 such that areas with multiple well pads in buffers that were avoided by deer should be limited.
1341 However, under similar ecological contexts as in our system (i.e., rugged terrain and ample
1342 vegetative cover) and similar deer and development densities, these behavioral responses are
1343 unlikely to elicit demographic effects. As such, we suggest that the development densities during
1344 our study could be used as a starting point for further work assessing the potential existence of
1345 thresholds of development above which demographic effects might occur, and future
1346 development planning could maintain similar thresholds to minimize population-level impacts in
1347 areas with similar habitat characteristics (i.e., ≤ 0.8 pads/km² on pinyon–juniper-dominated
1348 winter range in generally rugged terrain). In areas similar to our study area in land cover and
1349 topography, the RSF models for the high-development study area could be used to assess how
1350 deer would be anticipated to respond under different scenarios. Maps that show predictions from
1351 the high-development RSF model to the low-development area (Fig. 14) indicate how deer might
1352 respond behaviorally if the low-development area saw increased industrial activity. Such maps
1353 could be augmented with proposed development plans to further assess behavioral responses of
1354 deer and identify a strategy to extract natural gas with the least behavioral effect on deer.
1355 However, deer do not exist in these landscapes in isolation, and development strategies that are
1356 beneficial for them might affect more sensitive species, such as greater sage grouse. Thus,
1357 multiple species will need to be considered in development plans.

1358 Currently, many areas of the western United States place restrictions on drilling activity
1359 on winter ranges. Our results do not provide strong evidence for or against these restrictions
1360 because of the limited amount of drilling during our study (i.e., initiated as drilling declined on
1361 the landscape). It might be tempting to interpret the lack of demographic response to the
1362 production phase as evidence for removing drilling restrictions and speeding the transition to
1363 production, but this could be misguided. If the density differences recorded in this study were a
1364 function of an initial response by deer to drilling, removing restrictions could elicit local
1365 population declines through larger-scale avoidance as seen in mule deer and pronghorn in
1366 Wyoming (Sawyer et al. 2019, 2020). Thus, we propose that planning be based on conditions
1367 present on proposed development areas until further research focused on scenarios with more
1368 active drilling over longer periods of time can be conducted. Ultimately, the variability evident in
1369 our results when compared to stronger responses of deer and pronghorn from other systems,
1370 suggests development planners should acknowledge the dynamics involved in wildlife-energy
1371 development interactions. Considerations of topographic and vegetative diversity and whether or
1372 not there is evidence that animals are habitat limited should be incorporated into development
1373 planning options. This approach may ultimately foster a collaborative and likely more successful
1374 planning process.

1375 It remains to be seen whether the development in our area will limit mule deer
1376 populations at higher densities. The direct habitat conversion caused by roads, well pads, and
1377 facilities will at some threshold have demographic consequence for these populations. Thus,
1378 concerned managers should focus late-stage mitigation on recontouring and revegetating well
1379 pads, and reducing the overall road network and reclaiming roads or restricting public access
1380 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 \pm 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 \pm standard deviation of December to March change in percent ingesta-free body fat.

Figure 17. Mean \pm 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 \pm 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. 2016b)
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	

^aReference category (i.e., the effect represented by the intercept) was the low-development area in 2010.

^bReference category was the low-development area in 2012.

^cReference 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*

^aReference category (i.e., the effect represented by the intercept) was the low-development area in 2009.

^bReference category was the low-development area in 2013.

^cReference 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 \times male	0.01	0.04	-0.0684	0.0884
High development \times 2010	0.02	0.04	-0.0584	0.0984
High development \times 2011	-0.005	0.04	-0.0834	0.0734
High development \times 2012	0.03	0.04	-0.0484	0.1084
High development \times 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 \times year + study ^a	669.27	0.00	0.57	20
Season1 \times year	669.89	0.62	0.42	19
Season1 \times year \times study	678.27	9.00	0.01	26
Season2 \times year + study	678.66	9.39	0.01	38
Season2 \times year	679.29	10.02	0.00	25
Season2 \times year \times study	692.90	23.63	0.00	50
Year \times month + study	735.90	66.63	0.00	75
Year \times month	736.54	67.27	0.00	74
Year \times month \times study	835.93	166.66	0.00	148

^aStudy 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 \times month	1,037.44	1.98	0.17	35
Year \times month + study	1,038.86	3.39	0.08	36
Year + month	1,039.21	3.75	0.07	11
Year \times study	1,045.69	10.23	0.00	14
Year \times month \times study	1,074.23	38.77	0.00	70
Month	1,121.28	85.82	0.00	5

^aStudy 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 (\cdot), 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				
$p(\text{year} \times \text{survey}), \sigma \neq 0, \alpha = 0$	49	2,809	0.0	0.997
$p(\text{year} \times \text{survey}), \sigma = 0, \alpha = 0$	43	2,821	11.9	0.003
$p(\text{year} \times \text{survey}), \sigma \neq 0, \alpha \neq 0$	62	2,835	25.9	0.000
$p(\text{year} \times \text{survey}), \sigma = 0, \alpha \neq 0$	56	2,847	37.7	0.000
$p(\cdot), \sigma \neq 0, \alpha = 0$	30	3,121	311.8	0.000
$p(\cdot), \sigma = 0, \alpha = 0$	24	3,134	324.8	0.000
High development				
$p(\text{year} \times \text{survey}), \sigma = 0, \alpha = 0$	43	2,883	0.0	0.967

$p(\text{year} \times \text{survey}), \sigma \neq 0, \alpha = 0$	49	2,890	6.7	0.033
$p(\text{year} \times \text{survey}), \sigma = 0, \alpha \neq 0$	56	2,907	24.6	0.000
$p(\text{year} \times \text{survey}), \sigma \neq 0, \alpha \neq 0$	62	2,914	31.5	0.000
$p(\cdot), \sigma = 0, \alpha = 0$	24	3,135	252.6	0.000
$p(\cdot), \sigma \neq 0, \alpha = 0$	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.