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

9   **Range**

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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 **RÈSUMÈN**

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 mulets 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 mulets. 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 apparait que les cerfs mulets 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 entrainaient 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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143 **Contents**

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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. 2011*b*,

242 Laberee et al. 2014, Northrup et al. 2015), altered home range patterns in mule deer and elk

243 (Webb et al. 2011*a*, Northrup et al. 2016*b*), 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. 2011*b*, Webb et al. 2011*d*) 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. 2011*c*, 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   2011*c*; 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. 2016*b*). 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. 2011*c*), or during certain times of the year when habitat might be more limiting

296   (Marshal 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, 2016*a*). 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 (39.954^0N, 108.356^0W;

355   Fig. 1), which encompasses an area of 184 km^2. 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 ostesperma*)

361   shrubland complex. Other dominant shrubs included Utah serviceberry (*Amalenchier 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. 2014*b*) 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/km^2. 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. 2014*a*; 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/km^2 in south Magnolia,

434   1.2 km/km^2 in north Magnolia), pipeline densities (1.2 km/km^2 in south Magnolia, 0.5 km/km^2 in

435   north Magnolia), industrial facilities (0.1 facilities/km^2 in south Magnolia, 0.01 facilities/km^2 in

436   north Magnolia), and well pads (0.62–0.78 pads/km^2 in south Magnolia, 0.01–0.06 pads/km^2 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 ctmm

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. (2014*a*). 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. 2014*b*), 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 ($\frac{x_i - \bar{x}}{\text{SD}(x)}$, where x_i is the ith 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
$$[y_{tn}|\boldsymbol{\beta}_n] = \frac{e^{x'_{y_{tn}}\beta_n}}{\sum_{j=1}^{J} e^{x'_{j_{tn}}\beta_n}}$$

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

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

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

532   where y_{tn} is a resource unit represented by habitat covariates $\boldsymbol{x}_{y_{tn}}$ that is chosen by animal n at

533   time t from a set of available resource units J, represented by habitat covariates $\boldsymbol{x}_{j_{tn}}$. $\boldsymbol{\beta}_n$ are the

534   set of coefficients related to the k habitat covariates for individual n, and $\boldsymbol{\mu}_\beta$ and σ_β^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. 2016*b*). 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 km^2 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. 2011*c*; Northrup et al. 2015, 2016*b*). Further,

936   studies on other species have found similar behavioral responses to energy development and

937   related infrastructure, with elk (Webb et al. 2011*b*), 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. 2016*b*), 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. 2011*a*). 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.

MANAGEMENT IMPLICATIONS

Our findings support focusing mitigation efforts on reducing impacts during the construction and

drilling phases of hydrocarbon development and limiting human activity and noise during the

longer production phase. Such measures should include strategic spatial configuration of

infrastructure that reduces road networks or minimizes construction of new roads, encourages

multi-well pads and directional drilling (where possible) to reduce the footprint, noise (and

artificial light) reducing retaining walls, and remote liquid-gathering systems (Sawyer et al.

2009). Most of the wells in our study area are directionally drilled from pads with multiple wells,

which substantially reduced development density and resulted in a spatial configuration that

allowed deer to respond behaviorally.

Our results in combination with those of other studies on mule deer (Sawyer et al. 2017,

2020) support maintaining cover habitat and refuge areas free from development so that deer can

adapt their behavior without being displaced wholesale from their ranges. Landscape planning to

ensure the minimization of the industrial footprint (e.g., roads, pipeline, processing stations) is

critical for the maintenance of such cover habitat. More dispersed development, provided it does

not lead to a significantly larger road network, might be more effective at minimizing impacts to

deer and is supported by the surface disturbance thresholds documented by Sawyer et al. (2020).

Although focusing mitigation on the drilling phase of development seems intuitive, our results

offer some optimism that natural gas impacts might be more short-lived than previously thought

and provides for feasible options for mule deer conservation in development planning

considerations.

Our modeling framework also provides results that can be used to infer development

density thresholds and the subsequent behavioral responses. By focusing on the number of

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/km^2 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 ± standard deviation percent ingesta-free body fat determined using ultrasonography and palpation of the rump for doe mule deer captured in December (A) and March (B) between March 2009 and December 2015 in the low- and high-development winter range study areas in the Piceance Basin, Colorado, USA. Panel C shows mean ± standard deviation of December to March change in percent ingesta-free body fat.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

$p(\text{year} \times \text{survey})$, $\sigma \neq 0$, $\alpha = 0$	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
$p(.)$, $\sigma = 0$, $\alpha = 0$	24	3,135	252.6	0.000
$p(.)$, $\sigma \neq 0$, $\alpha = 0$	30	3,142	258.9	0.000

<u>SUMMARY OF CONCLUSIONS AND MANAGEMENT IMPLICATIONS</u>

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.